

3. The effect of abnormal 10 on the anaphase movement of knobbed and knobless acentric fragments.

Plants homozygous for abnormal chromosome 10 produce neocentromeres at knobbed regions of AI and AII chromosomes. Our earlier studies indicated that acentric fragments, derived from crossing over in bivalents heterozygous for a paracentric inversion, also exhibited neocentric activity if the fragment possessed a knob. Knobless fragments appeared to be passive at AI, but nothing was known of the fate of either fragment at the end of meiosis. A comparative study of the behavior of knobbed and knobless fragments in related plants of K10 K10 and k10 k10 constitution was made in order to determine the extent to which acentric fragments were preserved in the nucleus.

Counts were made of the frequency of AI cells with fragments (including cells having a single bridge and single fragment, a double bridge and two fragments, an acentric fragment only, and those with a single bridge and attached fragment). Interphase and quartet stages were examined and the frequency of a fragment in the cytoplasm was determined. The cytoplasmic fragments were expressed as percentage of total fragments excluded from the nucleus and the reciprocal of this value was adopted as an estimate of the rate of inclusion of the fragment within a TI or TII nucleus. The observed AI fragment frequencies and calculated frequencies of inclusion at the end of the first and second meiotic divisions are given in Table 1. Knobless fragments were derived from crossing over in In 3a/N3 heterozygotes in which both chromosomes 3 were knobless. Knobbed fragments were produced in In 7a/N7 plants homozygous for a knob in the inverted region. Cells were counted from two plants in each category; the frequency given is an average of the values in the two plants and the total number of cells is shown in parentheses.

		AI	Frequency of Fragment in Nucleus	
		Obs. Freq.	$(1 - \frac{\text{Frag. in Cytoplasm}}{\text{Total Frag.}})$	
		of Frag.	First	Second
			Division	Division
In 3a/ N 3 k3/k3	K10 K10	64.2 (407)	55.3 (442)	61.6 (383)
	N10 N10	28.7 (430)	23.9 (317)	35.5 (626)
In 7a/ N 7 K7/K7	K10 K10	83.1 (356)	98.9 (510)	91.4 (744)
	N10 N10	83.5 (539)	25.9 (699)	30.5 (403)

With In 3a/N3 heterozygotes the generation of fragments occurred at a higher rate in K10 K10 individuals than in the N10 N10. This is due to increased crossing over in the loop induced by K10. No increase in fragment frequency was noted in In 7a/N7 heterozygotes of K10 K10 constitution. The rate of fragment production in N10 N10 plants is already very high since the inverted segment is longer than in In 3a. It is believed that in k10 k10 plants, a maximum rate of fragment formation has been reached and that conversion of singles to doubles in the loop by K10 would not increase the fragment frequency since 25% of the double chiasmata (2 strand doubles) give cells without fragments. Variations in overall production of fragments, however, should not affect the data presented in the remainder of the Table since they are based only on that proportion of the AI cells that contain fragments.

It is clear that the knobbed acentric fragment in K10 K10 microsporocytes is nearly always included in the TI and TII nuclei. If the four categories of plants are ranked with regard to capacity to preserve the fragment as a nuclear chromosome throughout meiosis, the following order is obtained: K10 K10 In 7a/N 7 > K10 K10, In 3a/N 3 > N10 N10, In 7a/N 7 = N10 N10 In 3a/N 3. In K10 K10 plants the inclusion of the knobbed 7a fragment in the nucleus is not surprising since at AI it is often found near one pole. The attenuation of its

poleward tip is suggestive of spindle fiber attachment. The knobless 3a fragment in K10 K10 plants does not pass rapidly to the pole but shows a delayed poleward movement and is drawn into the nucleus in about one half of the cells with fragments. Even in N10 N10 plants, acentric fragments of both types were included in some of the interphase and quartet nuclei. This behavior was not anticipated and cannot be attributed to attachment of the fragments to centric chromosomes in AI, since the frequency of attached fragments was low.

During second division the knobbed 7a fragment in K10 K10 plants is found at the pole of the spindle as early as MII. About half of the knobless fragments in K10 K10 plants are also found at the pole at MII and these may represent fragments which had been included in the interphase nucleus. In neither case did the fragment show any indication of spindle fiber attachment. We believe that the movement of the fragment at second division is passive, resembling the poleward movement of acentric fragments and other particles in mitotic cells of the endosperm described by Ostergren, Molè-Bajer, and Bajer (1960). Thus, any acentric fragment incorporated into the nucleus at the end of the first division rapidly moves to the pole in the second division, with the exception of attached fragments which may be released into a dead zone at the equatorial plane of the spindle.

The question remains whether or not the fragment persists through additional mitotic divisions. Genetic tests of the transmission of deficient bridge chromatids by pollen grains in which the vegetative nucleus contains an acentric fragment are in progress and mitotic divisions following fertilization will also be examined for presence of the fragment.

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4. Evidence for an effect of the elongate gene on crossing over in chromosome 5.

The elongate gene has a number of effects when homozygous. These include, among others, the production of unreduced eggs in varying proportions with haploid eggs, pollen and ovule abortion, uncoiling of the