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Meiotic behaviour of telo-tertiary compensating trisomics of rye: evaluation for use in hybrid varieties

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Summary. Meiosis of four telocentric-tertiary compensating trisomics of rye (*Secale cereale* L.) was studied with the purpose of evaluating their suitability for use in maintaining genic male-sterile lines applied in hybrid varieties. They had been constructed from four different reciprocal translocations and three different telocentrics. In one trisomic a slight, but significant tendency was demonstrated for preferential pairing of the two normal chromosomes associated with the compensating complex. This promotes the desired segregation into one normal and one compensating karyotype. In all trisomics, however, too high a frequency of failure of chiasma formation in a critical segment of the complex was evident. This is correlated with the ease of recovery of the trisomics, but results in undesired segregational products. Interstitial chiasmata leading to the formation of branched configurations were also present, more in some trisomics than in others. These also result in undesired segregations. The behaviour at meiosis was so closely correlated with the length of the chromosome segments involved that a prediction of the most favourable combination of telocentric and translocation can be made. The telocentric should be large, the corresponding translocated segment large and the interstitial segment small. The non-translocated arm of the translocated chromosome should be large and the second translocated segment small. The combinations of translocations and telocentrics had not been selected for these criteria and did not meet the requirements for practical application.

Key words: Telo-tertiary compensating trisomic – Rye – *Secale cereale* – Meiosis – Hybrid variety

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Introduction

In compensating trisomics, one member of a pair of chromosomes is replaced by two rearranged chromosomes that together, but not separately, contain at least the complete genetic material of the missing chromosome. The total number of chromosomes is increased by one. One of the types reported by Khush (1973) is the telocentric translocation compensating trisomic, where one telocentric chromosome and one translocation chromosome together compensate for the absence of one normal chromosome (Fig. 1). This type usually contains so much extra chromosomal material that in plants their transmission through the pollen, in competition with pollen of normal chromosomal constitution, is very limited or even practically excluded. Female transmission, not being competition sensitive, is closer to theoretical expectation. For this reason, these types of compensating trisomics have been proposed (Sybenga 1982; de Vries 1985) to replace tertiary trisomics (Ramage 1965) in balanced chromosomal systems, for the maintenance of male-sterile lines in the construction of hybrid varieties. The essence of such systems is that a recessive male-sterility allele is located on the normal chromosome of the compensating complex, and the dominant normal allele is in or closely linked to the extra chromosomal material. Alternatively, the two normal chromosomes from which a segment is present in the translocation chromosome both carry the recessive allele. This allele must then be located in the translocation segment.

Further requirements are that the extra material with the dominant Ms allele is transmitted through the female and not through the male, and that no recombination between the ms gene and the extra material occurs. The latter is realized by the translocation that reduces recombination. Fertilizing homozygous sterile plants with the

pollen of such trisomics results in homogeneous sterile progeny, because only the pollen with the recessive allele of the male-sterility gene contributes to fertilization. Selfing the trisomic yields steriles and new, fertile trisomics, with frequencies depending on the female transmission of the extra chromosomal material. For details see Ramage (1965) and de Vries (1985). Potential advantages of the compensating trisomics over tertiary trisomics are the higher realisable transmission rate and a greater number of possible combinations of sterility genes, markers and extra chromosomal material with a given number of translocations. More than with tertiary trisomics, however, meiotic irregularities endanger correct transmission.

Comparable systems have been developed on the basis of alien addition chromosomes (wheat, Driscoll 1972) and duplications (maize, Patterson 1973).

The isolation of a series of four telo-tertiary compensating trisomics was reported by de Vries (1985). The present paper describes the meiotic behaviour of three of these and one more which has not been reported previously. Figure 1 shows the somatic chromosomes of a model karyotype and, in addition, the two different pairing modes with the corresponding metaphase-anaphase configurations when all paired segments have formed at least one chiasma. The normal chromosome involved is composed of the segments O1 (normal arm), T1 (interstitial segment) and R1 (end segment, corresponding with the translocated segment in the translocation chromosome). In the trisomic there is one copy of this chromosome, the homologue is replaced by the translocated chromosome (segments O3 and T3, corresponding with O1 and T1 in the normal chromosome) that lacks a segment R. The translocated segment S3 of this chromosome is an extra segment, of which a homologous segment is present in one other pair of normal chromosomes (S1 and S2). These two normal chromosomes further have the segments P (normal arm) and U (interstitial segment). Segment R must be present twice in the complement for normal genetic functioning. It is part of the extra telocentric (R2), which is equivalent with the incomplete arm of the compensated chromosome. Of this arm the interstitial segment T is present in three copies. The symbols O, P, R, S, T and U are the same as used in translocation heterozygotes (Sybenga 1975).

Since chromosome segments normally pair two-by-two, the trisomic segments must make a choice for pairing partner. There are three possibilities for S: S1 pairs with S2 and S3 is free: S1 pairs with S3 and S2 is free; S2 pairs with S3 and S1 is free (Fig. 1 b). When S3 pairs with either S1 or S2, and all other segments pair that have an opportunity to do so, a quinquivalent is formed. These are two possibilities. A third is that S1 pairs with S2, which gives a trivalent including the telocentric, the normal and the translocation chromosome, and a bivalent formed by the normal pair. With random pairing, the

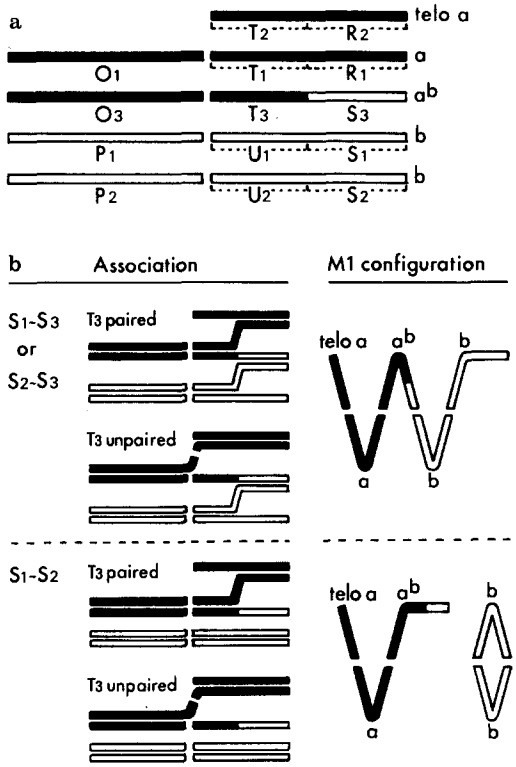

Fig. 1. a Model of a telo-tertiary compensating trisomic. One telocentric (T2, R2); a single normal chromosome of one type (01, T1, R1); one translocation chromosome partly homologous with the former chromosome (03, T3, S3); two normal homologues (P, U, S). The absence of the second copy (0, T, R) is compensated by the presence of the translocated chromosome (03, T3, S3) and the telocentric (T2, R2). 0 and P: standard chromosome arms; T and U: interstitial segments; R and S: translocated segments. The translocated chromosome P, U, R is not present. **b** Meiotic pairing configuration of a, and the two basic metaphase I/anaphase I configurations with chiasmata in all except the interstitial segments

ratio of the frequencies of quinquivalents versus trivalents + bivalents thus is expected to be 2:1.

In quinquivalents as well as in trivalents + bivalents, T3 can pair with T1 or with T2 or remain unpaired: again three pairing modes. In the first two cases, an interstitial chiasma in the translocation chromosome can form, which results in a branched configuration of either five or three chromosomes. This is the origin of the branched metaphase I configurations involving the telocentric (8, 9, 10, 11, 17) in Table 1 and Fig. 3. Pairing between T3 and T2 is not depicted in Fig. 1. The resulting metaphase I configurations after chiasma formation are not frequent, and it may be assumed that the interstitial segment usually follows the pairing pattern of the adjacent end segments O or R, and is infrequently capable of initiating pairing and forming chiasmata by itself. Branched multivalents can also arise from chiasma formation in the

Table 1. Frequencies of different meiotic metaphase I configurations of Fig. 3 in four telocentric-tertiary compensating trisomics of rye. Class A: configurations clearly based on quinquivalent pairing; class B: configurations based on quinquivalent or trivalent + bivalent pairing with the telocentric associated; class C: telocentric free and no multivalents present

Configuration code	Trisomics									
	240		248		305		306a		306b	
Class A										
1	51	0.102	2	0.004	7	0.014	53	0.066	9	0.020
2	31	0.062	0	0.000	0	0.000	57	0.071	11	0.025
3	98	0.196	161	0.322	234	0.468	187	0.234	50	0.111
4	63	0.126	0	0.000	2	0.004	141	0.176	106	0.236
5	4	0.008	0	0.000	1	0.002	0	0.000	1	0.002
6	5	0.010	0	0.000	0	0.000	0	0.000	1	0.002
7	17	0.034	0	0.000	0	0.000	0	0.000	2	0.004
8	0	0.000	26	0.052	0	0.000	0	0.000	0	0.000
9	1	0.002	0	0.000	0	0.000	0	0.000	0	0.000
10	0	0.000	0	0.000	0	0.000	0	0.000	1	0.002
11	1	0.002	0	0.000	0	0.000	0	0.000	0	0.000
12	8	0.016	0	0.000	1	0.002	2	0.003	6	0.013
13	2	0.004	0	0.000	0	0.000	0	0.000	6	0.013
14	11	0.022	32	0.064	47	0.094	2	0.003	18	0.040
15	6	0.012	0	0.000	0	0.000	1	0.001	0	0.000
16	5	0.010	0	0.000	3	0.006	1	0.001	53	0.118
Subtotal	303	0.606	221	0.442	295	0.590	444	0.555	264	0.586
Class B										
17	0	0.000	10	0.020	0	0.000	0	0.000	0	0.000
18	140	0.280	237	0.474	156	0.312	343	0.429	126	0.281
19	31	0.062	0	0.000	0	0.000	4	0.005	8	0.017
Subtotal	171	0.342	247	0.494	156	0.312	347	0.434	134	0.298
Class C										
20	26	0.052	32	0.064	49	0.098	9	0.011	52	0.116
Total	500	1.000	500	1.000	500	1.000	800	1.000	450	1.000

interstitial segment U of the normal chromosomes P-U-S, together with a chiasma in S after S1/S3 or S2/S3 pairing (Fig. 1). This results in configurations 1, 2, 5, 6, 12, 13 and 15 (Table 1, Fig. 3) and is much more frequent.

On the basis of the two fundamental pairing configurations (quinquivalent and trivalent/bivalent) in a 2:1 ratio, chiasma formation results in the specific metaphase I configurations that have been the subject of the present analysis. The orientation of these configurations determines the anaphase I segregation on which, in turn, the chromosomal composition of the gametes rests. This chromosomal composition of the gametes finally determines whether or not a specific telo-tertiary compensating trisomic is in principle suitable for maintaining genic male-sterile lines. The combination of a bivalent formed by the two normal chromosomes and a trivalent formed by the compensating complex carries a smaller segregational risk than a quinquivalent (de Vries 1983). Therefore, the pairing behaviour of segment S is of considerable importance and preferential pairing between S1 and S2 should contribute to the functionality of the compensating trisomic by increasing the frequency of trivalent + bivalent formation.

Materials and methods

Four different telo-tertiary compensating trisomics (Fig. 2) were studied. Their isolation, except for 306, was described by de Vries (1985). They were derived from translocations 240 (3RS/5RL), 248 (1RS/6RS), 305 (2RS/5RS) and 306 (1RS/6RL). The telocentrics involved were 1RS (248 and 306), 3RS (240) and 5RS (305). The plants analysed were of various backgrounds but genetically not very different. They were grown in a conditioned greenhouse at 18°–21 °C. PMCs were studied in permanent acetocarmine preparations after aceto-alcohol (1 : 3) fixation. Preliminary studies had shown that for a quantitative analysis of this material, C-banding was not required. All anthers used were at early to mid-metaphase I. Anthers with more than about 25% anaphases or later stages were excluded, to limit the inclusion of early anaphase stages that might have started shedding their chiasmate associations. For each of trisomics 240, 248 and 305, 500 cells were studied. For 306, two different plants with 800 and 450 cells, respectively, were analysed.

Results

The metaphase I configurations and their frequencies for each of the telo-tertiary compensating trisomics are given in Fig. 3 and Table 1, respectively. For different reasons

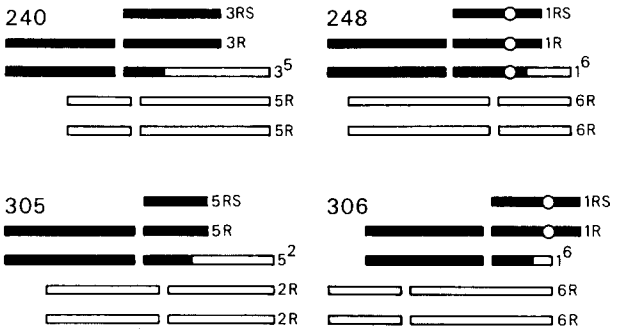

Fig. 2. Structure of the four telocentric-tertiary compensating trisomics based on translocations 240, 248, 305 and 306, and the telocentrics 3RS, 1RS and 5RS. Ring in short arm of 1R represents NOR

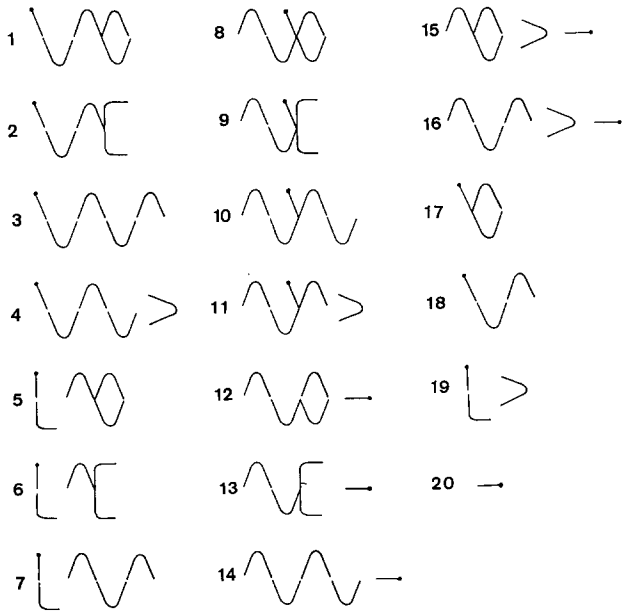

Fig. 3. The 20 metaphase I configurations listed in Table 1, resulting from the combination of presence and absence of chiasmata in different segments of the pairing configurations of a telo-tertiary compensating trisomic (Fig. 1)

the emphasis has been on pairing and chiasma formation rather than on orientation. Metaphase I reorientation is not uncommon in rye, so only late metaphase I configurations are relevant for final segregation, and these are not the best category for chiasma studies. In addition, it is difficult to conclude when the final orientation has been realised. Therefore, only if the pattern of chiasma formation did not give conclusive results, would an analysis of orientation have to be made.

Randomness of pairing

The configurations with code numbers 1–16 (Fig. 3 and Table 1, class A) must have been derived from quinquivalent pairing, those of class B (code numbers 17–19) can result from trivalent + bivalent pairing, but also from quinquivalent pairing with chiasma failure in critical segments. Similarly, configuration 20 (class C) may be derived from quinquivalent or trivalent + bivalent pairing. The fact that class A consistently contains less than the number expected with random pairing (two thirds of the total) could be interpreted to mean that quinquivalents frequently break down into smaller configurations. However, preferential pairing between the two normal completely homologous chromosomes (P-U-S) in segments S1 and S2 over pairing of either one with S3 in the translocated chromosome would have the same effect. In this case, the bivalent formed by the homologues would be expected to tend to form a ring. A free ring bivalent would also be formed after quinquivalent pairing if a chiasma had formed in interstitial segment U and no chiasma had formed in S (Fig. 1). This is expected to be much less frequent than ring formation in a normal bivalent in rye, where chiasma formation is usually distal from the middle of an arm. Bivalents accompanying the trivalent of the complex are not always, and not even often, reliably distinguished from the remaining bivalents in the cell, even after C-banding (de Vries 1984).

Therefore, in the present material, indirect methods are necessary for estimating the approximate frequency of ring bivalents belonging to the compensating complex. In Table 2, the frequencies of ring and open bivalents and pairs of univalents (when applicable) are given for class A for the four trisomics. The same frequencies may be assumed to be present for the same chromosomes in classes B and C, where they cannot be distinguished from the bivalent(s) formed as part of the compensating complex. When the ring and open bivalent and the univalent pair frequencies of class A are subtracted from the total bivalent frequencies in B and C, the remaining bivalents and univalent pairs in these classes may be assumed to represent the pair associated with the trivalent (or smaller configuration) of the complex. This approach has been used repeatedly in the past (see, e.g. Sybenga 1975). It is sensitive to variation between cells, as is common, and sometimes frequent in meiotic material without being readily explained. Still it can yield useful information.

This does not yet complete the estimate of the frequencies of the different bivalent types associated with the complex. Not all open bivalents are necessarily derived from quinquivalent breakdown. Especially with relatively low overall chiasma frequencies, such as with trisomics 240 and 306 in Table 2, trivalent + bivalent pairing may still result in relatively frequent open bivalents. In principle, the frequency of this event may be assumed to be equal to the frequency of open bivalents among the normal chromosomes in the cell. How this is estimated is shown below for the example of trisomic 240. It should be noted that especially the sub-acrocentric

Table 2. Metaphase I of meiosis in four telocentric-tertiary compensating trisomics. The frequencies of ring bivalents (r), open bivalents (o) and univalent pairs (u) observed in cells with configurations recognisably derived from quinquivalent pairing (class A), from trivalent + bivalent pairing or non-recognisable products of quinquivalent breakdown (class B), and in cells with only the telocentric representing the complex (class C). Also shown: the cells with open bivalents and univalents pairs in classes B and C attributed to quinquivalent pairing (V-pairing) and the final estimated totals of quinquivalent (total V-pairing) and trivalent + bivalent (III + II pairing) pairing. Average chiasmate association frequency b. The derivation of the frequencies of the two pairing modes is explained in the text

Total cells	Trisomics				
	240	248	305	306a	306b
	500	500	500	800	450
Class A					
r	1,027	1,062	1,401	2,007	1,153
o	416	43	73	205	165
u	72	0	1	8	2
Total	1,515	1,105	1,475	2,220	1,320
b	0.815	0.981	0.975	0.950	0.936
Cells	303	221	295	444	264
Added V-pairing	+48	+76	+28	+148	+131
Total V-pairing	351	297	323	592	395
Class B					
r	676	1,367	888	1,753	628
o	295	115	46	320	167
u	55	0	2	9	9
Total	1,026	1,482	936	2,082	904
b	0.803	0.961	0.973	0.919	0.885
Cells	171	247	156	347	134
V-pairing	−28	−60	−0	−143	−85
III + II from C	+6	+16	+21	+4	+6
Total III + II	149	203	177	208	55
Class C					
r	95	186	274	48	237
o	70	38	69	14	123
u	17	0	0	1	4
Total	182	224	343	63	364
b	0.714	0.915	0.899	0.873	0.820
Cells	26	32	49	9	52
V-pairing	−20	−16	−28	−5	−46
III + II pairing	−6	−16	−21	−4	−6

chromosome pairs 5R and 6R (in 240, 248 and 306) have lower than average chiasma frequencies in their short arm and consequently higher open bivalent frequencies. As long as the average chiasma frequency is high, this presents no problem. However, with reduced chiasma frequencies, the actual open bivalent frequencies for 5R and 6R may be much higher than estimated from the cell average. Table 2 contains the best estimates available, but they are not corrected for short arm size.

For 240, in order to obtain the numbers of ring and open bivalents in class B, not involved in the trisomic complex, the total number of cells in this class (171, Table 2) must be divided by the number of cells in the quinquivalent class A (303), which gives the cell number ratio of 0.564. This, multiplied by the number of ring bivalents, open bivalents and univalent pairs in A, gives the corresponding numbers for B (579, 235 and 41, respectively) Subtracting from the observed numbers gives the 97 ring bivalents, 60 open bivalents and 14 univalents pairs as the best estimate for the pair of chromosomes 5R in this trisomic plant (compare Fig. 2).

In this material, chromosome 5R is difficult to distinguish consistently at meiosis from some other chromosomes, especially 6R, even with C-banding. If 5R behaved like the average bivalent, the ratio of open bivalents to ring bivalents would be the same in 5R as in the normal bivalents, as observed in class A. This ratio is 416/1,027 = 0.405. Multiplying this by the estimated ring bivalent number in class C (97), which is assumed to be attributable entirely to trivalent + bivalent pairing, will give the best available estimate of the frequency of open bivalents in the group trivalent + bivalent pairing. This amounts to $0.405 \times 97 = 39$. As many as 60 were estimated in class B. The remaining 21 should be classified as derived from quinquivalent pairing rather than trivalent + bivalent pairing. Because there is one pair 5R per cell, this number represents the number of cells that should be included in the population of cells with quinquivalent pairing. By similar reasoning, 72/1,027 = 0.070 times the number of 97 rings in class B are expected as univalent pairs resulting from trivalent + bivalent pairing, which is 7 out of 14. The remaining 7 again are to be attributed to quinquivalent pairing. Thus, in 21 + 7 = 28 of the 171 PMCs of class B (Table 2), quinquivalent pairing has resulted in a trivalent with bivalent at metaphase I.

For class C a comparable approach is possible. The cell number ratio (class A/class C) is 0.086. The normal chromosomes, thus, are estimated to have formed 88 rings, 36 open bivalents and 6 univalent pairs. Subtraction from the observed numbers in class C gives 7 rings, 34 open bivalents and 11 univalent pairs formed by the complex. All rings are most likely attributable to trivalent + bivalent pairing, but the open bivalents have two possible origins. As above, if the ring:open bivalent ratio for 5R is the same as for the average chromosome, as apparent in class A, $416/1{,}027 = 0.405 \times 7$ should be the number of open bivalents attributable to trivalents + bivalents. This is only 3. The remaining 31 are from quinquivalent pairing. Similar reasoning results in 1 univalent pair from trivalent + bivalent pairing and 10 univalent pairs from quinquivalent pairing. Open bivalents and univalent pairs together from class C to be attributed to quinquivalent pairing add to 41, and rings, open bivalents and univalent pairs attributable to trivalent + bivalent pairing amount to 7 + 3 + 1 = 11. However, in class C only the univalent telocentric has been separated from the seven remaining pairs, so there are two pairs more

than the five normal pairs of class A. The number of chromosome pairs from class C to be distributed over the two types of pairing should, therefore, be divided by 2 to give the numbers of cells corresponding with these pairs. The numbers are not even and, rather arbitrarily, 20 are considered to be from quinquivalent pairing and 6 from trivalent + bivalent pairing. Together, these add up to the number of cells in class C (26).

For trisomic 240, we can now add up all cells atributed to the two pairing modes. Quinquivalent pairing: 303 (class A) + 21 + 7 (from class B) + 20 (from class C) = 351. Trivalent + bivalent pairing: 97 + 39 + 7 (class B) + 6 (class C) = 149. With random pairing, a ratio of 2:1 or 333:167 cells would be expected. The fit is reasonable with a slight but not quite significant excess of quinquivalent pairing (χ^2 2.91; $P > 0.05$). There is no reason to assume that the two entirely homologous chromosomes 5R pair preferentially with each other rather than either one of the two with the translocated segment of 5R in chromosome 3R/5R.

There is still a complication. It is quite possible, and with low average chiasma frequencies even probable, that the open bivalent excess of 5R in classes B and C is, at least in part, due to its sub-acrocentric nature. Thus, an excess of bivalent + trivalent pairing, potentially based on preferential pairing between the two homologous chromosomes 5R, might remain undetected. The great length of the translocated segment and previous experience with polysomics of this translocation do not suggest preferential pairing, however.

Trisomic 248 shows a different pattern (Table 2). The trivalent + bivalent class B is even larger here than the quinquivalent class A. A total of 1,.367 − 1,187 = 180 rings are estimated in class B, and as many as 115 − 48 = 67 open bivalents. With a ring:open bivalent ratio as in the quinquivalent class A, only 7 open bivalents are expected and the remaining 60 would actually be from quinquivalent pairing. The analysis of trisomic 248 can be further extended as for trisomic 240, and the most relevant results are summarised in Table 2. The conclusion is that there has been quinquivalent pairing in 297 cells and trivalent + bivalent pairing in 203 cells. The difference with random pairing is very significant and preferential pairing of the chromosomes 6R may be assumed, especially as the correction applied is exaggerated because of the sub-acrocentric shape of 6R. Preferential pairing of 248 with the breakpoint near the end in the region of most active pairing initiation agrees with the behaviour of this translocation in tetraploids (Sybenga 1973).

Trisomic 305 is more regular. The ratio quinquivalent pairing:trivalent + bivalent pairing is 323:177, quite close to the expected ratio. Chromosome pair 2R, here present as the two homologues associated with the compensating complex, is not far from metacentric and may not be expected to form higher than average numbers of open bivalents. With a large translocated segment and the break positioned well outside the region of major pairing initiation, preferential pairing is not expected. For this compensating trisomic data on the segregation of different karyotypes and a marker gene (*ti*, tigrina on 5RS; de Vries and Sybenga 1983) are available for a testcross progeny (de Vries 1985).

Of a total of 128 plants, 81 had 14 normal chromosomes, 78 with the recessive allele and 3 with the dominant allele. The latter are recombinants, unacceptable if the gene had been the male-sterility gene. The apparent compensating karyotype was found in 38 plants and all had the dominant allele of the marker gene. This is a rather low recovery of the trisomic type and, in addition, meiotic analysis of 19 of these trisomics showed that 2 were telocentric trisomics instead of compensating trisomics. A further 7 progeny plants had the recessive allele and were trisomic for an unidentified metacentric chromosome. One plant had 16 chromosomes, inlcuding 2 telocentrics, and one plant probably had 13 chromosomes. The segregational characteristics make this compensating trisomic uninteresting for practical use, as could have been predicted from its meiotic behaviour.

The fourth trisomic, 306, behaves unexpectedly mainly because of the apparent difference between the two sister plants. For 306a, there is considerable multivalent breakdown, which may be due to chiasma failure in the small exchanged segment in 1R/5R (Fig. 2). The ratio of quinquivalent:trivalent + bivalent pairing of 592:208 (800 cells) compared with an expected 533:267 shows an excess of quinquivalent pairing. This may well be the result of over-correction caused by more than average formation of open bivalents by the sub-acrocentric chromosome 6R, especially with the relatively low chiasma frequency. There is no reason to assume preferential pairing between the two chromosomes 6R.

The sister plant has even lower chiasma frequencies, which may in part explain the considerable difference between the two plants. The ratio of 395 quinquivalent pairing versus only 55 trivalent + bivalent pairing (450 cells) shows a large excess of quinquivalents, and is clearly caused by over-correction due to a high frequency of open bivalents formed by 6R. Preferential pairing between the two homologous chromosomes 6R is not indicated; it would only be detectable with much higher chiasma frequencies. Preferential pairing would not have been unexpected in this trisomic with a small size of the interchanged segment and the breakpoint in the main pairing initiation segment. There is no other information on preferential pairing with translocation 306.

Chiasma formation

The frequencies (b = bound arms) of chiasmate association of the arms of the bivalents not recognized as being

part of the telocentric tertiary compensating trisomic complexes are shown in Table 2, separately for the three classes of configurations. With decreasing size of the configuration of the complex, the bound-arm frequency decreases, especially for class C. The most prominent reason is the breakdown of the large configuration as a result of lack of chiasmata. This results in open bivalents with fewer than average numbers of chiasmata. In addition, such breakdown will take place particularly in cells that have a general tendency for lower chiasma frequencies, and this at the same time results in lower chiasma frequencies for the chromosomes not involved in the complex. As an exception, open bivalents will increase less when, as in 6R in 306 and 1R in 248 where the interstitial segments are large, ring bivalents are shed from quinquivalents by absence of a chiasma in the translocated segment (306) or the telocentric (248), but with a chiasma in the interstitial segment.

Of considerable interest are the frequency and distribution of chiasmata in the compensating complex, and their expected effects on segregation. With predominating alternate orientation of multivalents, as is common in rye, the chiasma pattern is of crucial importance, mainly for two reasons: (a) Absence of chiasmata in critical segments results in smaller configurations which orient and segregate independently. Some of the segregational combinations thus are not viable or not of the desired type. Plant a of interchange 306 has a low overall chiasma frequency and carries a great risk of unbalanced segregation. Low chiasma frequencies are common in inbred lines of rye (Sybenga 1958), for which the system of balanced trisomy is proposed. (b) Chiasmata in interstitial segments result in branched configurations with recombined chromatids that present special segregational problems.

With respect to the chiasma pattern, the four telo-tertiary compensating trisomics show characteristic differences that are of considerable interest for their segregational stability. In most cases the most common configurations are 3 and 18 (Fig. 3, Table 1), and these are the most favourable for balanced segregation. The bivalent accompanying the trivalent in configuration 18 is a normal bivalent and its segregation, also when independent from that of the trivalent, does not lead to any irregularity. Configurations 1 and 2 also will not cause serious problems. The interstitial chiasmata do not result in chromatids with structural rearrangements and segregation will usually be regular. They are common in 240 and 306, which have ample opportunity for interstitial chiasma formation in the long arm of 5R and 6R, respectively.

It is somewhat surprising that the same 240 and 306 also have several configurations of type 4, with one chromosome 5R or 6R, respectively, as a univalent. Absence of a chiasma in the short arm is not uncommon, but absence of chiasmata in the long arm is more unusual. Apparently, in this arm, exchange of pairing partner suppresses chiasma formation in the interstitial segment when the end segment is bound to the translocation segment of the translocated chromosome. It would seem that 306 especially would have enough space left for a chiasma in the long arm, but this is apparently not so. The univalent will tend to be lost and in the progeny only normal chromosome combinations 3R + 5R (in trisomic 240) or 1R + 6R (in trisomic 306) will appear. Thus, transmission of the compensating complex is reduced, as was indeed found by de Vries and Sybenga (1983) for trisomic 240. In the offspring of a backcross with a normal pollen parent, only 28 out of 130 carried the complex. No such data are available for 306. One may conclude that when a subacrocentric chromosome is involved as the normal pair in a telo-tertiary compensating trisomic, the translocation should preferably not be in the long arm. Yet this will be the most common type, partly because a long arm has a greater probability of being involved in a translocation, and partly because, as is our experience, translocations are more readily detected on the basis of chromosome morphological changes when the short arm remains short and the long arm is altered.

In contrast, configurations 5–7 are quite unfavourable because they are composed of two fragments that will tend to orient independently, giving 50% unbalanced segregational products. They are infrequent except in 240, where especially configuration 7 is formed. This is not expected because 3RL is not really a short arm.

Configurations 8–11 have the telocentric interstitially associated. Only 248 has a significant frequency, because the segment between the NOR and the breakpoint has a considerable capacity of pairing and forming chiasmata, as is known from other material of translocation 248 (Sybenga 1975). This association does not result in structurally rearranged chromatids when only the pairing combinations of Fig. 1 are realised. It enables the telocentric to co-orient with either 1R or 1R/6R, of which only the former leads to balanced segregational products. If the telocentric is associated with the translocated chromosome, undesired recombined chromatids will be formed.

Configurations 12–16 have an unbound telocentric. As expected, 14 is generally the most common. Not, however, in 306, even though it is the same telocentric as in 248. The difference between 306 and 248 is probably due to the smaller interstitial and translocated segments in 1R/6R in 306 that interfere less with the association of the telo with 1RS than in 248. It is striking that configuration 16, which is the equivalent of 4 except for the telocentric association, again is quite frequent in 306b, with low chiasma frequency. In 240, 248 and 305, the frequency of the telocentric not being bound is directly correlated with its length.

In the trivalent + bivalent combinations, the regular chain trivalent (18) is practically the only configuration except in 240, where in configuration 19, as in 5–7, a considerable frequency of unassociated arms 3RL can be observed. In 248, configuration 17, with an interstitially associated telocentric as in configuration 8, is present with a frequency that may not be overlooked.

In conlcusion, none of the four telocentric-tertiary compensating trisomics tested shows sufficient real or apparent preferential pairing between the two completely homologous chromosomes to consistently produce the desired configuration 18 of a chain trivalent and a (ring) bivalent. Only in 248 is a significant tendency to preferential pairing evident. In all cases, the pattern of absence and presence of chiasmata in critical segments causes more or less serious defects in the composition of the configurations, which disturbs balanced segregation.

In the desired type, the telocentric (T2 + R2 in Fig. 1) must be large to assure chiasmate association, but the interstitial segment must be small enough (or have other properties) to prevent chiasma formation. The non-translocated arm of the translocation chromosome (O3) must be long and so must be the non-translocation arm (P) of the normal bivalent. The terminal segment of this pair is also present on the translocated chromosome (S3). The shorter the segment S, the better, it seems. Yet segments S and T, and perhaps a short proximal, chiasma-free segment of O should be large enough to carry the male-sterility gene and a selective marker, which may not be recombined with S1 or S2 or with T1. One purpose of the translocation is to prevent such recombination by disturbing the pairing pattern, in spite of a high general chiasma frequency. When selecting translocations and telocentrics for constructing telocentric-tertiary compensating trisomics to be applied in hybrid varieties, these requirements should be kept in mind. The present combinations do not meet the requirements. Their telocentrics were selected for easy maintenance as trisomics and the translocations for somatic recognition.

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