

and Festuca, since genes required for nondisjunction have been found in these plants. However, it remains to be determined whether somatic losses observed in the present experiments resulted from nondisjunction. This requires cytological examination of fractional seedlings, which is currently underway. For preliminary results, see the following article.

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3. Isochromosome formation and the process of nondisjunction.

In the preceding article, sectorial loss of the  $B^9$  chromosome in endosperm and sporophyte tissue is reported and attributed to somatic nondisjunction. Cytological examination of root tips of the fractional seedlings has been made for three plants. Surprisingly, the losses of the  $B^9$  in these plants may be attributed to isochromosome formation, rather than nondisjunction. In one plant, two root tips gave chromosome counts of 20 and 21. The root tip with 21 chromosomes contained no telocentrics (as seen in metaphase) but did contain one chromosome with a large heterochromatic knob at each end (observable in prophase). In addition, two smaller knobs were seen halfway between the center of the chromosome and the distal knobs. The normal  $B^9$  chromosome carries a large terminal knob ( $K9^L$ ) and a second smaller knob (derived from the heterochromatic region of the B) in a median position. The extra chromosome found, therefore, was probably a  $B^9$  isochromosome. In a second plant, only one root tip has been examined, but again metaphase and prophase cells indicate the presence of a  $B^9$  isochromosome. A third plant was examined which showed multiple sectoring for loss of Yg, rather than single sector formation. Of four root tips that were examined, two contained 21 chromosomes, with one telocentric. One  $B^9$  was apparently present in these roots. The other two root tips carried 22 chromosomes, only one of which was telocentric. Prophase cells showed one chromosome with the isochromosome knob pattern and another with one-half this pattern. One  $B^9$  and one isochromosome  $B^9$  were likely present. Somatic nondisjunction of the  $B^9$ , followed by isochromosome formation could account for the findings in this plant.

In the previous article, evidence suggested that somatic sectoring is controlled by the same gene(s) that induces nondisjunction at the

second pollen mitosis. The finding of isochromosomes in the fractional seedlings suggests that isochromosome formation may be a normal step in nondisjunction. The B chromosome may carry a gene(s) responsible for splitting the centromere of the B isochromosome following the second pollen mitosis. This gene(s) may be primarily active during or immediately after the second pollen mitosis and relatively inactive at other cell divisions. In this respect it would follow the activity cycle of the gene(s) responsible for initiating nondisjunction (see previous article). Evidence from maize and other organisms allows the following explanation for nondisjunction of the maize B chromosome:

1. A gene(s) located distally in the B chromosome becomes active during the second pollen mitosis and induces a "stickiness" in the heterochromatic knob adjacent to the B centromere.
2. The inability of the chromosome to disjoin results in mis-division of the centromere and isochromosome formation. (Whether this step is essential to nondisjunction or simply a by-product of nondisjunction is not known).
3. The chromosome migrates to one pole.
4. During anaphase or later another gene(s) on the B chromosome becomes active and causes a splitting of the centromere of the isochromosome.
5. The heterochromatic knob adjacent to the B centromere also splits following nondisjunction. This step may or may not be controlled by genes on the B chromosome.

The sequence given above accounts for isochromosome formation. Residual activity of the gene(s) that induces heterochromatin stickiness may cause formation of isochromosomes in early somatic divisions of the embryo (see previous article). Activity of the gene(s) controlling centromere splitting may often be inadequate in somatic divisions to complete nondisjunction. The hypothesis also accounts for results of Rhoades, Dempsey, and Ghidoni (1967). They reported an abortive type of nondisjunction of A chromosomes that is induced by large numbers of B's. Rhoades et al. found that chromosomes carrying heterochromatic knobs are subject to loss of the knobbed arm at the second pollen mitosis. The best explanation of the data was that the knobs on the A chromosomes become sticky at the second pollen mitosis and this prevents disjunction. After anaphase bridge formation, one of the centromeres separates from its knobbed chromatid arm, and a telocentric and acentric are formed.

The acentric is lost. The findings are unusual in that (1) the primary site of nondisjunction is the heterochromatic knob and not the centromere in the A chromosomes, and (2) the anaphase bridge does not break in a conventional manner but splits adjacent to one of the two centromeres. The results can be explained, however, if the gene(s) that induces nondisjunction is specific for heterochromatin (the knob adjacent to the B centromere) and if another gene(s) produces an enzyme that attacks centromeres (splitting the B isochromosome; producing an A telocentric). The proposal is also consistent with the findings of Crouse (1960) on X chromosome nondisjunction in Sciara. She used translocations to demonstrate that a heterochromatic region close to the centromere is responsible for nondisjunction.

Finally, it has often been suggested that the telocentric nature of the B chromosome is a contributing factor in nondisjunction. Yet the B chromosome of rye, which undergoes nondisjunction in a manner similar to the B of maize, is a metacentric. In rye, two "sticky" regions appear on either side of the B centromere and prevent disjunction. The sticky regions are induced by a separate gene(s) on the B chromosome. In maize, the induction of a sticky region in one arm of a metacentric results in an unusual type of disjunction (Rhoades, Dempsey, and Ghidoni 1967). The possibility that nondisjunction might occur in maize chromosomes with heterochromatic knobs in both arms has not been tested. However, if the isochromosome B<sup>9</sup>'s are recovered in the greenhouse crop, they can be tested for nondisjunction. These chromosomes should have sticky regions in both arms. Nondisjunction by these chromosomes would indicate that the telocentric nature of the B is not essential for its nondisjunction.

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Characters	$\bar{y}_{ij} / \bar{y}_{Ij}$			$\bar{y}_{Ij} / \bar{y}_{Ij}$			Significance of differences	
	Plants	Mean	Standard error	Plants	Mean	Standard error	"t" values	Probability level
Plant height (cm)	82	110.73	1.83	26	105.92	3.40	1.27	0.3-0.2
Ear height (cm)	82	52.70	1.19	26	53.50	1.97	0.36	0.8-0.7
Stem diameter (mm)	82	13.78	0.18	26	13.00	0.41	1.97	0.1-0.05
Internode number	82	11.12	0.11	26	10.92	0.18	2.72	0.01-0.001
Leaf length (cm)	82	64.40	0.79	26	61.15	1.90	1.84	0.1-0.05
Leaf width (mm)	82	77.89	0.85	26	73.53	2.10	2.27	0.05-0.02
Pollen shedding time*	82	13.17	0.37	26	15.46	0.75	2.93	0.01-0.001
Silking time*	82	17.41	0.38	26	20.34	0.80	3.60	> 0.001
Shedding - silking period (days)	82	4.24	0.18	26	4.88	0.28	1.74	0.1-0.05
Ear length (mm)	84	109.13	2.79	24	103.75	5.36	0.90	0.4-0.3
Middle ear diameter (mm)	84	38.44	0.31	24	36.12	0.78	3.25	0.01-0.001
Row number	84	15.58	0.18	24	15.16	0.42	1.03	0.4-0.3
Kernels per row	84	26.38	0.76	24	24.12	1.30	1.42	0.2-0.1
Weight of 100 kernels (g)	84	18.17	0.28	24	17.25	0.66	1.45	0.2-0.1
Kernels per ear	84	411.35	13.25	24	372.00	26.37	1.38	0.2-0.1
Total kernels weight (g)	84	75.04	2.85	24	64.64	5.18	1.72	0.1-0.05