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Transmission of Chromosomes Through the Eggs and Pollen of Triticale × Wheat F_1 Hybrids

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Summary. The substitution patterns of rye chromosomes in hexaploid triticale×wheat F_2 hybrids, along with the transmission patterns of rye chromosomes through egg cells and pollen when several of the F_1 hybrids were test crossed to triticale and wheat were investigated. The data indicated that the rye chromosome transmission through both the egg and pollen was random in number and in composition. The test crosses suggested that it was best to use wheat pollen for the transmission of rye chromosomes through the egg cells of the F_1 hybrids and triticale egg cells for the transmission of rye chromosomes through F_1 hybrid pollen. A deviation from random segregation in the F_2 and the transmission rate was observed for rye chromosomes 1R, 4R/7R, and 6R. The transmission rates of 1R and 6R varied depending on the direction in which the cross was made. The results also indicated that there was little or no compensation between the R- and D-genomes and that the chromosomes of these two genomes appeared to be transmitted independently of each other.

Key words: C-banding – Hybrid cytogenetics – Hexaploid triticale

Introduction

Crossing between triticale (×*Triticosecale* Wittmack) and wheat (*Triticum aestivum* L. em Thell) is a common practice in triticale breeding programs around the world.

The resulting secondary triticales have been shown to differ in their chromosome constitution from primary triticales in that some rye (*Secale cereale* L.) chromosomes have been replaced by their homoeologues from the D-genome of wheat in specific order (Gustafson and Zillinsky 1973, 1978; Darvey and Gustafson 1975; Merker 1975; Gustafson and Bennett 1976; Rogalska 1978). In addition to R/D chromosome substitutions, rye chromosomes were noted that had been modified by the loss of large blocks of telomeric heterochromatin (Merker 1976; Roupakias and Kaltsikes 1977). The substituted triticales (Gustafson and Zillinsky 1973; Zillinsky 1979; Sowa and Gustafson 1979) and triticales with modified rye chromosomes (Gustafson and Bennett 1982; Bennett and Gustafson 1982) were reported to have improved fertility and other desirable agronomic characteristics as compared to primary triticales.

However, all observations on the substitution and modification pattern were made on hexaploid spring triticales, most of which originated from the CIMMYT breeding program. In contrast it was shown that R/D substitutions were generally absent from hexaploid winter triticales (Lukaszewski and Apolinarska 1981; Seal and Bennett 1982). In addition, the structure of rye chromosomes, often modified in spring triticales due to telomeric heterochromatin deletion, was unchanged in winter triticales. It was suggested that unlike in spring triticale, a selection pressure may act on winter triticales to restore or maintain the complete R genome and the normal rye chromosome structure (Lukaszewski and Apolinarska 1981).

Therefore, this study was undertaken to examine the substitution pattern observed in hexaploid spring and winter triticale×wheat hybrids. Because the possibility existed that natural selection might act as early as F_1, namely on chromosome transmission through the egg cell and/or pollen of the F_1 (selection against pollen carrying a 2R/2D substitution was noted before (Lukaszewski et al. 1980), zygote survival or F_2 seed viability results are presented on the transmission of chromosomes through egg cells and pollen of several triticale×wheat F_1 hybrids.

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Materials and Methods

The triticale×wheat F_1 hybrids were produced from the following accessions:

winter triticale: primary DC3, 94-3; secondary Mo2355
spring triticale: 'Beagle'
winter wheat: *T. aestivum* cv. 'Atlas 66', 'Grana'
spring wheat: *T. aestivum* cv. 'Alfa', 'INIA 66', 'Kasper'.

All triticale lines contained a complete rye genome without deletions or translocations as revealed by C-banding, and none of the wheat cultivars had a 1B/1R substitution or translocation.

The following hybrids, Mo2355×'Atlas 66', DC3×'Kasper', 'INIA 66'×94-3 and 'Beagle'×'Alfa', which for the remainder of the paper will be referred to as the F_1, were reciprocally crossed to wheat ('Grana') and triticale ('Beagle'). The test-cross progenies were analyzed on a plant-by-plant basis using a C-banding technique. The technique was essentially the University of Manitoba technique (Bennett et al. 1977), except that cold water was used as a pretreatment (0–2 °C, 24 h), the hydrolysis time in the 0.2 N HCl was reduced to 1 h and the three-step ethanol treatment was replaced with an absolute ethanol treatment for 60 min.

It was assumed that all of the gametes from the male and female test-cross parents contributed the same number (21) and the same set (ABD or ABR) of chromosomes to the test-cross progenies. Therefore, all the differences both in chromosome number and constitution found in the analyzed progenies were considered to have resulted from the variation among the gametes produced by the triticale×wheat F_1 hybrids.

Rye chromosomes were identified on the basis of the C-banding pattern according to Darvey and Gustafson (1975).

Results

The fertility of the four F_1 hybrids varied greatly; the 'Beagle'×'Alfa' F_1 showed the lowest and the DC3×'Kasper' F_1 the highest seed set both in test crosses and in self-pollination. The seed set in the F_1×triticale and wheat×F_1 test crosses was in general lower than in the reciprocal combinations, and the seed germination rate was close to zero in those combinations except for wheat×(DC3×'Kasper'), which was 57.3 percent (Table 1).

In the analyzed material a surprisingly high number of translocations of rye/rye and rye/wheat types as well as telocentric and modified rye chromosomes was found. Out of 305 plants analyzed and karyotyped, 93 plants were found in which 134 chromosomes of rye were present either as translocations, as telocentric chromosomes or as chromosomes modified by the deletions of telomeric heterochromatin. The frequencies with which individual chromosomes of rye were involved in translocations or were present as telocentrics did not show much variation except for chromosome 7R/4R, whose frequency was higher than for the remaining 6 chromosomes. The translocations and modifications of rye chromosomes will be described in a separate publication. For the sake of the present study, if an arm of a chromosome of rye was present, whether in wheat-rye translocation or as a

Table 1. Seed set and seed viability in triticale×wheat F_1 and in test crosses to wheat and triticale

Pedigree	Number of spikes	Number of seeds	Seeds per spike	Number of seedlings	Germination rate (%)
Mo2355×'Atlas 66' (F_2)	63	64	1.02	32	50.0
(Mo2355×'Atlas 66')×*T. aestivum*	8	75	9.37	61	81.3
T. aestivum×(Mo2355×'Atlas 66')	4	3	0.75	0	0.0
(Mo2355×'Atlas 66')×triticale	6	30	5.00	2	6.7
triticale×(Mo2355×'Atlas 66')	8	45	5.62	40	88.9
DC3×'Kasper' (F_2)	78	152	1.95	77	50.8
(DC3×'Kasper')×*T. aestivum*	7	77	11.00	67	86.9
T. aestivum×(DC3×'Kasper')	7	82	11.71	47	57.3
(DC3×'Kasper')×triticale	6	7	1.17	0	0.0
triticale×(DC3×'Kasper')	7	71	10.14	62	87.3
'INIA'×94.3 (F_2)	38	41	1.08	28	68.3
('INIA'×94.3)×*T. aestivum*	4	8	2.00	3	37.5
('INIA'×94.3)×triticale	2	5	2.50	0	0.0
'Beagle'×'Alfa' (F_2)	30	8	0.27	4	50.0
('Beagle'×'Alfa')×*T. aestivum*	6	24	4.00	16	66.7
T. aestivum×('Beagle'×'Alfa')	2	0	0.00	0	0.0
('Beagle'×'Alfa')×triticale	5	3	0.60	1	33.3
triticale×('Beagle'×'Alfa')	4	0	0.0	0	0.0
Total: F_2	209	265	1.27	141	53.2
F_1×*T. aestivum*	25	184	7.36	147	79.9
T. aestivum×F_1	13	85	6.54	47	55.3
F_1×triticale	19	45	2.37	3	6.7
triticale×F_1	19	116	6.11	102	87.9

telocentric, it was scored as if it were a complete chromosome. When the two arms of two different rye chromosomes were involved in a translocation and constituted one chromosome (translocation $5R^S/6R^S$) it was regarded as if one chromosome of rye was present when the number of rye chromosomes was scored. However, when frequencies of the individual chromosomes were scored, it was regarded as if two chromosomes were present (5R and 6R in the above example).

The chromosome constitution of 30 DC3×'Kasper' F_2 plants and 16 Mo2355×'Atlas 66' F_2 plants was also analyzed. No significant difference in the chromosome numbers and chromosome constitution was found between the F_2 populations. The number of chromosomes for the 46 F_2 plants ranged from 38 to 48, while the number of rye chromosomes ranged from 2 to 11 (Fig. 1) and the number of pairs of rye chromosomes from 0 to 4. None of the F_2 segregation ratios for the 7 rye chromosomes (i.e. homozygous ++, heterozygous +− and homozygous −− for the presence/absence of the given chromosome) significantly deviated from the 1:2:1 ratio, although the ratios for chromosomes 1R and 6R were on the border line of being significant at the 5% level. No significant deviations from the expected frequency of 75% of the plants with a given chromosome were found in F_2 (classes ++ and +−). However, plants containing chromosomes 1R or 6R showed the highest deviations (87% and 63%, respectively; Table 2).

Table 2. Segregation into classes of homozygous (++), heterozygous (+−) and homozygous (−−) for the presence/absence of the individual chromosomes of rye in the triticale×wheat F_2 generation

Chromosome	++		+−		−−		Plants with ++ and +−	
	No.	%	No.	%	No.	%	No.	%
1R	9	19.6	31	67.4	6	13.0	40	87.0
2R	8	17.4	28	66.9	10	21.7	36	78.3
3R	10	21.7	23	50.0	13	28.3	33	71.7
4R/7R	7	15.2	24	52.2	15	32.6	31	67.4
5R	7	15.2	28	60.9	11	23.9	35	76.1
6R	10	21.7	19	41.3	17	37.0	29	63.0
7R/4R	8	17.4	26	56.5	12	26.1	34	73.9

No significant differences in the transmission rate of chromosomes were noted between different F_1 hybrids, and therefore they will be treated jointly. On the other hand, differences were noted between different test crosses. In general, the numbers of chromosomes transmitted through F_1 gametes ranged from 16 to 27, the number of rye chromosomes from 0 to 7 (Table 3) and the number of the D-genome chromosomes from 0 to 7. More chromosomes were transmitted in the test crosses to triticale than to wheat (mean number of chromosomes per gamete 21.68 ± 0.18 and 20.53 ± 0.20, respectively), and more rye chromosomes were transmitted through egg cells than through pollen in crosses to the same partner (mean number of rye chromosomes per egg cell and pollen in crosses to wheat, 3.18 ± 0.12 and 2.43 ± 0.21, respectively; mean number of rye chromosomes per egg cell and pollen in crosses to triticale, 5.33 ± 0.33 and 3.99 ± 0.14, respectively; Table 3, Fig. 2). The available data on both the total chromo-

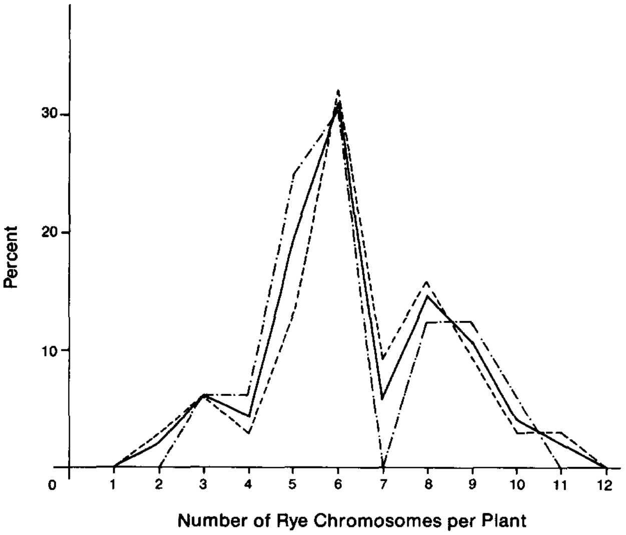

Fig. 1. Distribution of rye chromosomes in F_2 populations of winter triticale×winter and spring wheat. - - - winter×spring; –·–·– winter×winter; — F_2 total

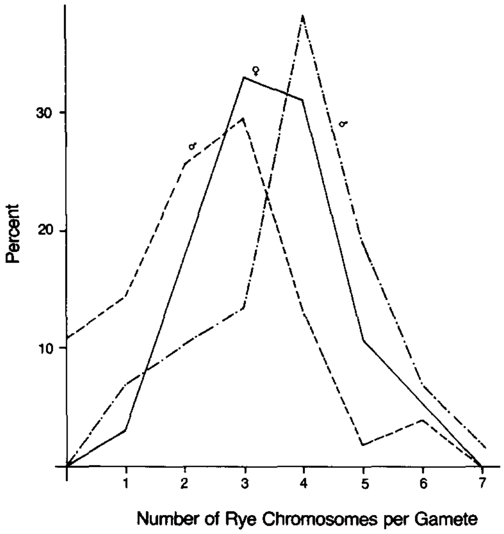

Fig. 2. Number of rye chromosomes per male and female gamete in (triticale×wheat) F_1 in crosses to wheat and triticale. ♀—F_1 × *T. aestivum*; ♂ –·–·– triticale×F_1; ♂ - - - *T. aestivum*×F_1

Table 3. Number of rye chromosomes of triticale × wheat F_1 gametes

Test combination	Number of plants analyzed	Number of rye chromosomes per gamete								Mean number of rye chromosomes per gamete
		0	1	2	3	4	5	6	7	
F_1 × *T. aestivum*	115	2 (1.7)[a]	11 (9.6)	20 (17.4)	34 (29.3)	30 (26.1)	15 (13.1)	3 (2.6)		3.18 ± 0.12
T. aestivum × F_1	47	5 (10.6)	7 (14.9)	12 (25.5)	14 (29.8)	6 (12.8)	1 (2.1)	2 (4.3)		2.43 ± 0.21
F_1 × triticale	3						2	1		5.33 ± 0.33
Triticale × F_1	94		(4.3)	9 (9.6)	14 (14.9)	38 (40.4)	17 (18.1)	10 (10.6)	2 (2.13)	3.99 ± 0.14
Total	259	7 (2.7)	22 (8.5)	41 (15.8)	62 (23.9)	74 (28.6)	35 (13.50)	16 (6.2)	2 (0.8)	3.36 ± 0.09

[a] ‰

Table 4. The transmission rate of individual rye chromosomes through the egg and pollen of the triticale × wheat F_1 hybrids

Test combination	Number of plants analyzed	Number of rye chromosomes							Total
		1R	2R	3R	4R/7R	5R	6R	7R/4R	
F_1 × wheat	115	59 (51.3)[a]	52 (45.2)	58 (50.4)	50 (43.5)	52 (44.3)	43 (27.8)	56 (48.7)	358
Wheat × F_1	47	9 (19.1)	15 (31.9)	14 (29.8)	21 (44.7)	15 (31.9)	22 (46.8)	14 (29.8)	110
F_1 × triticale	3	1 (33.3)	2 (66.7)	2 (66.7)	3 (100)	2 (66.7)	3 (100)	3 (100)	16
Triticale × F_1	94	56 (59.6)	47 (50.0)	47 (50.0)	67 (71.3)	53 (56.4)	55 (58.5)	53 (56.4)	378
Total	259	125 (48.3)	116 (44.8)	121 (46.7)	141 (54.4)	121 (44.8)	112 (43.2)	126 (48.6)	862

[a] %

some number and the number of rye chromosomes transmitted through gametes made it possible to calculate the number of D chromosomes transmitted. The transmission of D chromosomes was not significantly affected by the direction of the test cross (mean number of D chromosomes per egg cell and pollen 3.76 ± 0.25 and 3.64 ± 0.14, respectively), except for the F_1 × triticale cross, where the mean number of D chromosomes per egg cell was 2.33. However, since only 3 seeds in that combination were viable, the results have no statistical validity.

Significant differences were noted in the transmission rate of the chromosomes 1R, 4R/7R and 6R depending on the direction in which the test cross was made and on the test partner (Table 4). When the F_1 was used as female in crosses to wheat, chromosome 6R was transmitted with significantly lower frequency than random. In the reciprocal cross rye chromosomes in general were transmitted with lower frequency than random (mean number of rye chromosomes per gamete 2.43, 34.7% transmission rate), but chromosomes 4R/7R and 6R did not significantly deviate from the 50% transmission rate (44.7% and 46.8%, respectively), while chromosome 1R was transmitted with a frequency lower (19.1%) than any other chromosome. In crosses to triticale only the triticale × F_1 combination can be considered, because of the sample size, and in this combination chromosome 4R/7R was transmitted with a frequency 21.3% higher than random, while the remaining 6 chromosomes did not significantly deviate from the 50% transmission rate.

Discussion

Theoretically, the triticale × wheat F_1 hybrids are capable of producing a wide variety of gametes which, provided the gametes have 21 chromosomes, can range in their chromosome constitution from wheat (ABD) through 126 R/D combinations to triticale (ABR). Variation in chromosome number can greatly increase that range. The present study indicated that an apparently continuous range of R/D combinations was present and that none of the populations showed any skewness toward either ABD or ABR constitutions. The total transmission rate for individual rye chromosomes in all test combinations did not deviate from random (Table 4), while the number of rye chromosomes per gamete showed normal distribution (Table 3). This suggested that there was no selective pressure against gametes carrying certain sets or numbers of rye chromosomes that could limit the wide spectrum of the possible chromosome constitution of the F_1 gametes. However, differences were found in the range and number of rye chromosomes transmitted between eggs and pollen of F_1, as well as between different test partners. It seemed that those differences were due to the incompatibility of certain types of the F_1 gametes and testers rather than to particular properties of the F_1 gametes themselves.

The seed from the wheat×triticale crosses is generally inviable, most likely due to endosperm imbalance, while reciprocal crosses are generally successful. It would be expected, therefore, that all the wheat-like egg cells from the triticale×wheat F_1 would produce inviable seed when fertilized by triticale pollen and triticale-like pollen from the F_1 would produce inviable seed in crosses to wheat. Moreover, seed set in the triticale×wheat crosses is never complete, and is usually about 50%, which indicates that the actual number of the triticale-like eggs produced by the F_1 may be higher than shown by seed set and the germination rate in the test crosses to wheat. The above factors can affect the results of any analysis concerning the chromosome constitution of gametes which has been based on the chromosome complement of progeny obtained from test crosses. Apparently this was the case in the present study. The triticale×wheat F_1 fertility and seed viability was high when it was used as a female in crosses to wheat, while in crosses to triticale the seed set was considerably lower (actually only one combination was successful) and the resulting seed was largely inviable (Table 1). A similar situation occurred in the reciprocal crosses where wheat pollinated with the F_1 pollen gave fewer viable seeds than when triticale was used as a tester. This was clearly demonstrated by the shift toward F_1 male gametes, containing a lower number of rye chromosomes, yielding viable seed when combined with wheat egg cells rather than triticale egg cells (Fig. 2). Therefore, only wheat pollen for the transmission of rye chromosomes through egg cells of the F_1 and triticale egg cells for the transmission of rye chromosomes through F_1 pollen can be regarded as adequate testers, though not ideal.

It has been shown that the elimination frequency of rye chromosomes from the wheat-rye F_1 hybrids with genome constitution ABR was strongly correlated to the chromosome length/DNA content (Lukaszewski et al. 1980). No correlation of that kind was found in this study despite similarities both in the materials and methods used. Merker (1979) found that in F_1 hybrids between normal wheat and wheats containing one, two and three rye chromosomes, chromosome 1R was transmitted in a random manner both through egg cells and pollen, while chromosomes B, D and E were transmitted through egg cells with frequencies of 36, 26.3 and 31 percent, respectively. Male transmission of the chromosome E was 25% (Merker 1979). According to Darvey and Gustafson's (1975) nomenclature, chromosomes D and E are 4R/7R and 6R, respectively, while chromosome B is most likely chromosome 3R. It was interesting to note that in the study by Merker (1979) the male and female transmission rates for chromosome 6R were calculated on the basis of the F_2 segregation only and no test crosses were made. The observed segregation ratio in F_2 was well explained by the transmission rates of 31% and 25% but did not give any indication as to which gametes' survival was affected by the presence/absence of the chromosome 6R.

In the present study ratios in F_2 for any of the 7 chromosomes of rye did not significantly deviate from the random segregation 1:2:1 (Table 2), but frequencies of plants with chromosomes 1R, 4R/7R or 6R showed the highest deviations from the random 75%. In test crosses no significant differences in the transmission rate of chromosomes 2R, 3R, 5R and 7R/4R were found, while chromosomes 1R, 4R/7R and 6R deviated from the expected ratio for random transmission in some of the test crosses. It appeared that in the F_1×wheat cross the seed which originated from the female gametes carrying chromosome 6R was less viable, while in the reciprocal cross the seed from pollen carrying chromosome 1R was less viable (Table 4). Darvey and Gustafson (1975) suggested that chromosome 1R was the major nucleolus-organizing chromosome in rye, and biochemical studies on ribosomal RNA have demonstrated the presence of ribosomal RNA on chromosomes 1R and 4R/7R (Rimpau and Flavell, pers. comm.). No RNA has been detected on chromosome 6R; however, it is known to carry a secondary constriction as a univalent at first metaphase, like chromosome 4R/7R (Riley and Chapman 1958). Because of their possible affinity with nucleolus-organizing activity, chromosomes 1R, 4R/7R and 6R may cause the seedlings with those chromosomes to have pre-determined selective survival rate advantage or disadvantage, depending on their mode of inheritance, while their presence or absence did not seem to affect the gamete survival. Possible nucleolar activity of chromosome 6R has been suggested as a reason for its preferential retention in substituted spring triticales (Gustafson and Bennett 1976).

It was surprising that in crosses to wheat (wheat× F_1) the transmission rate of chromosome 1R was significantly lower than for any other chromosome. Several European wheats carry a 1B/1R substitution or translocation (Mettin et al. 1973; Zeller 1973; Blüthner and Mettin 1977), and it has been suggested that the nucleolus organizer present on the short arm of chromosome 1R is advantageous in hexaploid wheat as compared to the nucleolus organizer present in chromosome 1B (for review, see Gustafson 1976, 1982). Those 1B/1R substitutions and/or translocations occurred spontaneously in the breeding programs, therefore it was surprising to find in the present study that the F_1 gametes contributing chromosome 1R to wheat gave less viable seed. The data presented here suggest that if 1R substitution into wheat was desired in a breeding program, the first backcross with AABBDR hybrid should be made using wheat as the male partner for better results.

In all test cross combinations using wheat as a parent there was no correlation between the number of R and D chromosomes transmitted, while for the triticale × F_1 combination the correlation was low ($r = -0.53$) but significant. This indicated that there was little compensation between R- and D-genomes and most of the time the chromosomes of those two genomes were transmitted independently of each other. The correlation for triticale × F_1 may have resulted from the tendency to keep the number of chromosomes as close to 21 as possible, and gametes deviating from that did not survive or yield viable seed. Lack of compensation between R- and D-genomes, but good compensation between homoeologues was reported by Gupta (1961), and may explain the differences in the transmission rate of rye chromosomes between this study and that of Merker (1979).

The frequency of both male and female gametes carrying 3–4 rye chromosomes was high in most of the combinations analyzed, constituting 23.9 and 28.6 percent of all gametes tested, respectively. However, the frequency of F_2 plants with seven rye chromosomes was low (6.4% of F_2), while the classes of plants with 6 and 8 rye chromosomes per plant were numerous (31.2 and 12.5 percent, respectively). This indicated selection pressure against genotypes with seven rye chromosomes and possibly the operation of a disruptive selection pressure for genotypes carrying complete D- or R-genomes. On the other hand, the decrease in the distribution pattern observed when 6 to 8 chromosomes are present (Fig. 1) bears close resemblance to that found by Gustafson and Zillinsky (1978) for the substitution pattern in the unselected population of the triticale × wheat hybrids and for the substitution pattern in advanced secondary triticales present in a breeding program (Merker 1975).

The results indicated that there was no clear evidence of any selection pressure against female or male gametes produced by the triticale × wheat F_1 hybrids. The transmission of chromosomes through egg cells and pollen seemed to be random both in number and composition. There was however evidence that some combinations of gametes result in inviable seed, so the F_2 progeny with 7 rye chromosomes are less viable than others and seedlings with chromosomes 4R/7R or 6R have less chance to survive than other combinations of chromosomes, while those with chromosome 1R have a better-than-average chance to survive. Therefore, if there is a natural selection pressure to restore or maintain complete R- or D-genomes in triticale, it acts on some other stage in the breeding program (e.g. winter survival, fertility, plant type, hardiness).

Literature

Bennett, M.D.; Gustafson, J.P. (1982): The effect of telomeric heterochromatin from *Secale cereale* L. on triticale (× *Triticosecale* Wittmack). 2: The presence or absence of blocks of heterochromatin in isogenic backgrounds. Can. J. Genet. Cytol. **24,** 93–100

Bennett, M.D.; Gustafson, J.P.; Smith, J.B. (1977): Variation in nuclear DNA in the genus *Secale.* Chromosoma **61,** 149–176

Blüthner, W.D.; Mettin, D. (1977): Chromosomensubstitutionen und Translokationen zwischen Weizen und Roggen und deren Bedeutung für die Züchtung. Arch. Züchtungsforsch. **7,** 15–27

Darvey, N.L.; Gustafson, J.P. (1975): Identification of rye chromosomes in wheat-rye addition lines and triticale by heterochromatin bands. Crop Sci. **15,** 239–243

Gustafson, J.P. (1976): The evolutionary development of triticale: the wheat-rye hybrid. Evol. Biol. **9,** 107–135

Gustafson, J.P. (1982): Cytogenetics of triticale. In: Cytogenetics of Crop Plants (eds. Swaminathan, M.S.; Gupta, P.K.; Sinha, U.), in press

Gustafson, J.P.; Zillinsky, F.J. (1973): Identification of D-genome chromosomes from hexaploid wheat in a 42-chromosome triticale. In: Proc. 4th Int. Wheat Genet. Symp., pp. 225–232. Columbia, Missouri: Mo. Agr. Exp. Stn.

Gustafson, J.P.; Bennett, M.D. (1976): Preferential selection for wheat-rye substitutions in 42-chromosome triticale. Crop Sci. **16,** 688–693

Gustafson, J.P.; Zillinsky, F.J. (1978): Influences of natural selection on the chromosome complement of hexaploid triticale. In: Proc. 5th Int. Wheat Genet. Symp., vol. 2 (ed. Ramanujam, S.), pp. 1201–1207. New Delhi: New Delhi Press

Gustafson, J.P.; Bennett, M.D. (1982): The effect of telomeric heterochromatin from *Secale cereale* L. on triticale (× *Triticosecale* Wittmack). 1: The influence of several blocks of telomeric heterochromatin on early endosperm development and kernel characteristics at maturity. Can. J. Genet. Cytol. **24,** 83–92

Gupta, P.K. (1961): Ph. D. Thesis University of Manitoba

Lukaszewski, A.J.; Apolinarska, B. (1981): The chromosome constitution of hexaploid winter triticale. Can. J. Genet. Cytol. **23,** 281–285

Lukaszewski, A.J.; Apolinarska, B.; Lapinski, B. (1980): Chromosome elimination in the (*Triticum persicum* × *T. dicoccoides*) × *Secale cereale* F_1 hybrids. Hod. Rosl. Aklim. Nasien. **24,** 365–372

Merker, A. (1975): Chromosome composition of hexaploid triticale. Hereditas **80,** 41–52

Merker, A. (1976): The cytogenetic effect of heterochromatin in hexaploid triticale. Hereditas **83,** 215–222

Merker, A. (1979): The breeding behavior of some rye-wheat chromosome substitutions. Hereditas **91,** 245–255

Mettin, D.; Blüthner, W.D.; Schlegel, G. (1973): Additional evidence on spontaneous 1B/1R wheat-rye substitutions and translocations. In: Proc. 4th Wheat Genet. Symp., pp. 179–184. Columbia, Missouri: Mo. Agr. Exp. Stn.

Riley, R.; Chapman, V. (1958): The production and phenotypes of wheat-rye chromosome addition lines. Heredity **12,** 301–305

Rogalska, S. (1978): Chromosome constitution of plants of selected lines of secondary hexaploid triticale. Hod. Rosl. Aklim. Nasien. **22,** 294–301

Roupakias, D.G.; Kaltsikes, P.J. (1977): The effect of telomeric heterochromatin on chromosome pairing of hexaploid triticale. Can. J. Genet. Cytol. **19,** 543–548

Seal, A.; Bennett, M.D. (1982): The rye genome in winter hexaploid triticales. Can. J. Genet. Cytol. **23,** 647–653

Sowa, W.; Gustafson, J.P. (1979): Relation between chromosomal constitution in triticale and several agronomic characters. Hod. Rosl. Aklim. Nasien. **24,** 397–404

Zeller, F.J. (1973): 1B/1R wheat-rye chromosome substitutions and translocations. In: Proc. 4th Wheat Genet. Symp., pp. 209–221. Columbia, Missouri: Mo. Agr. Exp. Stn.

Zillinsky, F.J. (1979): The influences of chromosome substitutions on some agronomic characteristics of hexaploid triticale. Hod. Rosl. Aklim. Nasien. **24,** 383–388

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