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Linear Differentation of Cereal Chromosomes

III. Rye, Triticale and 'Aurora' Variety

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Summary. The BSG test was used in an investigation of the linear differentiation in rye variety 'Zhitkinskaya', common wheat variety 'Aurora' and two secondary Triticale namely AD-196 and F-1239.

Chromosomes of 'Aurora' variety and wheat chromosomes within Triticale may be easily divided into "constant" and "variable" chromosomes as described previously (Iordansky et al. 1977; Zurabishvili et al. 1977).

It is necessary to emphasize that the diversity of "variable" chromosomes underlies karyotypical polymorphism within wheat and Triticale species. The polymorphism observed exists in parallel with strict homomorphism of homologous chromosomes.

In IB chromosomes of 'Aurora' variety, the short arm is substituted by the rye chromosome arm. The karyotype of Triticale AD-196 consists of six pairs of rye chromosomes and fifteen pairs of wheat chromosomes.

Key words: Linear Differentiation - BSG Test - Constant and Variable Chromosomes

Introduction

Identification and more detailed morphological investigations of wheat chromosomes by means of the BSG test opens up new prospects not only for phylogenetic studies (Zurabishvili et al. 1974; Gill and Kimber 1974; Iordansky et al. 1977; Zurabishvili et al. 1977) but also for understanding the mechanisms of appearance and stabilization of karyotypes (and genomes) in complex species and genera hybrids.

Of particular interest and practical importance in this respect is a study of secondary Triticales derived from two wheat and one rye species, as well as of those varieties in which complete or partial substitution of a wheat for a rye chromosome is expected on the basis of genetic data.

A differential staining technique has been repeatedly used for the chromosomal analysis of Triticale (Merker 1973, 1973a, 1975), Triticale wheat hybrids (Merker 1975) and also of wheats with rye-substituted chromosomes (Bennet and Smith 1975). Yet in all those studies, the authors confined themselves to identification of rye chromosomes without karyotyping wheat chromosomes, which could not be afforded because of their insufficient linear differentiation in the samples.

For this reason Bennet and Smith in the abovementioned work with 'Aurora' and 'Caucasus' varieties could only confirm expected translocation between rye and wheat but could not identify the wheat chromosome involved.

A parallel examination of rye chromosomes is necessary for a karyologic study of Triticale chromosomes. In most published works, the pattern of linear differentiation varies considerably (Shmargon 1938; Schapova 1974; Verma and Rees 1974; Gill and Kimber 1974a) due to differencies in the staining procedure or modifications of other techniques. This makes the comparison of the results especially difficult. In addition, the rye chromosomes were shown to be rather polymorphous in the heterochromatin localization (Weimarck 1975).

In view of the great practical importance of the chromosomal analysis of distant hybrids and varieties of wheat, we have used the BSG test to study linear differentiation patterns in chromosome of rye, two secondary Triticales, and the 'Aurora' variety in which the substitution of an arm in one of the chromosomes was presumed (Zeller 1973; Mettin et al. 1973).

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Materials and Methods

We used seeds of *Secale cereale* L., var. 'Zhitkinskaya' and *T.aestivum* L., var. 'Aurora' as well as seeds of Triticale AD-196 and F-1239, obtained from Prof. A.F. Shulyndin (the V.Y. Yuryev Institute of Plant Breeding and Genetics, Kharkov, USSR).

The techniques of sample preparation and of chromosomal analysis were described earlier (Iordansky et al. 1977).

Results

Secale cereale L., var. 'Zhitkinskaya' (Fig.1)

Each pair of the chromosomes can be identified on the basis of the morphology and differential staining patterns. All the rye chromosomes have large blocks of telomeric heterochromatin, which in chromosomes 3 and 4 are located on both arms. Centromeric heterochromatin, though much more weakly stained is observed in all the chromosomes. Small intercalary heterochromatin bands are seen in chromosomes 1, 2, 3, 5 and 6. No difference was found between the staining patterns of homeologous chromosomes.

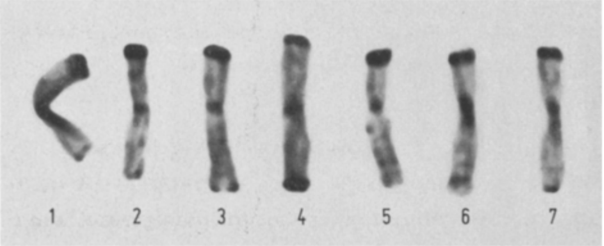

Fig.1. Differentially stained chromosomes of *Secale cereale L.* var. 'Zhitkinskaya'

Triticale F-1239 (Fig.2)

This hybrid contains 7 pairs of rye chromosomes, 6 of which (I, III, IV, V, VI and VII) are fairly similar to the corresponding chromosomes of the 'Zhitkinskaya' variety. Only metacentric chromosome II, with large and equal in size telomeric regions, cannot be identified with any rye chromosome. In Triticale AD-196 such a chromosome also has not been found.

The wheat chromosomes of the hybrid are much more difficult to analyze. The comparison of these chromosomes with chromosomes of all the species and varieties we have studied (see Zurabishvili et al. 1967; Table 1) makes it possible to single out a group of familar "constant" chromosomes (1, 2, 3, 5, 9, 10, 11 and 12) and a "variable" group (4, 6, 7, 8, 13 and 14).

Knowing that the hybrid originated from the common and the durum wheats, we have carried out a more detailed comparison of the chromosomes of these species with those of Triticale F-1239. Unfortunately, we had not at our disposal the seeds of original common or durum wheat variety, and this complicated the analysis considerably.

Among the "constant" Triticale chromosomes a similarity has been found between chromosomes 2, 5, 6 and 8 and *T.durum* chromosomes 2, 5, 4 and 7,

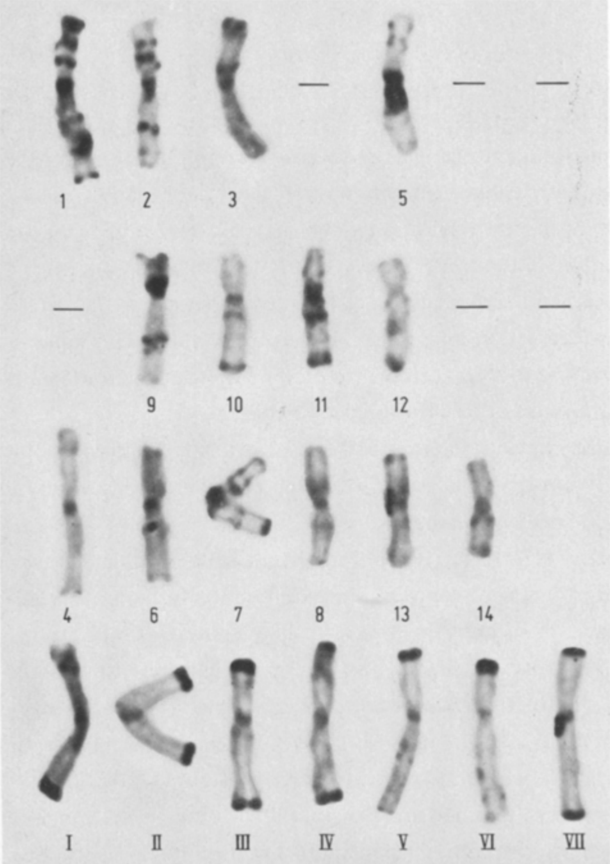

Fig.2. Differentially stained chromosomes of *Triticale* F-1239

respectively, while chromosome 9 is more similar to chromosome 9 of *T. aestivum*.

Since homologous chromosomes 1, 10, 11, 12 and 14 in the original species are hard to distinguish, we failed to establish their exact origin in the hybrid.

The short arm in chromosome 3 can be attributed to either *T. aestivum* or *T. durum*, while the origin of the long arm remains unclear. However, without the complete knowledge of the structural variability (polymorphism) of the common and durum wheat chromosomes we cannot state unequivocally the existence of translocations in these chromosomes.

"Variable" chromosomes 6, 8 and 14 are found in *T. durum;* chromosome 14 occurs also in the 'Chinese Spring' variety. Wheat chromosomes 4 and 7 are unique for the F-1239 and their origin is unknown.

The important feature of the hybrid complement is that it is balanced; i.e., the homologous chromosomes are morphologically similar.

Triticale AD-196

The well defined differentiation of the chromosomes of this hybrid facilitates identification of each pair of the chomosomes (Fig.3). The rye genome, unlike that of Triticale D-1239, is represented by 6 chromosome pairs that attract special attention in the chromosome complement of AD-196. It should be noted that the difference between the wheat chromosomes of the two hybrids has also been found: "constant" chromosomes 1 and 3 are absent in AD-196 which instead has two more "variable" chromosomes. Only four pairs of chromosomes of rye were found to be similar in AD-196 and F-1239 (4, 5, 6 and, to a lesser extent, 1) when the differential staining patterns were compared. When the karyotype of AD-196 was compared to those of the common and the durum wheat, it was found that chromosomes 3, 5, 8, 9 and 10 are similar to the durum wheat chromosomes; chromosome 1 is similar to chromosome 4 of the common wheat var. 'Aurora'; chromosomes 13 and 14 are found in Triticale F-1239. Chromosomes 4, 6, 7 and 15 are unique and their origin remains unknown.

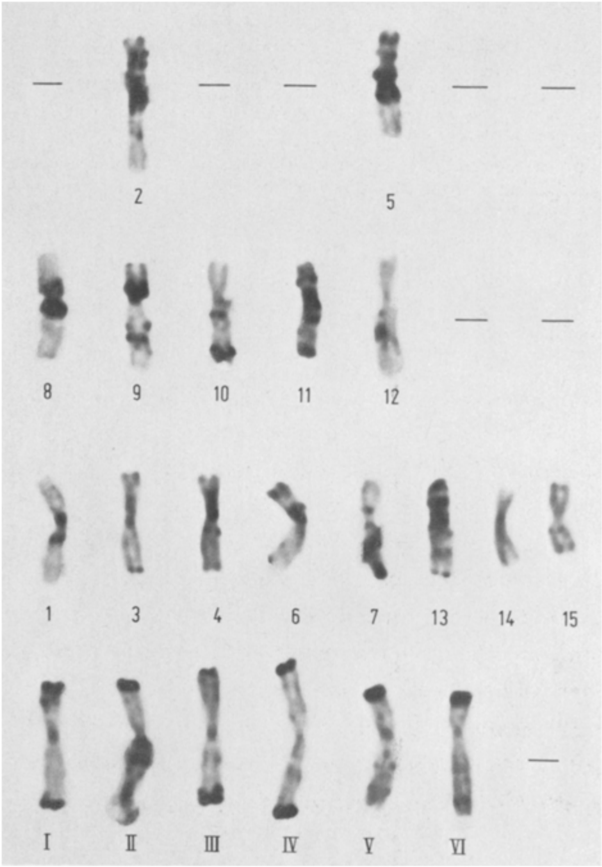

Fig.3. Differentially stained chromosomes of *Triticale* AD-196

T. aestivum L. var. 'Aurora' (Figs.4 and 6)

On the basis of the total content and distribution of heterochromatin, these chromosomes are similar to the 'Diamant' variety chromosomes. As in the latter, the 'Aurora' chromosomes can be divided into two groups according to the amount of heterochromatin, (1, 2, 3, 5, 8, 9, 11 and 4, 6, 7, 10, 12-21) but individual chromosomes in the two varieties differ considerably. Above all one should notice the absence of similarity between chromosomes 5, 6, 7, 14-16, 18-20 of the 'Aurora' variety to the corresponding chromosomes of the 'Diamant'. Chromosome 1 of the 'Aurora' attracts special attention among the unique chromosomes: its short arm with large telomeric heterochromatin is similar to the short arm of chromosomes III and VII of rye (Fig.1), while the long arm is similar to the long arm of 'Diamant' chromosome 1.

Interphase Nuclei

The structure of differentially stained interphase nuclei of rye, Triticale and var. 'Aurora', as in other

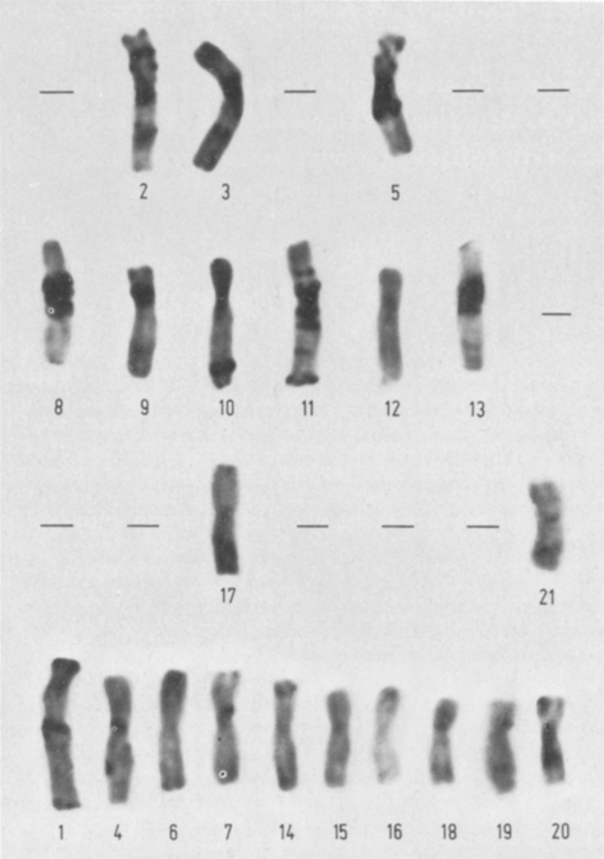

Fig.4. Differentially stained chromosomes of *T. aestivum* var. 'Aurora'

species studied, is in a good agreement with the particularities of their chromosome structure (Fig.5).

There are few large chromocentres in rye nuclei differing strikingly from the numerous small chromocentres of the common wheat. Therefore, parent chromocentres are easily distinguishable in Triticale. The 'Aurora' nuclei are particularly illustrative in this respect: two large rye chromocentres are clearly seen on the background of small wheat chromocentres.

As can be judged without resorting to the use of quantitative analysis, the relative location of rye chromocentres is random--no nearing tendency was observed.

Discussion

A considerable amount of work has been devoted to the investigation of conventionally stained rye chromo-

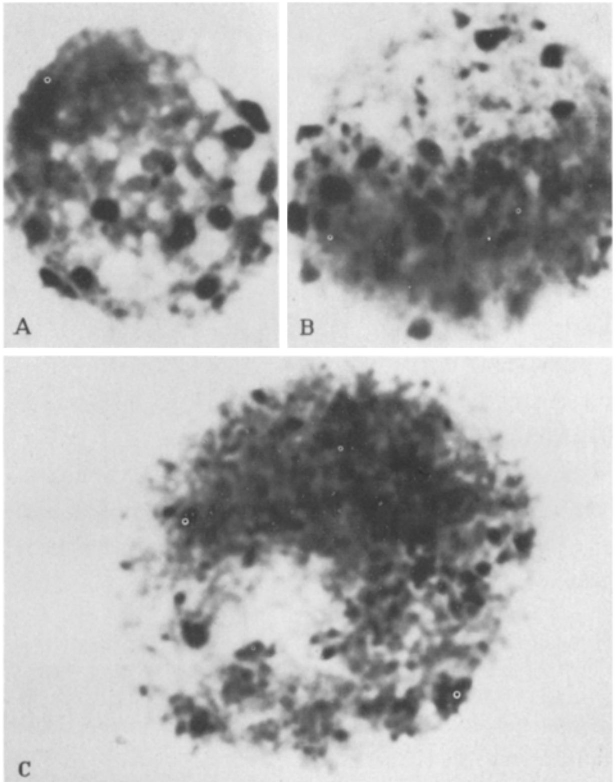

Fig.5. Differentially stained interphase nuclei A - *Secale cereale* B - Triticale AD-196
C - *T. aestivum*, var. 'Aurora'
Rye chromocentres are shown by arrows

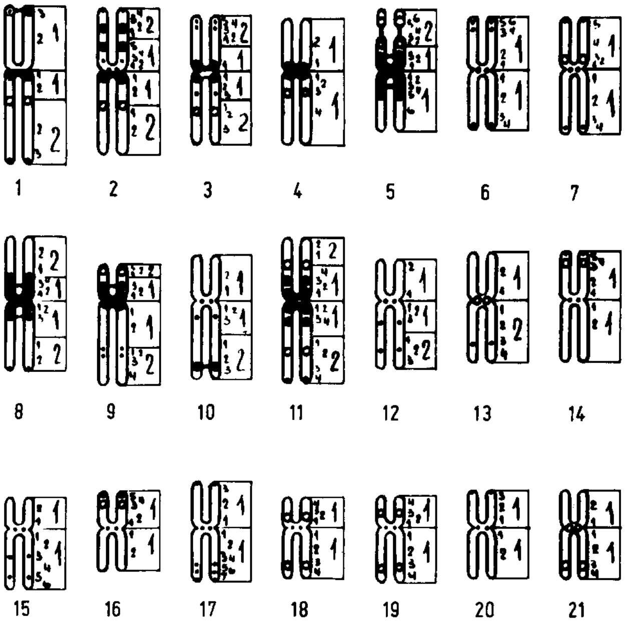

Fig.6. Idiogram of differentially stained chromosomes of *T. aestivum* var. 'Aurora'

somes (see a review by Tudose 1970). Nowhere, however, has the polykaryogram technique been used (Lejeune 1965; Zurabishvili et al. 1974), and this makes it impossible to evaluate the validity of identification of individual chromosomes. In addition, due to either true polymorphism, or variations in the techniques used, the homology between differentially stained chromosomes found in the publications of different authors is rather difficult to establish (Shmargon 1938; Sarma and Natarajan 1973; Schapova 1974; Verma and Rees 1974; Gill and Kimber 1974a; Weimark 1975). We, therefore, gave up comparing the data from published sources and confined ourselves to the comparison of the 'Zhitkinskaya' variety chromosomes with those of the 'Imperial' variety (Gill and Kimber 1974a). This permitted us to establish, with sufficient reliability, the homology between 7 pairs of chromosomes of these varieties.

Little or no difference was found between homologous rye chromosomes in the 'Zhitkinskaya' variety and in the karyotypes of Triticale studied. Chromosome III in AD-196 and chromosome II in F-1239 were so morphologically original that it was impossible to consider them as structural derivatives of a chromosome similar to those found by Weimarck (Weimarck 1975). Hence, based on the material studied, neither polymorphism of rye chromosomes nor the subdivision of them into "constant" and "variable" ones, as observed in wheat, can be stated with confidence (Zurabishvili et al. 1976). Preferential cross-pollination of rye seems to be an important factor affecting the structure and the evolution of its karyotype.

The observed predominance of the localization of large bands in the telomeric regions, densely stained by the BSG technique, is in good agreement with available data on the localization of rye constitutive heterochromatin which was obtained by different methods, (Lima-de-Faria 1959; Darlington and Haque 1966; Natarajan and Ahnstrom 1970) as well as on the localization of large chromomers in pachytene chromosomes (Lima-de-Faria and Jaworska 1972). The total length of the densely stained bands constitutes about 10 per cent of the whole karyotype length and this agrees fairly well with the 10 to 12 per cent of the quickly reassociating DNA (Cot = 0.01) in the rye genome (Ranjeakar et al. 1974).

These data confirm the ability of the BSG method to reveal the constitutive heterochromatin regions in the chromosomes. This is also supported by the Wagenaar's observation on the telomeric association of chromosomes in the somatic cells of rye (Wagenaar 1966; Godin and Stack 1975).

It is much more difficult to identify chromosomes in hybrids than in their parent species. Therefore, taking into account the impossibility of differentiating among Feulgen stained chromosomes of common wheat (Zurabishvili et al. 1974), and the absence of polykaryogram analysis data on wheat and rye, the identification of Triticale chromosomes (Shigenaga and Larter 1971; Shigenaga et al. 1971; Merker 1973) and of substitution lines (Lelley 1973) seems rather unconvincing. Merker (1973a) and Weimarck (1974) obtained differentially stained preparations of Triticale chromosomes but limited themselves to the general description and identification of wheat from rye chromosomes without analyzing their karyotype structure.

According to our observations, the karyotype structure of Triticale is rather complex. Each set of chromosomes is represented by a unique mosaic of common wheat, durum wheat and rye chromosomes. The origin of some chromosomes is unknown while inter-species translocations that took place in the centromeric site may be supposed in others. However, despite the general intricacies of AD-196 and F-1239 genomes, their strictly balanced character cannot be overlooked. It manifests itself with a large similarity in the morphology and heterochromatin distribution pattern of homeologous chromosomes.

Detailed pedigrees of these hybrids were not published. It is known, however, that the hybrids belong to the so-called "trispecies" Triticale (Shulyndin 1970, 1972; Sisodia and McGinnis 1970; Fyodorova 1973) and were obtained from common wheat, durum wheat and rye.

Irrespective of a crossing sequence leading to the appearance of a secondary or a "trispecies" Triticale, the synthesis of such hybrids should include zygote formation containing 35 chromosomes of wheat, of which 21 (A, B, D) originate from common wheat and 14 (A, B) originate from durum wheat. Taking into account genetic differences between the A and B genomes of tetra and hexaploid wheat (Kostov 1940; Pisarev and Shilko 1970; Makhalin 1974) and our own observations on structurally unidentified homologs of *T.aestivum* and *T.durum* (Zurabishvili et al. 1977), one can readily imagine how complex and heteromorphous the F_1 karyotype may be. And this concerns wheat chromosomes only, totally disregarding chromosome set of rye.

If Mendelian segregation is assumed, then only - $1/2^{14}$ or a very small proportion of F_2 plants should be completely homozygous; i.e., contain only homologous (homomorphous) pairs of chromosomes which originate from A and B genomes of common or durum wheat. As early as 1938, Sapegin (1938), analyzing a F_2 segregation from the crossing of durum and common wheat, found that the number of homozygotes (about 1 %) was much higher than theoretically expected. He supposed that in F_1 meiosis, chromosomes segregate not quite randomly; i.e., some of them are temporally linked to each other. This disturbs the Mendelian segregation in interspecific wheat hybrids and results in the appearance of unexpected and irregular segregations which were called "mad" segregations by N.N. Vavilov (Vavilov and Yakushkina 1925).

Now that one knows the associative properties of heterochromatin and various types of associations and linkages of chromosomes related to it (Prokofieva-Belgovskaya 1966; Wagenaar 1969; Du Praw 1970; Ahokas 1971; Yunis and Yasminech 1972; Badaev et al. 1973; Godin and Stack 1975), it is easy to imagine an actual mechanisms of such temporal or permanent associations due to highly repetitive DNA sequences in the heterochromatic regions (Mayfield and Ellison 1975). The formation of temperal interchromosomal links seems to increase within the the parent sets of unbalanced heteromorphous karyotypes of F_1 hybrid wheat, and this results in both apparent decrease in the number of "linkage groups" and disturbances in Mendelian segregation.

The repeated self-pollination and fertility selection following the hybridization should contribute to both increasing the probability of appearance of plants with balanced karyotypes and the homomorphism by all the chromosome pairs and preserving (revealing) of such rare and valuable plants. The appearance of this balanced character of karyotype in the fertility selection of self-pollinating plants suggests that the similarity of structure and distribution of heterochromatin in homologous chromosomes is an essential condition for their normal conjugation.

Bearing in mind the formation mechanisms of secondary Triticale karyotype and a considerable number of "variable" chromosomes in *Triticum*, it is easy to explain the observed difference between AD-196 and F-1239 karyotypes. It appeared as a result of possible karyotypic differences in wheat and rye used in breeding these hybrids, and also as a result of an accidental combination of common and durum wheat chromosomes in the formation of F_1 gametes. Subsequent self-pollinations and fertility selection led to stabilization of the karyotypes by preferential conservation of plants with certain sets of homomorphous chromosome pairs.

The most apparent feature of the common wheat var. 'Aurora' karyotype, which was genetically predicted (Zeller 1973; Mettin et al. 1973), is the substitution of the short arm of variable chromosome 1 (IB) for the yet unidentified arm of a rye chromosome. All the rest of the known "constant" chromosomes are present in the karyotype except for the chromosome which is similar to chromosome 14 of the 'Chinese Spring' variety (see Zurabishvili et al. 1977; Table 1). At the same time the 'Aurora' karyotype manifests a considerable originality with respect to the "variable" chromosome content. Only two of them (17 and 21) are morphologically similar to the corresponding chromosomes of the 'Diamant' variety while the remaining nine (6, 7, 13-16, 18-20) have, to our knowledge, no relationship to any of the chromosomes of the common or other wheat species.

Exactly as in the case of the comparison of the 'Diamant' and the 'Chinese Spring' karyotypes (Iordansky et al. 1977), the differential staining of 'Aurora' chromosomes reveals a karyotype originality which can be attributed in the first place, to the uniqueness of "variable" chromosomes. These unique intravarietal "variable" chromosomes can, therefore, be used as markers in hybridization and genetic analysis of both ordinary varieties and Triticale and other hybrids. "Constant" chromosomes, though manifesting a certain degree of polymorphism, are less suitable for this purpose. Only the 'Chinese Spring' "constant" chromosomes might be an exception since they are highly enriched with constitutive heterochromatin.

By investigating numerous varieties used in 'Aurora' breeding (Lukyanenko 1970) it would be possible to assess the contribution made by each of them to the 'Aurora' karyotype and to clarify the origin of the rye chromosome fragment.

The comparison of the karyotypes of known forms of polyploid wheat (Zurabishvili et al. 1977, Table 1), shows clearly that each of them contains two groups of chromosomes: the "constant" and the "variable" group. The uniqueness of each karyotype is determined primarily by the "variable" chromosomes, the morphological diversity of which is rather high and, to our point of view, due to intensive introgression. Such diversity is particularly high in common wheat. Its varieties differ considerably from each other by the karyotype structure making it impossible to establish a specific *T.aestivum* karyotype and poses the task of the analysis of the existing diversity of chromosome types in this cultured "superspecies".

It should be noted that intervarietal karyotypic differences within *T.aestivum* species may be far greater than interspecific ones. The latter were not found at all in comparing *T.durum* with *T.corthlicum*. This observation seems to indicate the relative character of the existing classification within the genus *Triticum*. "Constant" chromosomes, though manifesting a certain level of interspecific and intervarietal polymorphism, constitute a basis of each karyotype and can be used in future reconstruction of an initial prekaryotype of polyploid wheat.

The employment of the BSG test has considerably widened potential of chromosomal analysis. In the near future, investigation of linear differentiation of chromosomes will most likely become one of the principal techniques used in solving the problems of philogeny, genetics and selection of wheat and other cultured cereals.

Conclusions

1. The patterns of linear differentiation of chromosomes of rye var. 'Zhitkinskaya', common wheat var. 'Aurora' and Triticale AD-196 and F-1239 were studied using the BSG test.

2. In the karyotypic structure of common wheat var. 'Aurora' as well as of Triticale AD-196 and F-1239 one can identify the same division of chromosomes into "constant" and "variable" as in other wheat species.

3. Common wheat varieties have a considerable karyotypic polymorphism mainly due to the "variable" chromosomes, and this shows that no specific karyotype exists in *Triticum aestivum L.*

4. The short arm of IB chromosome of the 'Aurora' variety is substituted for unidentified rye short arm.

5. The karyotype of secondary Triticale is represented by a complex and unique mosaic made up of homomorphic pairs of parent species chromosomes, the AD-196 hybrid, containing only six pairs of rye chromosomes.

6. The "variable" chromosomes, which are different in different hybrids and varieties, can be used as markers in crossings or genetic analysis.

7. The mechanisms leading to the appearance of balanced karyotypes of Triticale and common wheat varieties and to the morphological diversity of these karyotypes are discussed.

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