determined although it could be placed distal to the Wx locus. Tests of the presence of Ds in this chromosome in the progeny of the remaining 9 plants were not completed.

The project was discontinued at this juncture even though crosses had been made to obtain plants with proper constitution to determine the location of Ds in the chromosomes carrying the null segment. The main questions -- whether crossing over occurs and where this may occur -- appeared to be answered by the results already obtained. It was occurring, and between Ds and Sh and not between the null segment and Ds. At the time, it was considered that the rewards that could be expected by pursuing this project would be too meager to justify the considerable amount of effort involved in the pursuit. It should be emphasized, however, that this Ds, in the presence of Ac, causes modification in expression of Sh, located proximal to it, and this has occurred to Sh in those chromosomes that have the null segment located just distal to Ds.

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1. An analysis of chromosomal behavior during meiosis in asynaptic maize: Distribution of bivalents.

The expression of the asynaptic gene is highly variable, bivalents per cell ranging between 0 and 10. Swaminathan and Murty (Genetics 44: 1271-1280, 1959) made the interesting observation that although variation in bivalent frequency follows a binomial or Poisson distribution when the mean value per cell is low, marked deviation from a binomial distribution can be noted when this value is high and approaches half of the potential number of bivalents. This was explained on the assumption that certain pairs of homologous chromosomes entered into bivalent association more frequently than others. These authors based their conclusions on an analysis of

Beadle's (Cytologia 4: 269-287, 1933) data on asynaptic maize as well as data on asynapsis in other organisms. The present study was undertaken to examine the situation more critically and determine as far as possible the cause of the deviation. The recent data of Miller (Genetics 48: 1445-1463, 1963) were analyzed for the purpose. The method of analysis is outlined below.

The expectations for the frequency of varying numbers of bivalents can be obtained from the expansion of the binomial $(p+q)^{10}$, where p is the coefficient of synapsis or the probability that a pair of homologues would enter into synapsis (= one-tenth of the mean number of bivalents per cell), and q is the probability that a given pair would show asynapsis and equals (1-p). In case all homologous pairs within a meiocyte and all meiocytes behave alike (or if 'p' varies but slightly), observed frequencies should not differ significantly from these expectations. Deviations from a binomial distribution may result under two different situations and correspondingly two models can be set up as follows, depending on (1) differential behavior of homologous pairs within a meiocyte or (2) differences between cell populations.

Model 1 --- Assuming the first situation, suppose there are two groups within a meiocyte with n_1 and n_2 chromosomes (so that $n_1+n_2 = 10$) with two different values of 'p' (and correspondingly two different values of 'q'). Let these values be p_1, p_2 and q_1 and q_2. It can be proven by assigning different numerical values to n_1, n_2, p_1, p_2, q_1 and q_2 that (1) the deviation would follow unimodal distribution; (2) the frequencies at the extremes would be less than those expected from binomial distribution; and (3) the frequencies in the middle would be higher than those expected from binomial distribution. The pattern of deviation can be roughly represented by Figure 1.

Model 2 --- According to this model, the population of meiocytes (= N) may comprise groups (say, N_1 and N_2) such that (1) each of N_1 cells has p_1 and q_1 as coefficients of synapsis and asynapsis respectively and (2) each of N_2 cells has p_2 and q_2 as the same coefficients. It can be proven that the deviation according to this model would be characterized by the following. (1) Frequencies at the ends would be more than those expected from binomial distribution. (2) Frequencies in the middle would be correspondingly less. (3) The deviating distribution would be either unimodal or bimodal depending on the ratio $N_1:N_2$. The patterns of deviation have been indicated in Figure 2.

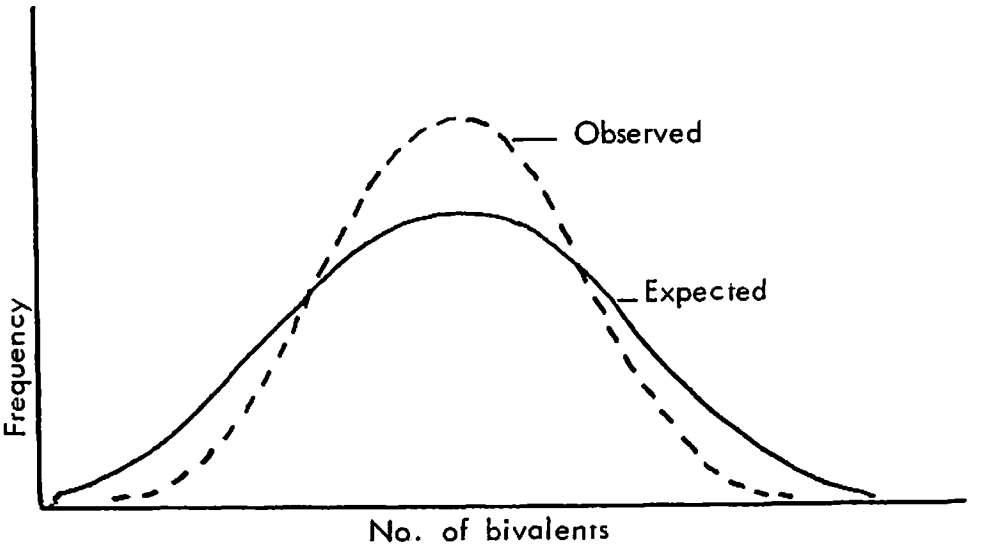

Fig. 1
Deviation from binomial distribution according to Model 1. (p = 0.5)

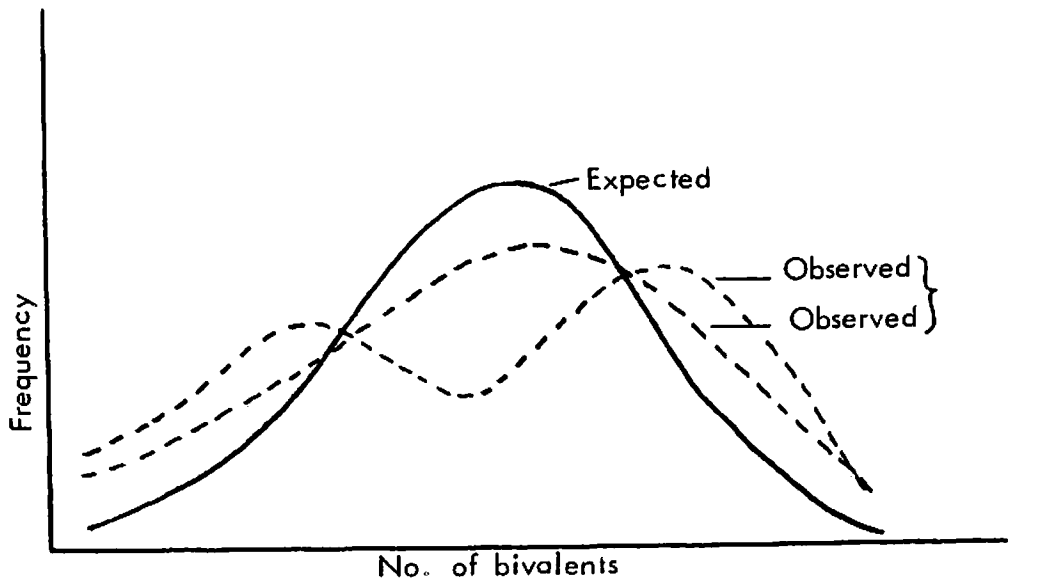

Fig. 2
Deviation from binomial distribution according to Model 2. (p = 0.5)

The results of actual analysis of Miller's data have been presented in Table 1. The following observations can be made:

(1) For 'p' values close to 1, the frequencies of bivalents follow a binomial distribution.

(2) For 'p' values much below 1, the observed frequencies differ significantly from those expected on the basis of binomial distribution.

(3) The deviation is of the type expected according to Model 2.

The conclusion that can be drawn from this study is different from that of Swaminathan and Murty, who inferred a differential behavior of chromosomes within meiocytes (equivalent to Model 1). However, no evidence was offered by them from the analysis of data and their inference was based on the extrapolation of certain types of preferential or nonrandom behavior of chromosomes within single cells in other organisms. The correspondence of the deviation in the present study to Model 2 may mean several possibilities such as (1) variation in chromosomal behavior (different 'p' values) in different regions (e.g. upper, middle and basal) of the same anther, (2) variation in different anthers, (3) variation in different spikelets. But there is no indication of particular chromosomes within a meiocyte being highly different in their behavior (i.e. with 'p' values deviating significantly from the average).

It is relevant to mention here that the observations of Rees and Naylor (Heredity 15: 17-27, 1960) and Rees (Heredity 17: 427-38, 1962) regarding variability in chromosomal behavior within individual anthers of rye are consistent with the present finding as to the variable expressivity of the asynaptic gene in different groups of meiocytes. As postulated by Rees (1962), such differences may be causally related to the division sequence, i.e. how early or late meiosis takes place in a meiocyte. Presumably the variable metabolic status of the cells undergoing meiosis at different times affects the expressivity of genes controlling meiotic behavior of chromosomes.

The present study helps to emphasize the fact that interesting variations in chromosomal behavior can be noted by recording and analyzing the data on individual anthers, spikelets and plants and even different regions of the same anther separately before pooling the data. Further, it may be noted that such an analytical method as employed in the present investigation would elicit more

Table 1
Analysis of Distribution of Bivalents and Pattern of Deviation from Binomial Distribution

Plant Number as in Miller (1963)	Mean No. of bivalents per cell (p)	Frequency of bivalents of varying number (Upper figures are actual observations and lower ones are those expected from binomial distribution)											Deviation significant (S) or non-significant (NS)
		0	1	2	3	4	5	6	7	8	9	10	
# 3	0.015	178 171.9	16 26.2	5 1.8	1 0								S
# 4	0.200	17 5.4	10 13.4	4 15.1	7 10.1	5 4.4	3 1.3	2 0.3	2 0				S
# 5	0.408	38 1.1	13 7.3	18 22.7	25 41.6	22 50.1	21 41.4	13 23.7	13 9.3	13 2.4	15 0.4	9 0	S
# 6	0.704	4 0	8 0	6 0.3	9 1.7	8 7.0	13 20.0	18 39.4	27 53.4	31 47.5	42 25.0	34 5.9	S
# 7	0.727	0 0	0 0	2 0.1	7 0.5	5 2.4	4 7.8	13 17.2	16 26.2	20 26.2	18 15.5	15 4.1	S
# 8	0.886					1 0	1 0.3	7 2.2	6 9.9	28 28.9	35 49.9	52 38.8	S
# 9	0.888						0 0	8 3.8	13 14.7	43 43.6	67 76.9	69 61.0	NS
#10	0.900				1 0	0 0	2 0.1	0 0.6	2 9.7	6 9.7	15 19.4	24 17.4	S
#11	0.917						1 0.1	1 1.2	8 7.5	23 31.0	39 76.1	119 84.1	NS
#12	0.976									9 4.6	30 38.6	161 156.9	NS
#13	0.995									2 0.5	18 21.5	430 428.0	NS
#14	0.995										5 4.8	95 95.2	NS

information from the data gathered from cytological studies, and thus would provide a useful supplement to the latter.

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1. Polarized variation in R-locus expression among gametes from single plants.

It is a common assumption in genetics that within the same organism gametic equivalence for a specific phenotype is the rule under conditions where explanations invoking segregating modifiers can be eliminated. In the tassel of a single heterozygous plant (Rr) it is expected that all pollen which carries the R gene will produce the same endosperm phenotypes when testcrosses are made to inbreds which carry those genes necessary for pigment production. The data presented below show that this equivalence for R-locus expression for pollen from within a single tassel cannot be taken for granted.

RR^{st} plants in corn grass background (a background selected for its tillering ability) were pollinated with rr to isolate Rr heterozygotes. Because of the effect of R^{st} (paramutation) the ability of R to produce pigment is reduced and symbolized by R'. The R'r heterozygotes were grown under field conditions; numbered plants on the first and fifth day of anthesis were testcrossed to Inbred W22 rr. Testcross kernels were then scored for amount of endosperm pigment present by matching R' phenotypes against a set of standard kernels which ranged from 0 - 22, colorless through completely pigmented respectively.

It can be noted from the data that the earliest pollen samples from a tassel have produced the lightest phenotypes; those pollinations made from florets which shed pollen on the fifth day were measurably darker.