GENETIC INTERACTION IN RYE EXPRESSED AT THE CHROMOSOME PHENOTYPE

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FOR our understanding of the organization of the chromosome, it is essential to detect genetic interactions which are expressed at the level of the chromosome phenotype. Gene interactions studied by methods of progeny analysis give information concerning effects on the phenotype of the organism and little or no information about the genetic interplay within the chromosome body.

This paper contains a description of an effect on the chromosome phenotype dependent on interaction between two separate loci.

Plan of the experiments

In most tissues of rye the B chromosome of the standard type, divides in the normal way into two chromatids which disjoin and move to opposite spindle poles. In the microenvironment of the pollen grain this B chromosome type reacts differently. At the first pollen division the two chromatids do not finish their separation process at two localized segments, one situated on each arm, and the two chromatids move together to one spindle pole (MÜNTZING 1946). These segments responsible for nondisjunction are located one at the end of the short arm, the other at equal distance from the kinetochore in the long arm (Figure 13 and Table 1).

Two new chromosome types derived from the standard B chromosome, are the small isochromosome, which a pachytene analysis revealed to be a mirror image of the short arm of the standard type, and the large isochromosome which is a mirror image of the long arm of the standard chromosome (Figure 13 and Table 1) (MÜNTZING and LIMA-DE-FARIA 1949, 1953; LIMA-DE-FARIA 1952).

TABLE 1

B chromosome types of rye; their structure at pachytene and behavior at the first pollen mitosis (compare with Figure 13)

Chromosome type	Structure at pachytene	Regions with delayed reproduction	Nondisjunction at first pollen mitosis
Standard chromosome	Short and long arm	+	+
Large isochromosome	Mirror image long arm	+	+
Small isochromosome	Mirror image short arm	+	—
Deficiency chromosome	Short and long arm without knob region	+	—

Although the small isochromosome possesses two regions that usually react to the microenvironment of the pollen grain by delayed reproduction, when these are alone, without the long arm, they do not function, with the result that the small isochromosome does not show nondisjunction in the pollen grain (Figure 13).

On the contrary, the large isochromosome which has two regions like the small isochromosome, but which are situated in the long arm, exhibits delayed reproduction at these segments with resulting nondisjunction (Figure 13; MÜNTZING 1946).

A third derivative of the standard chromosome was found by MÜNTZING (1948) which in root tips turned out to be composed of the short arm and a small part of the long arm. This chromosome type did not show nondisjunction. It was thought at that time that the region where nondisjunction is manifested would be absent in the long arm. A pachytene analysis revealed, however, that the segment where delayed reproduction is manifested was present both in the short and long arm but that instead the distal knob region of the long arm was absent (Figure 13 and Table 1; MÜNTZING and LIMA-DE-FARIA 1952). It was concluded that the presence of the knob region is instrumental in the manifestation of delayed reproduction at the two segments present in both the long and short arm. In this case, the genetic interaction takes place within the chromosome.

To check this phenomenon further, an experiment was devised in which the knob region was placed in one chromosome to see whether it would interact with the segments of delayed reproduction present in another chromosome.

MATERIALS AND METHODS

Crosses were performed between the following plants (the chromosomes of the normal complement are also called A chromosomes).

Four female parent plants with the following chromosome constitution were used. Nos. 1 and 2: 14 A chromosomes plus two standard chromosomes of the Turkish variety. Nos. 3 and 4: 14 A chromosomes plus two standard chromosomes of the Wasa variety.

The male parent in these crosses was a single plant with 14 A chromosomes plus four standard chromosomes of the Turkish variety and one deficiency chromosome (Table 2).

RESULTS

When the standard and deficiency chromosomes are present in the same pollen grain, the standard chromosome should undergo nondisjunction and the deficiency chromosome should not exhibit this phenomenon if there were no interaction between the knob region of the standard chromosome and the segments of delayed reproduction of the deficiency chromosome.

In the plant used as a male parent, in the absence of gross meiotic irregularities there is a high probability that every pollen grain gets one or several of the four standard chromosomes present in each pollen mother cell. Thus, the de-

TABLE 2

Chromosome constitution of parents and of main part of progeny in the cross studied. For sake of simplicity only the main types of products of meiosis are represented

	Female parent			Male parent					
Somatic constitution		14A 2ST					14A 4ST 2DF		
Main types of products of meiosis	7A	7A 1ST	7A 2ST	7A 1ST	7A 2ST	7A 3ST	7A 1ST 1DF	7A 2ST 1DF	7A 3ST 1DF
Nondisjunction	7A	7A 2ST	7A 4ST	7A 2ST	7A 4ST	7A 6ST	7A 2ST 2DF	7A 4ST 2DF	7A 6ST 2DF
Zygote × 7A	14A 2ST	14A 4ST	14A 6ST	14A 2ST 2DF			14A 4ST 2DF		14A 6ST 2DF
× 7A 2ST	14A 4ST	14A 6ST	14A 8ST	14A 4ST 2DF			14A 6ST 2DF		14A 8ST 2DF
× 7A 4ST	14A 6ST	14A 8ST	14A 10ST	14A 6ST 2DF			14A 8ST 2DF		14A 10ST 2DF

ficiency chromosome has a high probability of being accompanied by one or several standard chromosomes in the pollen grain (Table 2).

When pollen of this plant is used to pollinate the four plants used as female parents, the behavior of the deficiency chromosome at the first pollen mitosis can be disclosed by the analysis of the progeny. The results of the cross are summarized in Table 3. As seen from the first vertical column, the number of stand-

TABLE 3

Distribution of the standard and deficiency chromosomes in the progeny of the cross 14 A chromosomes + two standard chromosomes × 14 A chromosomes + four standard chromosomes + one deficiency chromosome

Number of standard chromosomes per plant	Number of plants with standard chromosome	Number of plants with deficiency chromosome	Number of plants with one deficiency chromosome	Number of plants with two deficiency chromosomes	Number of plants with three deficiency chromosomes
0	2	0	0	0	0
1	3	1	1	0	0
2	36	7	0	6	1
3	11	6	4	0	2
4	93	27	0	25	2
5	13	4	2	1	1
6	35	4	1	3	0
7	2	0	0	0	0
8	1	0	0	0	0
Total	196	49	8	35	6

ard chromosomes varied from zero to eight per plant. Of the 196 plants: 36 have two standard chromosomes, 93 have four, and 35 have six standard chromosomes. On the other hand, plants with one, three and five standard chromosomes are only three, 11, and 13, respectively. This means that, in most cases, the standard chromosome exhibited nondisjunction, but that this phenomenon does not occur always as revealed by the presence of plants with one, three, and five standard chromosomes.

Since the deficiency chromosome lacks the nondisjunction mechanism, it is seldom recovered in the progeny. Not to lose it from the progeny, many crosses must usually be made. In this cross, however, 49 deficiency chromosomes are found among 196 plants (25 percent). This result gives clear indication that there has been a mechanism increasing the number of deficiency chromosomes, due to the presence of the standard chromosome in the pollen grain. This phenomenon becomes, however, clearer, when one analyzes the distribution of the deficiency chromosome in the progeny. Of the 49 deficiency chromosomes, 27 occur in plants with four standard chromosomes. This means that the male nucleus contained two standard chromosomes and fertilized a female nucleus with also two standard chromosomes.

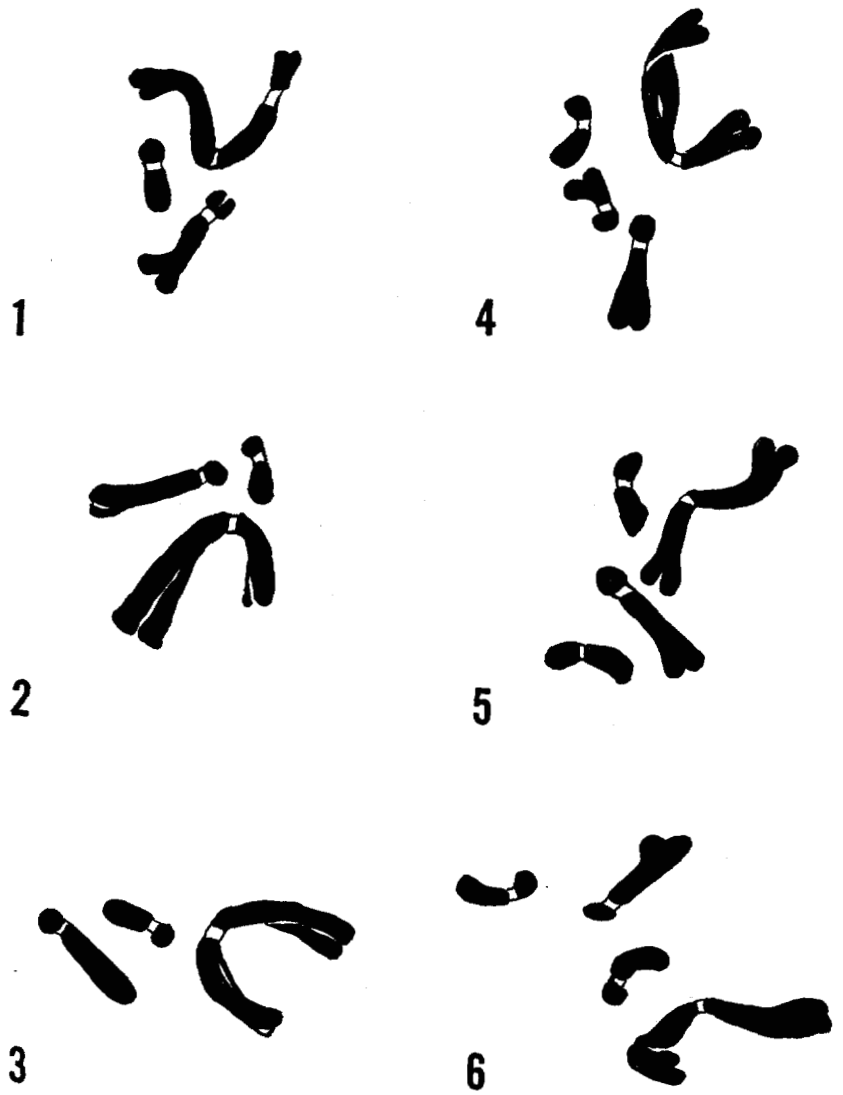
That nondisjunction has occurred in the deficiency chromosome is shown by the last three vertical columns of Table 3. Plants where this chromosome occurs alone i.e., where it had normal disjunction, are only eight among 49 (16.3 percent), but plants which carry two chromosomes are 35 (71.4 percent). The comparison of Tables 2 and 3 also shows that pollen grains with too many B chromosomes (6–10) are less effective in fertilization than pollen grains with few B's.

There are, besides, six plants that carry three deficiency fragments (12.3 percent). This may be attributed to exceptional cases of two nondisjunctions: one in the first pollen mitosis followed by another in the second pollen mitosis, in one of the two chromosomes present in the microspore.

To control that the deficiency chromosome did not alter its structure during the two generations, a study was made of metaphase root tip chromosomes and of pachytene in the parent plants and in the progeny. As seen in Figures 1–12, the deficiency fragment has the same structural pattern in both cases.

DISCUSSION

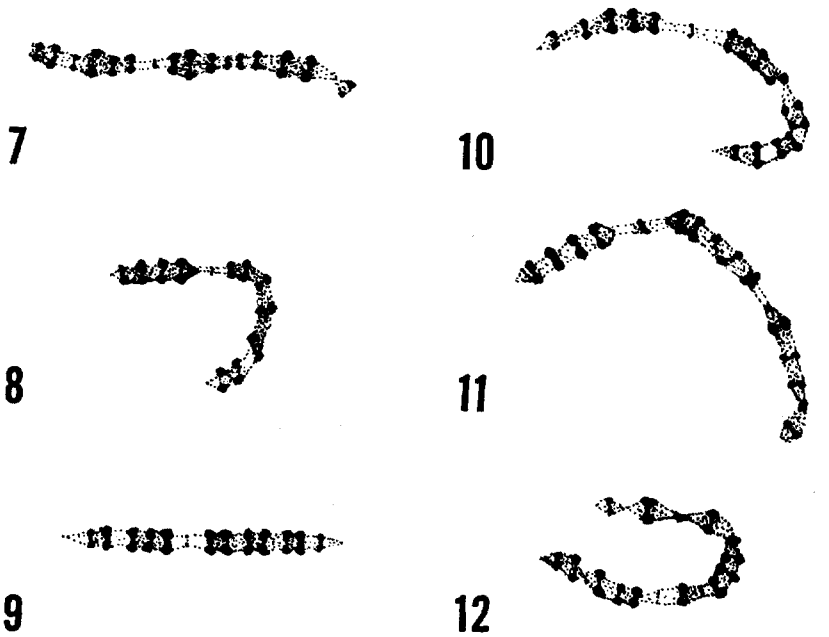
The fact that the deficiency chromosome exhibits nondisjunction when a standard chromosome is present in the same pollen grain is evidence of a genetic interaction among the knob region of the standard chromosome and the segments of delayed reproduction in the deficiency chromosome. The only chromosome segment missing in the deficiency chromosome which is present in the standard chromosome is the knob region (Figure 13). A mechanical association between the two chromosomes cannot be invoked in this case, as it is sometimes done when genetic interactions take place at pachytene where pairing occurs. In case the deficiency chromosome would have paired at pachytene with the standard chromosome, this pairing would have been disrupted by the passage through the two meiotic divisions. At anaphase, of the first pollen mitosis, there is no particular



FIGURES 1–6.—Root tip chromosomes. Figures 1–3. One standard and one deficiency chromosome at the side of an A chromosome in three metaphase plates of the male parent of the cross shown in Table 2. Figures 4–6. One standard and two deficiency chromosomes together with an A chromosome (submedian kinetochore) in three metaphase plates from plants of the progeny of the cross shown in Table 2. 5000×.

spatial, or mechanical relation between the two chromosome types. Thus, the interaction is purely genetic, and manifested at the level of the chromosome phenotype.

ROMAN (1947) has demonstrated in maize by means of translocations between A and B chromosomes that the kinetochore region of the B chromosome is necessary for the manifestation of nondisjunction. Rearranged chromosomes must



FIGURES 7–12.—Pachytene chromosomes. The deficiency chromosome at pachytene in the male parent of the cross represented in Table 2 (Figures 7–9) and in the plants of the progeny of the same cross (Figures 10–12). In Figures 7–9 are represented single chromosomes which have divided precociously showing each their two chromatids, in Figures 10–12 are drawn three bivalents composed each of their two paired chromosomes. 3000×.

carry this region to manifest nondisjunction. In ROMAN's study, there has been, however, no cytological analysis of the chromosomes at the pollen mitosis, and the regions where nondisjunction is manifested in the B chromosome are unknown. BOSEMARK (1956) found in Festuca that the simultaneous presence in the pollen grain of B chromosomes with and without nondisjunction capacity led to the manifestation of this phenomenon in the latter type.

Other examples of interactions among segments expressed at the chromosome phenotype are found in the literature. Among them are the Dissociation-Activator system of MCCLINTOCK (1951) where one segment present in one chromosome determines the phenotypic expression of a segment in another chromosome. Another example is the interaction system in maize between the distal region of the long arm of abnormal 10 and the telomeres of the chromosomes of the normal complement. These exhibit active mobility on the spindle when abnormal 10 is present in the nucleus (RHOADES 1952).

These cases and others, which I reviewed in 1956 and 1962, add evidences that the chromosome phenotype is determined by a well-defined system of gene interactions which follow a definite pattern along the chromosome.

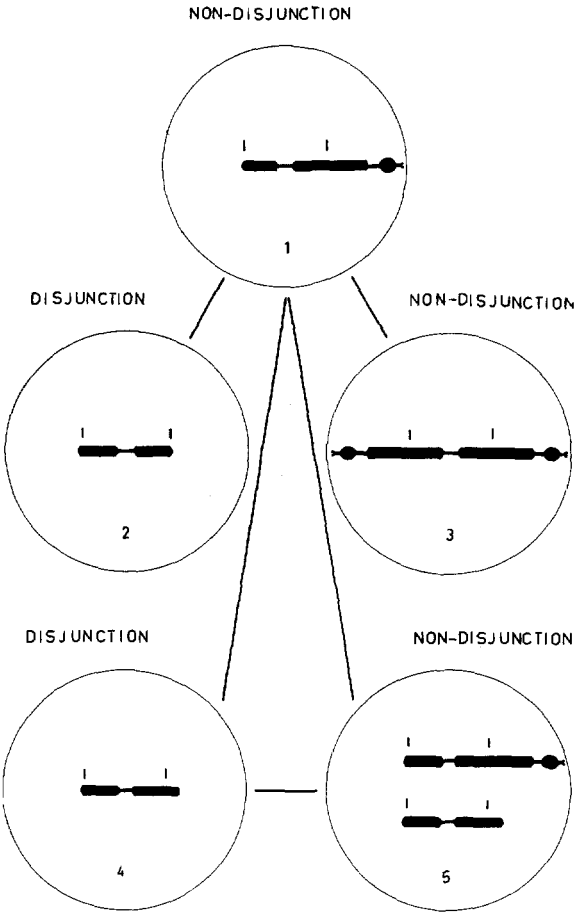


FIGURE 13.—The occurrence of nondisjunction in the standard chromosome and its derivatives at the first pollen mitosis. The chromosomal structure shown is that of the chromosome types at pachytene (schematically drawn). 1, standard chromosome, 2, small isochromosome, 3, large isochromosome, 4, deficiency chromosome, 5, standard chromosome and deficiency chromosome present in the same pollen grain. The regions marked with vertical dashes are the segments which exhibit delayed reproduction.

SUMMARY

At the first pollen mitosis the standard B chromosome of rye manifests delayed reproduction at two well-defined segments, one in the short and the other in the long arm. This results in nondisjunction. Another B chromosome called deficiency chromosome derived from the standard type does not manifest nondisjunction in the first pollen mitosis, although it has the two segments which in the original B chromosome type perform this function.

When the deficiency chromosome is placed together with the standard chro-

mosome in the same pollen grain, nondisjunction is manifested by the deficiency chromosome. In the progeny of crosses between plants with these two chromosome types, among a total of 196 plants, 49 carry the deficiency chromosome and of these, 35 contain two deficiency chromosomes.

The region present in the standard chromosome which is absent in the deficiency chromosome is the knob region. Any type of pairing that may have occurred at pachytene between the two chromosome types is disrupted by the two meiotic divisions. It is concluded that the knob region of the standard type is instrumental in the manifestation of delayed reproduction at the two segments of the deficiency chromosome.

This type of genetic interaction is expressed at the level of the chromosome phenotype.

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