Behaviour of Wheat and Rye Genome Chromosomes in Triticale-A Review

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The chromosome behaviour of wheat and rye genomes were discussed in triticales with reference to cytological and other characters. Rye chromosomes show preferential involvement in meiotic disturbances and were attributed to differential meiotic duration, genome allo-cyly and to the amount of heterochromatin. Both wheat and rye chromosomes influence each other homologous and homoeologous pairing either through increase in the dose of genome or individual chromosomes or genes. Cytoplasmic-nuclear interactions also regulate the meiotic chromosome pairing of wheat and rye chromosomes and other characters in triticales. Chromosome substitutions and translocations involving A, B, D and R-genome chromosomes occur in most of the triticales. Variability in the expression of individual genes of wheat and rye noticed in triticales.

The degree of chromosome pairing in triticales were influenced by both wheat and rye genomes. In wheat-rye combination, rye and wheat genomes influence both homologous and homoeologous pairing, they also compete each other in nucleolus formation. Rye chromosomes preferentially involved in meiotic irregularities and its genes are either suppressed or partially expressed in triticales which may be due to pressure asserted by wheat genome or its cytoplasm. In the following review, the behaviour of wheat and rye genomes with reference to several cytological and other features in triticales are discussed.

Chromosome pairing

(i) Dosage Effect—Wheat-wheat and wheat-rye homoeologous pairing increased with increase in the dose of rye genome chromosomes in triticales-rye hybrids. A reduction in the dosage of wheat genomes in wheat-rye combinations, increases the probability of wheat-rye homoeologous pairing. An increase in the dosage of rye genome, increases the level of homoeologous pairing between wheat chromosomes. High level of homoeologous pairing noticed due to increase in the dosage of homoeologous group 3 chromosomes (3B and 3R). Hybrids with double doses of 5R causes high degree of homoeologous pairing perhaps by suppressing the effect of *ph* allele of 5B. Bernard and Bernard (1985) noticed that the highest number of rye chromosomes were involved in homoeologous pairing (1.6/pmc) in ABDR hybrids nullisomic for 5B, while the frequency of homoeologous pairing in ABDRR hybrids was similar in the presence or absence of 5B, suggesting that dosage effect of the rye genome in promoting homoeologous pairing. A correlation between chromosome instability and the wheat *ph1* gene dosage has been detected in wheat $\times$ rye and barley $\times$ wheat F_1 hybrids (Mello-Sampayo *et al.* 1988, Vieira *et al.* 1991). In hybrids derived from crosses between triticales (8x, 6x, 4x) and diploid rye (Figs. 1-2), it was noticed that an increase in the relative proportion of wheat chromosomes in the hybrids had a suppression effect on homologous as well as homoeologous pairing of rye and relative increase in rye complement promoted homoeologous pairing between wheat chromosomes. Similarly, in the hybrids ABRRR, ABRR, the wheat comple-

Figs. 1-13. 1, $7''+14'$ in $6x$ triticales $\times 2x$ rye hybrids. 2, $9''+3'$ in $4x$ triticales $\times 2x$ rye hybrids. 3-4, Meiotic metaphase of $6x$ triticales ($6x=42$). 5-6, Mitotic anaphase bridges in $6x$ triticales. 7-12, Meiotic irregularities in $6x$ triticales. 7, Univalents. 8, Dividing univalents. 9, Laggards. 10, Anaphase bridges. 11, Micronuclei. 12, Asynaptic cell with a single ring bivalent. 13, Giemsa C-banding of somatic metaphase chromosomes in $6x$ triticales showing substitutions of rye chromosomes.

ment AB, has shown to reduced the homologous pairing between rye chromosomes relative to that found in triploid (RRR) and diploid (RR), and the presence of rye chromosomes in these hybrids increase the homoeologous pairing between the chromosomes of wheat (AB) (Naranjo *et al.* 1979).

(ii) **Role of Individual Chromosomes and Genes**—Certain rye chromosomes eg. 2R and 5R has a promotional effect and chromosome 4R has a suppression effect on homoeologous pairing in triticale. It was also noticed that a single dose of the short arms of rye chromosomes 7R/4R and 5R as well as 1R have an adverse effect on chiasma formation in hybrids between the varieties of Chinese Spring and Holdfast. Miller and Riley (1972) suggested that the activity of rye chromosome arm 5RL is similar to that of 5BL of wheat in preventing homoeologous pairing. Orellana *et al.* (1984) noticed that the strongest diminution of wheat pairing (75%) was produced by 5R of rye and the weakest diminution of wheat pairing (1%) was produced by 3R. Where as the diminution of rye chromosome pairing produced by wheat chromosomes ranges from 6.9 to 48.4%.

(iii) **Interaction of Genomes**—An increase in chromosome pairing in certain wheat $\times$ rye hybrids may not only the result of specific effects of chromosomes and genes of wheat and rye, the new interaction of genetic systems of wheat and rye also influence chromosome pairing (Stefanowska 1988). Galindo and Jouve (1989) observed a strong negative intergenomic interaction between the rye and wheat genomes in triticale mainly affecting the meiotic pairing of rye chromosomes. The role of wheat chromosome 1B in the interaction with rye genome has also been emphasized since a higher degree of meiotic stability in monosomic 'Rosner' and low degree of meiotic instability in 'Rosner' trisomic for 1B.

(iv) **Cytoplasmic—Nuclear Interactions**—Hexaploid triticales containing the extracted AABB component and the cytoplasm from hexaploid wheat had an improvement in meiotic stability (Thomas and Kaltsikes 1972). Rye cytoplasm in tetraploid triticales did not increase the meiotic stability of rye chromosomes (Melz and Schlegel 1987). Triticale lines some of which contained hexaploid wheat cytoplasm and others tetraploid wheat cytoplasm had a significantly lower number of univalents per cell and improved fertility. A 2R/2D substitution in triticale gave high seed fertility in *aestivum* cytoplasm over *cereal* cytoplasm (Yasumuro *et al.* 1987).

(v) **Role of Heterochromatin**—In both hexaploid and octoploid triticales and in wheat-rye addition lines, the rye univalents were correlated with the presence of telomeric heterochromatin (Reddy 1988a). Telomeric heterochromatin of rye effects the chiasma position in rye and univalent formation in the wheat-rye amphiploid and in wheat (Gupta and Reddy 1991). A strong correlation was found between the increased heterochromatin content and pairing failure (Reddy 1990). Rye chromosomes with only one telomeric band were present as rod bivalents (Fig. 3) paired in the non-heterochromatic ends and those with telomeric bands on both the arms were found more frequently as univalents. A number of studies also attributed the variation in chromosome pairing and chiasma frequency to the distribution of heterochromatin of rye chromosomes. In both diploid and tetraploid rye, chromosome 2R, with prominent bands on both the telomeres was present as univalent in highest frequency (43.82%) in comparison to 3R (7.69%) with small bands (Lukaszewski and Gustafson 1986). Further it was shown that in advanced hexaploid triticale lines with homozygous deletions of telomeric heterochromatin on one or more of rye chromosomes 1R, 3R, 4R and 5R were associated with improved meiotic stability compared to that found in controls (Fig. 4). Huelgenhof *et al.* (1988) noticed pairing stability in homozygous deficient lines with a correlation between percentage of heterochromatin with mean univalent frequency. Effect of rye heterochromatin on pairing in wheat is also reported recently (Bernardo *et al.* 1988) and the influence being more pronounced for large arms than for the short ones.

The presence of extra homologous for 1A or 1D or 2A or 2B or 3B increased non-homo-

logous pairing and the extra homologue for 7A decreased non-homologous pairing. Darvey and Larter (1973) found that monosomic or trisomic condition of chromosome 1B leads to better or worse meiotic stability respectively. Bernard and Bernard (1985) analysed the role of D-genome participation in homoeologous pairing in different hybrid combinations involving triticales at different ploidy level and it was concluded that D-genome chromosome participation in homoeologous pairing is less than one.

Many cases of genes influencing meiosis has been reported. Lelley (1975) based on lack of correlation between chiasma frequency and univalents within the plant and a significant correlation between the plants, suggested that rye chromosome pairing in triticales is under the control of polygenes and it was also suggested that genes for asynapsis in rye genome can reduce chromosome pairing in triticales. Schlegel and Weryszko (1979) identified several alleles in rye that effect homoeologous pairing between wheat and rye chromosomes. In an analysis of different tetraploid triticales, Lukaszewski and Gustafson (1986) noticed variation in rye pairing frequencies in 4x triticales corresponded to those found in inbred ryes, indicating that the tetraploid lines differed from each other in the rye genes controlling chromosome pairing.

Nucleolar activity

In octoploid triticales, wheat chromosomes 1B and 6B and rye chromosome 1R and also 6R taking part in nucleolus formation. Whereas, in hexaploid triticales, only the wheat chromosomes 1B and 6B participate in nucleolus formation while the activity of rye NOR chromosomes was suppressed (Lukaszewski and Gustafson 1986). Similarly, the activity of 5D of wheat was also shown suppressed in 6x forms. However, in octoploid triticales, there is strong evidence to show that 5D is activated by rye genome (Rangel-Figueriedo *et al.* 1985). Changes in the dosage of chromosomes 1B and 6B had a strong influence on nucleolar frequencies in triticales (Thomas and Kaltsikes 1983). In trigenic hybrids involving triticales and tritordeum, while both wheat and barley chromosomes were involved in the nucleolus formation, rye chromosome activity was suppressed (Feranandez-Escobar and Martin 1985). Petrovic *et al.* (1988) noticed that in most of the Yugoslavian wheats having 1B/1R substitution and/or translocations the NOR of rye was completely reduced. Recently, using specific DNA probes isolated from the rye spacer region it has been shown that the rye rDNA retains some potential for NOR activity when placed in a wheat background (Appeals *et al.* 1986). However, the level of rDNA appears to depend on the presence or absence of wheat chromosome 1B and/or 6B. Capesius and Appels (1989) has shown that in tetraploid triticales, the NOR activity of rye is suppressed by NOR of wheat and the suppression is directly related to suppression of RNA transcription of rye and thus a reduction in rRNA synthesis. The results discussed above, therefore, provide evidence for the existence of an activation-inhibition system of genetic control of NOR activity, acting at the level of interaction between chromosomes and between genomes.

Aneuploidy

Cytologically observable features in triticales are the presence of mitotic and meiotic irregularities, gametes with unbalanced chromosome number and plants with aneuploid chromosome number, (Figs. 5–11). Differential duration of cell cycles of wheat and rye, disturbances at premeiotic mitosis could account for many of the disturbances. Asynapsis and/or desynapsis were also attributed for these disturbances (Fig. 12). Neocentric activity of some rye chromosomes also seems to play a role in meiotic disturbances in triticales. The effect of

'Hybrid desynapsis' for pairing instability and aneuploid formation in intervarietal hybrids of wheat, also seems to be moderately expressed in triticale.

It was earlier proposed that the wheat and rye genomes in triticale behave autonomously i. e. genome allocyly, which may well be a factor in octoploid triticale, since the univalents formed are mainly those of rye. However, genome allocyly cannot explain the presence of occasional wheat chromosomes as univalents in octoploid triticales, nor the general presence of univalent wheat chromosome in hexaploid triticales. Another theory based on the assumption that the forced homozygosity of allogamous rye chromosomes may be the genetic cause of univalent formation, since, reduced chiasma frequency is available in inbred ryes.

In hexaploid triticale, chromosome 1B tends to be involved in aneuploidy more frequently (34%) than any other chromosomes (2R-9%) the remaining chromosomes were involved only a maximum of 5%. It was observed that the presence of chromosome 1B results in better or worse meiotic stability depending on whether or not it is in the monosomic or trisomic condition, respectively (Darvey and Larter 1973). This perhaps due to natural selection pressure towards the elimination of 1B and/or 6B. Several high yielding wheats, in fact contain either 1B/1R substitution or 1B/1R translocation supports this hypothesis.

Substitutions and translocations

Most of the present-day 6x triticales resulted from the crosses either with 8x triticales or with 6x wheats, contain substitutions or translocations of D-genome chromosomes for those of R, A and B-genomes. This was possible due to frequent failure or reduced homologous chromosome pairing, as well as homoeologous pairing in the hybrids. Substitutions of D-genome chromosome for R-genome chromosomes (Fig. 13) are well established (Reddy 1988b, 1992a, Gustafson *et al.* 1989) and substitutions of D-genome chromosomes for A- or B-genome chromosomes reported recently (Lukaszewski 1988, Hohmann and Krolow 1991). The replacement of R-genome chromosomes by D-genome chromosomes are mainly controlled by the genes present on D-genome chromosomes and the ability for the D-genome chromosome to compensate for rye chromosomes. Translocations between B, D- and R-genome resulted due to pairing failure of B, D- and R-genome chromosomes in the derived F₁ hybrid of triticale and wheat, as a univalents both R and B, D chromosomes have a tendency to misdivide. The resulting telocentric chromosome often fuse, forming new arm combinations. Both misdivision and fusion frequencies appear to be chromosome specific, and to be affected both by genotype and environment. The possibility of translocations among wheat chromosomes in triticale cannot be ruled out, however, no serious attempts were made to identify them, however, Schlegel and Schlegel (1989) listed the available 270 wheat intervarietal translocations involving A, B and D-genome chromosomes.

Expressivity of genes

Triticale, since carrying genes from both the wheat and rye genomes, it possesses characters from both the parents regardless of its nature of function. Ability to grow in sandy soils, longer spikes, winter hardiness, disease resistance from rye; good nutritional quality, early maturity, insensitivity for day length from wheat are some examples in this regard, however, the genes responsible for plant height and grain yield in rye and/or wheat seems not effective in triticale. Oettler *et al.* (1991) has shown that in hexaploid triticales, all the characters which affects the fertility are mainly controlled by rye genes while wheat genes controls largely the vegetative development. The aluminium tolerance from rye is poorly expressed in triticale this is because of tolerance system from rye is modified by suppressor genes of wheat

(Gustafson *et al.* 1991). Similarly, many characters governed by single genes in rye which do not often segregate in single gene ratios in triticales (eg. hairy neck). Many of the very good genes for disease resistance present in either of the parental species are never fully expressed in triticales. In some cases, triticales susceptible to diseases for which wheat or rye parents are resistant. The amount of acid phosphatase enzymes produced by the genes in triticales, and responsible of kernel shrivelling is lower than either of the parents and the factors responsible for this phenomena is still not yet identified. Changes in rye telomeric heterochromatin content was noticed in several triticales and a number of factors suggested for this variation (Reddy 1988a, 1989, 1990) but its final effect appears to be in gene modulation (Gupta and Reddy 1991). The reasons for the erratic expression of the genes are not clear, but obviously there are many complex reactions occurring between the genes of wheat and rye.

Influence of environmental factors on the expression of wheat and rye genomes

Increase in temperature shortened the meiotic cycle in wheat and rye and leads to many meiotic irregularities (Reddy 1992b). There are also indications that the environments can influence chromosome pairing and chiasma frequency in wheat and in triticales (Naranjo *et al.* 1989). Queiroz *et al.* (1991) identified low temperature stabilization genes *Ltp1* in 5DL, *Ltp2* in 5AS, *Ltp3* in 5BS and *Ltr* (low temperature recombination gene) in 5DS. UV radiation may be one of the factors responsible for heterochromatin deletions in many CIMMYT triticales lines grown at high altitudes (Reddy 1988a). Breeder selection has been shown to either increase or decrease the heterochromatin content from rye genome in each generation for establishment of a balanced nucleotype of triticales (Jouve *et al.* 1988). The karyotype stabilization of A and B chromosomes in tetraploid triticales and their selective advantage is also seems to be determined by genotype-environment interactions.

Conclusion

The genetics and cytogenetics of triticales are very closely associated with the interactions that occur between the genomes of wheat and rye. In most cases, genes from rye, when present in triticales background, do not express themselves in a manner similar to that observed in diploid rye. This is seen in characters governed by single genes which do not often segregate in single gene ratios when in a triticales. The rye chromosomes can even alter chromosome morphology when in a triticales background. In addition, pairing frequencies and heterochromatin content of rye chromosome can also change when present in a wheat background. From the above it is clear that the genetics and cytogenetics of triticales are very complex and continue to present challenges to the researcher.

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