An Indirect Test for a Role of the Synaptonemal Complex in the Establishment of Sister Chromatid Cohesiveness

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Abstract. The meiotic behavior of a special maize trisome was quantitatively observed at pachytene, metaphase I, anaphase I, prophase II, metaphase II and anaphase II. The data obtained are consistent with (but do not prove) the model that sister chromatid cohesiveness at anaphase I may be established during pachytene synapsis of the chromosome regions involved. The data suggest, however, that the normal prophase II maintenance of dyad integrity by cohesiveness of sister chromatid centromere regions does not depend upon prior synapsis of these regions, although monads separated from each other on the anaphase I spindle may be delivered to the same prophase II daughter nucleus. - The strands which some of the time connect sister chromatids which are separating equational at anaphase I show a positive Feulgen staining reaction.

Introduction

It has been recently proposed (Maguire, 1978a) that the synaptonemal complex (SC) may serve a previously unsuggested function, i.e. that of somehow providing for the sister chromatid cohesiveness presumably required for maintenance of chiasmata until anaphase I and possibly required in centromere regions for maintenance of dyad integrity between metaphase I and anaphase II.

In brief, the reasoning behind this suggestion was as follows. (1) Extension of the SC (assumed to be locally important to the process of crossing over) from end to end of each bivalent seems extravagant in the light of evidence that formation of the SC may be initiated at several, variously distributed points, at least in some organisms (Gillies, 1975; Holm, 1977; Zickler, 1977), the well known ability of rearranged segments to synapse with matching regions in normal sequence chromosomes, similarity of probable number of points of initiation per bivalent to average number of crossovers within them (Sved, 1966; Gillies, 1975) and similarity of synaptic and crossover frequencies in chromosome regions heterozygous for relatively short rearrangements (Maguire,
A structural basis for the production of the normally observed sister chromatid cohesiveness all along their length seems needed. (3) At least one meiotic mutant is known in which apparently precocious removal of the SC is associated with failure of chiasma maintenance in spite of the presence of crossovers (Maguire, 1978b). (4) There is evidence that precocious removal of the SC with ethanol treatment can produce the same effect, i.e. failure of chiasma maintenance in the presence of crossovers (Maguire, 1976). (5) There is a variety of circumstantial evidence that anomalous types of nondisjunction and disjunction of sister chromatids may be correlated with history of correspondingly anomalous synapsis and asynapsis respectively of the regions involved at pachytene.

The work described here sought to make quantitative observations which would allow comparisons between frequency of synapsis at pachytene, in material where synaptic behavior is variable in specific chromosome regions, with frequency of apparent sister chromatid cohesiveness at later meiosis in those same chromosome regions. A basic assumption is that truly synapsed chromosomes (with SC present) at pachytene in maize provide a configuration to a trained observer at the light microscope level which is as distinctive as is the SC itself (observable only with E.M. magnification). Nuclei appropriately fixed and stained and examined at this stage in thin sections with E.M. microscopy have consistently shown SC between homologues (Ting, 1969; Gillies, 1973).

Materials and Methods

A special maize trisomic stock, which has been described extensively elsewhere (Maguire, 1960), was crossed to KYS inbred. Plants were derived from this cross which contained the twenty normal maize chromosomes plus an extra chromosome which consisted of a segment of a *Tripsacum* chromosome that contained its centromere attached to approximately half of the short arm of a normal maize chromosome 2. This chromosome will be referred to as the T2 chromosome. In plants of such constitution trivalent configurations have been found consistently in about 2/3 of pachytene microsporocytes and also in about 2/3 of metaphase I microsporocytes (Maguire, 1965). KYS background was introduced in this case in order to improve the quality of pachytene preparations for detailed observations at that stage.

Microsporocyte samples were collected from plants of this constitution, fixed in ethanol-acetic 3:1 mixture and stored in a freezer pending examination in aceticarmine of Feulgen squash preparations. A tassel sample from a single plant was selected for study (on the basis of probable comparative abundance of appropriate meiotic stages) so that all observations could be made in material with homogeneous genetic background.

It is a basic assumption of this study that there is sufficient homogeneity in chromosome behavior at meiosis throughout the tassel in time and space so that the sample of those cells observed at a specific stage can be taken as generally representative for that stage. The possibility of sampling error should be kept in mind although it was probably minimized in this case by exclusive use of anthers from the first flowers of the intercalary region of lateral branches.

Each squash preparation was made from a single anther. Every slide at a stage of interest was systematically scanned. Almost all cells at metaphase I, anaphase I, early telophase I, mid-prophase II, metaphase II and anaphase II were easily classified for the traits to be scored in each case. However, in spite of half KYS background, many pachytene cells contained chromosomes too tangled to be unequivocally analyzed. It is believed that important bias was avoided in pachytene scoring by the following procedure. Each cell at mid-late pachytene was first examined under low power magnification (100×) for general quality of spread. Only those cells which had no apparent extensive superimposition of chromosomes were chosen for examination under oil immer-