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# Analysis of the Rye Chromosome Constitution and the Amount of Telomeric Heterochromatin in the Widely and Narrowly Adapted Hexaploid Triticales

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**Summary.** Investigations were made on the rye chromosome constitution and on the presence of telomeric heterochromatin in rye chromosomes of the 26 most widely and 24 most narrowly adapted triticale strains. Among widely adapted lines, 22 (85%) had a complete rye genome and four triticales only had chromosomal R-D genome substitutions. Twenty-three (96%) of the 24 most narrowly adapted triticales had substitutions between the chromosomes of the R and D genomes. The most widely adapted triticales accumulated fewer modified rye chromosomes in comparison to narrowly adapted lines. They had from one to three rye chromosomes with heterochromatic deletions: 46% of widely adapted lines had two modified rye chromosomes; 34% had three modified rye chromosomes, and 19% had a single modified rye chromosome. In widely adapted strains, the 1R, 4R, 5R and 6R modified chromosomes were observed; they were present in 80%, 73%, 50% and 11% of the cases, respectively. The most narrowly adapted triticales had from two to four modified rye chromosomes: 58% of the strains had three modified rye chromosomes; 29% had four modified rye chromosomes and 12% had two modified rye chromosomes. The modified 4R and 5R chromosomes were present in all of these lines. The 1R (modified), 6R (modified) and 7R (modified) were found in 83%, 25% and 16%, respectively, of the narrowly adapted strains.

Results support the previous observations (Pilch 1980b) that a wide adaptation of hexaploid triticales is associated with the presence of the full potential of rye genome, and that it is independent of the amount of telomeric heterochromatin possessed by rye chromosomes.

**Key words:** Triticale – Rye – Hexaploids – Adaptation – Chromosomal substitutions – Modified chromosomes – Telomeric heterochromatin

## Introduction

In order to obtain improvements in triticale attention has been directed recently to the chromosomal substitutions between the R-rye and D-wheat genomes (Muntzing 1963; Darvey 1973; Darvey and Gustafson 1975; Kaltsikes and Roupakias 1975; Kaltsikes et al. 1975; Gustafson 1976; Gustafson and Bennett 1976; Gustafson et al. 1979a, b) and to the deletions of telomeric heterochromatin of rye chromosomes (Thomas and Kaltsikes 1974, 1976; Merker 1976a; Roupakias and Kaltsikes 1977; Bennett 1974, 1977, 1979; Gustafson et al. 1979a, b).

Zillinsky (1979a, b) and Skovmand (1979) reported that in the early stages of triticale breeding in the CIMMYT program, genetic improvements in fertility, straw strength, plant height, seed type and daylength insensitivity were observed to be more rapid among those selections with chromosomal substitutions. The optimum ratio of D-genome to R-genome chromosomes in those strains was 1:6 (Pilch 1980a).

Merker (1976b) presented 128 different possible combinations which can occur between R and D genome chromosomes in triticale. This means that substituted triticales have the possibility of a far reaching reorganization of the chromosomal and genomic composition. However, only a few combinations have been found in the breeding programs (Darvey and Gustafson 1975; Merker 1975; Rogalska 1977; Pilch 1980a, b).

Merker (1976b) suggested that chromosome substitution possibilities are limited in hexaploid triticale because of gene interaction or because of the lack of homoeology between wheat and rye genomes which can cause the establishment of the substitutions. Thus, certain D-genome chromosomes may lack specific genes essential for a successful substitution, or they may have genes that make a particular substitution impossible.

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Some varieties which have been released in 1978 and 1979 for commercial production (Zillinsky et al. 1980) had only one or two R-D genome substitutions.

Apart from chromosomal substitutions, the rye chromosomes modified by reduced or missing telomeric heterochromatin have been found in hexaploid triticales, and attention was directed to these segments of late-replicating DNA.

Thomas and Kaltsikes (1974, 1976), Merker (1976a) and Roupakias and Kaltsikes (1977) illustrated the role of heterochromatic deletions of rye chromosomes in the triticale meiotic stability improvements. Bennett (1974, 1977, 1979) found a relationship between these deletions of heterochromatin at the telomeres of rye chromosomes and the seed type improvement in triticale strains.

The research reported here was undertaken to investigate an association between adaptation and rye chromosome constitution and heterochromatic deletions of rye chromosomes in hexaploid triticales.

## Materials and Methods

The material for investigation was selected from the 10th International Triticale Screening Nursery (ITSN). This nursery had 245 entries, including wheat checks, and it was distributed in 1978-79 to 121 locations throughout the world. The triticale entries for the 10th ITSN were evaluated for their yield potential in Ciudad Obregon (Sonora state, Mexico) under uniform conditions in replicated yield trials. Among 750 tested advanced lines, the best ones, which were identified as having good yield potential, were selected for inclusion in the ITSN. The potential test plants were also grown in small multiplication plots and seeds from these plots were used to assemble the nursery.

This nursery was observed and selection of adapted triticale strains were made by co-workers at various locations throughout the world. Grain yield, resistance to diseases and pests and degree of grain shrivelling were used as indicators of adaptation. Co-workers utilized the same methods for recording agronomic and disease data. Yield, agronomic and pathological data, which provide information about the adaptation of the triticale entries, were obtained from various locations around the world. Statistical analyses of reported information were made using a new set of computer programs called the Small Grains Summary System. This program was developed by the Laboratory for Information Science in Agriculture (LISA), formally called the Information Sciences Genetic Resources (IS-GR) Program, Colorado State University, Fort Collins, Colorado, USA.

Results from 26 locations indicated ample broad adaptation among the triticales of this ITSN. The 26 highest yielders (the most widely adapted) and the 24 lowest yielding lines (the most narrowly adapted) from the triticale entries in this nursery were examined in order to identify their chromosome constitution and heterochromatin deletions of rye chromosomes. The entry numbers and identities of those strains are listed in Tables 1 and 2.

**Table 1.** 26 highest yielding triticales in the 10th International Triticale Screening Nursery (1978-79)

| Entry no. | Cross | Average yield, kg/ha |
|---|---|---|
| 56 | IA – IRA X BUI | 3843.0 |
| 153 | DRIRA – MA | 3830.2 |
| 157 | BUEY – BGL"S" | 3517.2 |
| 207 | BGL"S" | 3499.8 |
| 179 | CML X CNO-GALLO | 3394.7 |
| 11 | DRIRA | 3360.5 |
| 220 | UM 1296 | 3345.9 |
| 142 | $M_2$A-ARM"S" X BGL | 3314.1 |
| 137 | $M_2$A-ARM"S" X BGL | 3306.7 |
| 63 | BGL"S"/ARS-MEXIPAK MUT X BGL"S" | 3299.9 |
| 60 | BEAGLE | 3281.6 |
| 138 | $M_2$A – ARM"S" X BGL | 3279.3 |
| 168 | DRIRA-KANG | 3269.8 |
| 209 | BGL"S" | 3253.6 |
| 16 | $M_1$A | 3250.8 |
| 126 | BGL"S" – $M_2$A | 3238.2 |
| 191 | BGL"S"/BGL"S" X ITA-LEO | 3216.7 |
| 158 | BUEY – BGL"S" | 3214.1 |
| 145 | $M_2$A-ARM"S" X BGL | 3207.3 |
| 18 | $M_2$A | 3179.5 |
| 144 | $M_2$A-ARM"S" X BGL | 3174.7 |
| 113 | CIN"R" – BGL"S" | 3166.8 |
| 213 | BGL CORTO | 3165.4 |
| 20 | $M_2$A | 3164.2 |
| 161 | IA-$M_2$A X PI62/BGL"S" | 3163.9 |
| 203 | FS 1897 | 3153.6 |

**Table 2.** 24 lowest yielding triticales in the 10th International Triticale Screening Nursery (1978-79)

| Entry no. | Cross | Average yield, kg/ha |
|---|---|---|
| 40 | $M_2$A – CML | 2394.1 |
| 53 | IGA – $M_2$A | 2393.0 |
| 122 | IRA – $M_2$A X $M_1$A | 2384.6 |
| 244 | FS 381 – FS 477 | 2383.9 |
| 107 | $M_2$A – TI 71 | 2379.9 |
| 167 | TREAT 913-CIN X IA | 2372.7 |
| 178 | $M_2$A – IRA X CML | 2370.9 |
| 42 | $M_2$A – CML | 2357.3 |
| 48 | $M_2$A – IRA X $M_2$A – CIN | 2329.0 |
| 79 | CML – IRA | 2318.9 |
| 226 | $M_2$A – WW15 | 2307.8 |
| 112 | $M_2$A X UM940"S"-ARM"S"/AZ 67 | 2301.3 |
| 41 | $M_2$A – CML | 2295.0 |
| 105 | $M_2$A – TI 71 | 2285.4 |
| 27 | IRA(2) | 2285.2 |
| 163 | BGC-IA X TOB/$M_2$A | 2275.3 |
| 164 | $M_2$A-UP301 X BGL"S" | 2249.8 |
| 228 | $M_2$A – CML | 2236.6 |
| 234 | CML – FS 1377 | 2185.0 |
| 59 | $M_2$A – IRA | 2132.3 |
| 243 | IRA – CML | 2128.1 |
| 218 | UM 1216 | 1963.3 |
| 239 | BGC – TI 71 | 1837.2 |
| 238 | BGC – TI 71 | 1716.1 |

Modification of the Leishman staining technique (Pilch 1980b) was used in determining rye chromosome constitution and the amount of telomeric heterochromatin in rye chromosomes.

## Results and Discussion

Earlier investigation of rye chromosome constitution and the amount of telomeric heterochromatin in rye chromosomes of the most widely and narrowly adapted hexaploid triticales showed that wide adaptation of triticales was associated with the presence of the full potential of the rye genome (Pilch 1980b). Triticale lines with the complete set of rye chromosomes appeared to have an advantage in adaptation over a wide range of environments over substituted triticales. The most widely adapted triticale lines in that nursery had more telomeric heterochromatin of rye chromosomes in comparison to the most narrowly adapted triticales. Those results suggested also that adaptation of triticale strains was independent of the amount of telomeric heterochromatin possessed by rye chromosomes.

Results obtained from the 10th ITSN supported earlier findings (Pilch 1980b). Of 26 highest yielding triticale strains which were among the most widely adapted in the 10th ITSN, 22 entries (85%) had a complete rye genome (Table 3). Four triticale entries: 179, 16, 18 and 20, had substitutions between the chromosomes of the R and D genomes only. In entries 179, 18 and 20, the 2R chromosome was replaced. Entry 16 had the 2R and 7R chromosomes substituted by wheat chromosomes. Twenty three (96%) of the 24 most narrowly adapted triticale strains were found to have chromosomal substitution between R and D genomes, (Table 4). In these lines the 2R-2D substitution was present, except in entry 226 in which the 2R chromosome was present but 3R was replaced. One triticale strain with all rye chromosomes was identified among the narrowly adapted entries.

The most widely adapted triticales had more telomeric heterochromatin in rye chromosomes than the triticale strains which were among the narrowly adapted entries (Tables 3, 4). Bennett (1977, 1979) and Gustafson et al. (1979a, b) suggested that triticale cultivars could be improved by modifying the rye chromosome structure through the removal of late-replicating telomeric segments of heterochromatin, suggesting further that the elimination of these segments from rye chromosomes should be a major objective in the breeding of economically useful triticales that would contain all seven pairs of rye chromosomes. To achieve the desired chromosome structure in triticale, they also recommended that diploid rye and triticale lines having different rye chromosomes with deletions of telomeric heterochromatin be used as parents and that those identified be combined into a single triticale

**Table 3.** Rye chromosome constitution and the amount of telomeric heterochromatin of 26 highest yielding triticales in the 10th International Triticale Screening Nursery (1978-79)

| Entry no. | Rye chromosomes | | | | | | | No. of rye chromosome pairs |
|---|---|---|---|---|---|---|---|---|
| | 1R | 2R | 3R | 4R | 5R | 6R | 7R | |
| | −L | | | | −s | | | |
| 56 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | −S | | | |
| 153 | + | + | + | + | + | + | + | 7 |
| | −L | | | | | **S | | |
| 157 | + | + | + | + | + | + | + | 7 |
| | −L | | | | −S | | | |
| 207 | + | + | + | + | + | + | + | 7 |
| | −L | | | −S | −S | | | |
| 179 | + | | + | + | + | + | + | 6 |
| | −L | | | | −S | | | |
| 11 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | −S | | | |
| 220 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | −S | | | |
| 142 | + | + | + | + | + | + | + | 7 |
| | | | | | −S | | | |
| 137 | + | + | + | + | + | + | + | 7 |
| | −L | | | | −S | | | |
| 63 | + | + | + | + | + | + | + | 7 |
| | | | | | −S | | | |
| 60 | + | + | + | + | + | + | + | 7 |
| | −L | | | | −S | | | |
| 138 | + | + | + | + | + | + | + | 7 |
| | −L | | | −S | −S | | | |
| 168 | + | + | + | + | + | + | + | 7 |
| | −L | | | | −S | | | |
| 209 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | −S | | | |
| 16 | + | | + | + | + | + | | 5 |
| | −L | | | **S | | | | |
| 126 | + | + | + | + | + | + | + | 7 |
| | −L | | | | −S | | | |
| 191 | + | + | + | + | + | + | + | 7 |
| | −L | | | | | **S | | |
| 158 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | | | | |
| 145 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | −S | | | |
| 18 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | | | | |
| 144 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | | −S | | |
| 113 | + | + | + | + | + | + | + | 7 |
| | | | | | −S | | | |
| 213 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | −S | | | |
| 20 | + | | + | + | + | + | + | 6 |
| | | | | **S | | | | |
| 161 | + | + | + | + | + | + | + | 7 |
| | | | | | −S | | | |
| 203 | + | + | + | + | + | + | + | 7 |

S, L Chromosome short and long arms; − Reduced telomeric heterochromatin on both homologues; ** Lack telomeric heterochromatin on both homologues; + Large heterochromatic telomere on both arms of both homologues

that would retain all seven pairs of rye chromosomes.

The most widely adapted triticales investigated here only had from one to three rye chromosomes with heterochromatic deletions (Table 3). A plurality of them (46%) had two modified rye chromosomes, nine lines (34%) had three modified rye chromosomes, and five lines (19%) had a single modified rye chromosome (Fig. 1). The 1R, 4R, 5R and 6R modified chromosomes were identified in the widely adapted triticales

The 1R chromosome modified by reduced telomeric heterochromatin of the long arm was the most frequently found. It was present in 21 strains (80%). The 5R chromosome, which had reduced telomeric heterochromatin of the short arm, was the next most frequently observed (in 73% of triticales). The 4R chromosome, which had reduced or missing telomeric heterochromatin of the short arm, was found in 50% of the strains. The 6R chromosome, with reduced or missing telomeric heterochromatin of the short arm, was identified in 11% of lines.

The lowest yielding, narrowly adapted triticale entries accumulated more modified rye chromosomes, from two to four, in comparison to the most widely adapted strains (Table 4). Fifty-eight per cent of strains had three modified rye chromosomes; 29% had four modified rye chromo-

**Table 4.** Rye chromosome constitution and the amount of telomeric heterochromatin of 24 lowest yielding triticales in the 10th International Triticale Screening Nursery (1978-79)

| Entry no. | Rye chromosomes | | | | | | | No. of rye chromosome pairs |
|---|---|---|---|---|---|---|---|---|
| | 1R | 2R | 3R | 4R | 5R | 6R | 7R | |
| | −L | | | **S | −S | **S | | |
| 40 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 53 | + | | + | + | + | + | + | 6 |
| | **L | | | **S | −S | | | |
| 122 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 244 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 107 | + | | + | + | + | + | + | 6 |
| | | | | **S | −S | | −L | |
| 167 | + | | + | + | + | + | + | 6 |
| | −L | | | −S | −S | | −L | |
| 178 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | **S | | |
| 42 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 48 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | **S | | |
| 79 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 226 | + | + | | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 112 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | **S | | |
| 41 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 105 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 27 | + | | + | + | + | + | + | 6 |
| | **L | | | **S | | | | |
| 163 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 164 | + | + | + | + | + | + | + | 7 |
| | −L | | | **S | −S | | | |
| 228 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | **S | | |
| 234 | + | | + | + | + | + | + | 6 |
| | −L | | | | −S | | | |
| 59 | + | | + | + | + | + | + | 6 |
| | −L | | | **S | −S | | | |
| 243 | + | | + | + | + | + | + | 6 |
| | | | | −S | −S | | | |
| 218 | + | | + | + | + | + | + | 6 |
| | | | | **S | −S | | −L | |
| 239 | + | | + | + | + | + | + | 6 |
| | | | | −S | −S | −S | −L | |
| 238 | + | | + | + | + | + | + | 6 |

Explanations see Table 3

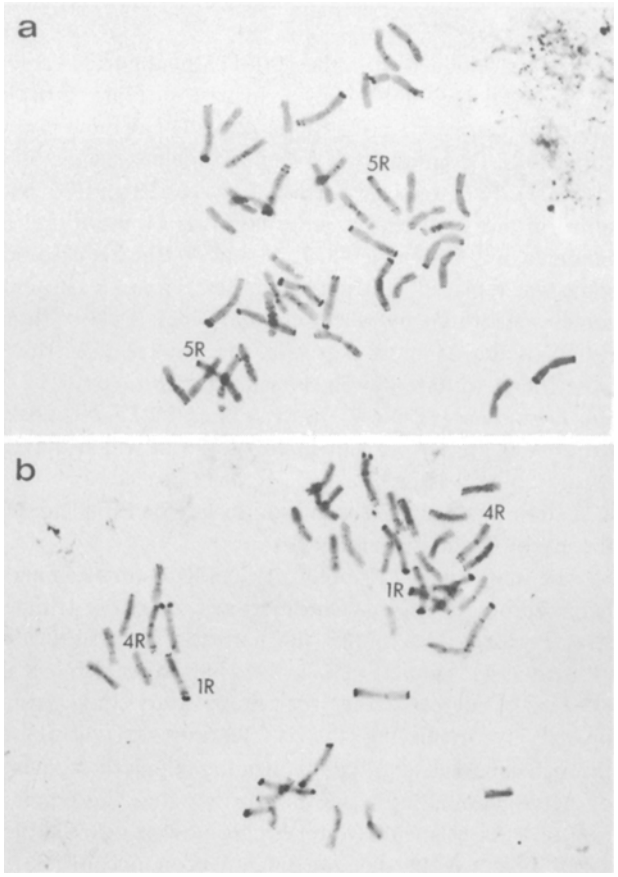


**Fig. 1a and b.** C-banded metaphase chromosomes of two high yielding related triticales, $M_2$ A-Arm'S' × Bgl, of the 10th ITSN having a complete rye genome. **a** entry 137 has reduced telomeric heterochromatin of the short arm of the 5R chromosome, **b** entry 145 has reduced telomeric heterochromatin of the long arm of the 1R chromosome and the 4R chromosome with missing telomeric heterochromatin of the short arm

somes and 12% had two modified rye chromosomes. The modified rye chromosomes 1R, 4R, 5R, 6R and 7R were found among the narrowly adapted triticales. The 4R (modified) and 5R (modified) were present in all narrowly adapted triticale lines. The 1R (modified), 6R (modified) and 7R (modified) were found in 83%, 25% and 16% of triticales, respectively.

These findings bring to question whether agronomic improvement of triticale cultivars can be successfully accomplished by the elimination of large blocks of telomeric heterochromatin from rye chromosomes, as suggested Bennett (1977, 1979) and Gustafson et al. (1979a, b).

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