factors to express the different frequencies of certain modes of pairing; thus $(1 - q)(1/3 + p)$ expresses the frequency that autosyndetic pairing occurs when two bivalents are formed. The details of the algebraic manipulations are too long to include here. The formula is as follows:

$$p = \frac{1/6 + 1/12 \text{ aeq} - R}{1/4 - 3/8 \text{ aq} + 1/8 \text{ aeq}}$$

where a = the frequency of adjacent disjunction of the quadrivalent, e = the frequency of equational orientation, q = the frequency of quadrivalent formation, and R = the frequency of the recessive class as found in a backcross.

The value aeq is equal to $2\alpha$, a mathematical term as used by Mather to express the frequency of double reduction, a phenomenon partly responsible for deviations from a 5:1 ratio. The value of $\alpha$ here can be estimated from the control ratio $4.03:1 = 5 - 2\alpha:1 + 2\alpha$ ($\alpha = .095$). However it seems inadvisable to substitute this value in the above formula since the value of q is probably lower in the structural heterozygote than in the control. Also the aq term causes some trouble. A rough estimate of the values of a and q can be made from cytological observations if we assume that all the groups of homologous chromosomes behave in about the same manner. The amount of equational separation (e) for the A locus can be derived for diploids from the data of Rhoades on the frequency of second division segregation in diploid eggs of el el plants. It is .74 (M G C News Letter 30, p. 40). If we assume that crossing over is the same frequency in the diploid and the tetraploid strains used, then this value may be taken as an estimate of "e".

In view of the fact that this study is as yet in a preliminary stage, the value of p cannot be estimated with any degree of accuracy until various things are known - the effect of crossing over within the inversion loop, amount of numerical nondisjunction (3 - 1 split of quadrivalent), etc. It is impossible to draw any definite conclusions as to some of the problems this work is endeavoring to answer such as: what magnitude of structural rearrangement is required to produce the autosyndetic pairing found in allotetraploids? However, the data presented here are in general agreement with those reported on structurally heterozygous triploids by Rhoades in the last issue and indicate that a substantial amount of preferential pairing does take place.

G. G. Doyle

4. Occurrence of crossover strands in the diploid gametes of as plants.

Asynaptic plants produce both haploid and diploid eggs as well as non-functional spores with unbalanced chromosomal complements. Haploid and diploid sperm are also produced, but zygotes coming from the functioning of 2n pollen grains are rare because of competition with 1n

grains. The crossover studies to be reported, therefore, involve only diploid eggs.

Asynaptic plants heterozygous for various linked markers were used as egg parents in backcrosses to diploid and tetraploid testers. When the pollen parents were diploid, the triploid progeny was analyzed for crossovers; when the pollen parents were tetraploid, the tetraploid progeny was dealt with. In most cases, a second backcross (or a self pollination) was necessary to determine the complete genotype of the original diploid gamete.

The kinds and frequencies of diploid eggs are given in the tables. The first sets of data, involving genes on chromosome 9, test crossing over in a single chromosome arm. The last set of data, involving chromosome 5 markers, tests regions on both sides of the centromere. The chromosome 9 studies shown in Tables 1 and 2 include both coupling and repulsion backcrosses. Table 1 gives the actual genotypes of the diploid gametes and their frequencies. In Table 2, this data has been re-arranged so that gametes coming from similar crossover events in the C.B. and R.B. tests may be summed, even though they are of different genotypes. Two crossover designations are given above each class; the first assumes doubling occurred at the first meiotic division, the second assumes doubling at the second division.

On the first hypothesis an equational first meiotic division followed by a failure of second division is postulated. Centromeres of sister chromatids pass into different nuclei. On the second hypothesis, the first division is completed normally and the dyads at each pole then disjoin into their component chromatids without a true second division, i.e., "sister" centromeres remain in the same nucleus. There is genetic evidence for the occurrence of both processes, but it is uncertain whether mixed events can occur in the same cell (equational division for some of the chromosomes and normal AI for others) or whether all the chromosomes of a cell behave in the same way. Cytological observations favor the former proposal.

Examination of the classes listed in Table 2 reveals that region (2) and (1-2) crossovers are far too frequent on hypothesis (1). Similarly the combined (2),(1-2) class of hypothesis (2) is larger than expected. Region (2) in both cases is the wx-centromere region which is only about 11 genetic units in length (Rhoades, MNL 30: 42). Thus neither hypothesis alone can fully account for the data, although hypothesis (2) is the better explanation in most cases.

Formation of a restitution nucleus at second division (hypothesis 2) will give all the types of diploid gametes obtained in the observed frequencies, with the exception of the (2), (1-2) class. Gametes in this questionable class possess one apparent non-crossover strand from each of the parental homologues. In order to learn more about the origin of this class, it was necessary to know whether or not such

Table 1.

Type of diploid gamete

**Cross group 1 (C Wx / c wx)**

|  | | Type of diploid gamete | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | | $\frac{C\ Wx}{c\ wx}$ | $\frac{C\ Wx}{C\ Wx}$ | $\frac{C\ Wx}{C\ Wx}$ | $\frac{C\ Wx}{C\ Wx}$ | $\frac{C\ Wx}{C\ Wx}$ | $\frac{C\ wx}{C\ Wx}$ | $\frac{C\ wx}{C\ wx}$ | $\frac{C\ Wx}{c\ Wx}$ | $\frac{c\ Wx}{c\ wx}$ | $\frac{c\ wx}{c\ wx}$ |
| 1. | $\frac{C\ Wx}{c\ wx}$ as/as X 4n c wx CB  Σ = 166 | 73 | 19 | 15 | 2 | 3 | 1 | 18 | 0 | 0 | 35 |
| 2. | $\frac{C\ Wx}{c\ Wx}$ as/as X 4n c wx RB  Σ = 132 | 0 | 0 | 8 | 3 | 60 | 25 | 11 | 23 | 2 | 0 |

**Cross group 2 (Sh Wx / sh wx)**

|  | | $\frac{Sh\ Wx}{sh\ wx}$ | $\frac{Sh\ Wx}{Sh\ Wx}$ | $\frac{Sh\ Wx}{Sh\ Wx}$ | $\frac{Sh\ Wx}{Sh\ Wx}$ | $\frac{Sh\ Wx}{Sh\ Wx}$ | $\frac{Sh\ wx}{Sh\ Wx}$ | $\frac{Sh\ wx}{sh\ wx}$ | $\frac{sh\ Wx}{sh\ Wx}$ | $\frac{sh\ Wx}{sh\ wx}$ | $\frac{sh\ wx}{sh\ wx}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. | $\frac{Sh\ Wx}{sh\ wx}$ as/as X 2n sh wx CB  Σ = 56 | 11 | 15 | 9 | 1 | 1 | 1 | 7 | 0 | 3 | 8 |
| 2. | $\frac{Sh\ wx}{sh\ Wx}$ as/as X 2n sh wx RB  Σ = 7 | 0 | 0 | 1 | 1 | 4 | 0 | 1 | 0 | 0 | 0 |

Table 2.

| Source of 2n gamete — hypothesis 1: hypothesis 2: | (2) (0) | (2) (2) (1-2) (1) | (1-2) (1-2) (1) | (1-2) (1) | (1-2),(0) (1),(2) (2),(1-2) | (1) (1-2) (1-2) | (1) (1-2) (1-2) | (1-1-2) (1-1) | (1-1-2) (1-1) (1-1) | (1) (1-2) (1-2) |
|---|---|---|---|---|---|---|---|---|---|---|
| $\frac{C\ 1\ Wx\ 2}{c\ \ \ \ \ wx}\ \frac{as}{as}$ o  X 4n c wx  GB | 19 | 35 | 15 | 18 | 73 | 2 | 0 | 0 | 0 | 3 |
| $\frac{C\ 1\ wx\ 2}{c\ \ \ \ \ Wx}\ \frac{as}{as}$ o  X 4n c wx  RB | 23 | 25 | 8 | 11 | 60 | 3 | 2 | 0 | 1 | 0 |
|  | — | — | — | — | — | 1 | 1 | 1 | 1 | 1 |
|  | 42 | 60 | 23 | 29 | 133 | 5 | 2 | 0 | 1 | 3 |
| $\frac{Sh\ 1\ Wx\ 2}{sh\ \ \ \ wx}\ \frac{as}{as}$ o  X 2n sh wx  GB | 15 | 8 | 9 | 7 | 11 | 1 | 3 | 0 | 1 | 0 |
| $\frac{Sh\ 1\ wx\ 2}{sh\ \ \ \ Wx}\ \frac{as}{as}$ o  X 2n sh wx  RB | 0 | 0 | 1 | 1 | 4 | 0 | 0 | 0 | 1 | 1 |
|  | — | — | — | — | — | 1 | 1 | 0 | 1 | 1 |
|  | 15 | 8 | 10 | 8 | 15 | 2 | 3 | 0 | 1 | 1 |

strands had experienced crossing over in the other chromosome arm (not tested in the chromosome 9 studies) and also whether or not such strands carry "sister" centromeres or "homologous" centromeres. For this reason, compounds of $\frac{A}{a} - \ominus \frac{Bt}{bt} \quad \frac{pr}{Pr}$ were used, in which crossing over can be detected in both arms and in which the centromere is marked by Bt.

When $\frac{A}{a} - \ominus \frac{Bt}{bt} \quad \frac{pr}{Pr}$ as/as plants were pollinated with 4n <u>a</u> <u>bt</u> <u>pr</u> testers, the following kinds of seed were produced:

| A Bt Pr | A Bt pr | A bt Pr | A bt pr | a Bt -- | a bt -- |
|---------|---------|---------|---------|---------|---------|
| 432 | 352 | 35 | 2 | 4 | 450 |

Due to extremely poor germination of bt types, only a part of this population could be tested for genotype. At present 98 plants have been analyzed and the results are given in Table 3.

The exceptional class corresponding to the (2),(1-2) class in the previous table is listed under (1-2). In this case, region (2) is from the centromere to Bt, a distance of approximately 1%, making a (1-2) double highly unlikely. Therefore, the heterozygous condition for Bt indicates that homologous, rather than sister, centromeres are present. The strands in these gametes have not undergone crossing over in the regions tested, and have probably come from univalent chromosomes which separated equationally at the first meiotic division. Occasional recovery of two strands with homologous centromeres (Bt/bt) that have experienced crossing over is indicated by the (1-2-3) class, which is more easily interpreted as the result of a single in (3) followed by an equational first division.

Since the majority of the data on types of diploid gametes is accounted for on hypothesis (2) while the exceptional class can only be explained by hypothesis (1), it appears that both events must occur during formation of diploid eggs. Pollen mother cells have been seen which contain a mixture of bivalents and univalents at AI. The univalents sometimes divide equationally after the dyads have reached the poles. This leads to a mixture of dyads and monads in each nucleus. It is possible that, when a majority of monads is present, the sister centromeres of the dyads disjoin without a spindle mechanism, to give a total of 20 separate centromeres in each cell. Dowrick (Heredity 7: 219-226) suggests that the capacity of the centromeres for division determines the occurrence of the second meiotic division. In the present case, the single condition of the majority of centromeres might prevent a second division. Thus, a chromosome pair tested genetically would sometimes contribute 2 chromatids with sister centromeres to the diploid spore (bivalent MI, dyad PII = hypothesis 2) and sometimes it would contribute 2 chromatids with homologous centromeres (univalent MI, monad PII = hypothesis 1). Diploid eggs may arise, therefore, by a combination of doubling (or centromere separation) at AI and at PII.

Table 3.

$$\frac{A\ 1\ \ 2\ Bt\ \ 3\ pr}{a\ \ \ \ \ bt\ \ \ \ Pr}\ \begin{matrix}as\\as\end{matrix}\quad \times\quad 4n\ a\ bt\ pr\quad RB$$

Source of 2n gamete

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Hypothesis 1:** (1-2) | (1-2) | (2) | (1) | (1) | (1-2-3) | (1-2-3) | (1-2-3) | (2),(3) (0),(1) | (3) | (1-2-3-3) |
| **Hypothesis 2:** (0) | (0) | (1) | (2) | (2) | (2) | (3) | (3) | (1-2) | (1-2-3) | (3-3) |
| A\|A Bt\|Bt pr\|pr | a\|a bt\|bt Pr\|Pr | A\|A Bt\|Bt pr\|pr | a\|a bt\|bt Pr\|pr | A\|A Bt\|Bt pr\|pr | a\|a bt\|bt Pr\|pr | A\|A Bt\|Bt pr\|pr | a\|a bt\|bt Pr\|pr | a\|a bt\|bt pr\|Pr | A\|A Bt\|Bt pr\|Pr | A\|A Bt\|Bt Pr\|Pr |
| 41 | —* | 82# | —- | 0 | — | 23 | 3 | 20 | 2 | 1 |

$\Sigma = 98$

* Blanks in the data represent failure of germination of seed.

# Require further tests due to possible segregation of another aleurone factor. These may be A/A instead of A/a.

The fact that crossover chromosomes are found in diploid eggs of as plants (which was first reported in 1947 by Rhoades, Genetics 32: 101) would be surprising if these eggs came from EMC's with only univalents. It seems likely, however, that EMC's containing both univalents and bivalents give rise to diploid eggs and therefore a certain amount of crossing over would be expected.

A calculation of the percent of crossover strands among the total strand population gives 12.9% C-Wx recombination in the coupling backcross and 9.9% C-Wx recombination in the repulsion backcross. The value for the Sh-Wx region in the coupling data in Table 1 is 21.4%. The last value is based on a small population of only 56 gametes, since triploid plants are more difficult to obtain than tetraploid ones. Using only the phenotypically Bt classes, a value of 14.2% is obtained for the Bt-Pr region in the chromosome 5 test. Most of these values are less than the standard values. Because of the unusual events which occur during formation of diploid gametes, it is difficult to predict the expected rate of exchanges. However, if some univalent chromosomes are present in the cell at the time of crossing over, a reduction in the recombination values would be expected.

## 5. A duplicate factor ratio.

A chance segregation of pale green plants occurring in the $F_2$ of crosses between KYS and two tester stocks may represent another occurrence of the $pg_{11}$ $pg_{12}$ duplicate factors found by Rhoades. In $F_2$'s segregating ws lg gl, 126 green: 12 pale green: 42 ws plants were found. This is close to the 15: 1 ratio of green: pale green expected if duplicate factors are involved. It seems likely that KYS is homozygous for or carries either $pg_{11}$ or $pg_{12}$ while the second factor of the pair is carried in the ws lg gl tester stock as well as in a Rg lg a et stock.

## 6. Further studies of KYS male sterility.

In the MNL 31: 81, mention was made of an aberrant $F_2$ from self pollination of Ms ms S s, which segregated male sterile plants. No male steriles (Ms ms s s) were expected since only S pollen functions in Ms ms S s heterozygotes. The Ms ms S s plant which was self pollinated came from a cross of as/KYS ♀ X KYS ♂ (Ms ms S s X ms ms s s). Two other Ms ms S s plants coming from the same cross (and the same ear) were selfed and gave no male steriles. Numerous other unrelated $F_2$'s also gave only normal plants. The single aberrant population remains unexplained. Although as was segregating, asynaptic plants can easily be distinguished from the male steriles on the basis of ear sterility.

Thirteen genetic testers were checked for ms and s constitution. Nine were Ms Ms S S, two were ms ms S S, and two were Ms ms S S. Our stocks of Mangelsdorf tester are ms ms S S. Evidently the s allele is restricted in its occurrence, whereas the ms mutation is more widely distributed.