

sh bz Wx, occurred much less frequently (142 vs 720) than the Sh Bz wx class. This is indicative that the Df 9S Dp 9L megaspores do not function as frequently as do the Dp 9S Df 9L spores.

Data from the reciprocal cross are as follows:

| <u>Sh</u> | <u>sh</u> | <u>Sh</u> | <u>sh</u> | <u>Sh</u> | <u>sh</u> | <u>sh</u> | <u>Sh</u> | |
|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-------|
| <u>Bz</u> | <u>bz</u> | <u>bz</u> | <u>Bz</u> | <u>bz</u> | <u>Bz</u> | <u>bz</u> | <u>Bz</u> | |
| <u>Wx</u> | <u>wx</u> | <u>Wx</u> | <u>wx</u> | <u>wx</u> | <u>Wx</u> | <u>Wx</u> | <u>wx</u> | Total |
| 754 | 540 | 0 | 0 | 13 | 9 | 31 | 40 | 1387 |

Here the Sh Bz wx and sh bz Wx classes are approximately equal in size since neither type of duplicate-deficient microspore develops into functioning pollen and both classes stem from singles between bz and the In or 2- and 3-strand doubles within the In where one exchange is between wx and the break point in 9L. In the female backcross the Sh Bz wx class constituted 23.3 percent of the progeny but only 2.9 percent in the male backcross. The difference may be ascribed to functioning Dp 9S Df 9L megaspores. Likewise in the female backcross the sh bz Wx class was 4.6 percent of the total while in the male backcross the percentage was 2.2. Here also the difference is due to functioning Df 9S Dp 9L megaspores which according to Li's data amount to 2.4% of the functioning ovules.

When plants heterozygous for this inversion were pollinated by bm pollen, some of the F₁ plants were phenotypically bm. These arose from functioning Dp 9S Df 9L megaspores which are deficient for the tip of 9L. The F₁ bm plants are hemizygous for the bm locus and show the bm phenotype. The bm locus can be placed in the distal end of 9L.

M. M. Rhoades
E. B. Patterson

4. Further studies on preferential segregation.

Plants of abnormal 10/normal 10 and K 3L/k 3L constitution were used as the female parent in crosses with a gl₆-lg₂-a₁ tester which had knobless chromosomes 3. (The symbol K 3L represents a chromosome 3 possessing the knob at position 0.6 in the long arm while k 3L denotes a knobless chromosome 3.) Both the K 3L and k 3L chromosomes of the female parent were carrying the Gl, Lg and A alleles. The A locus is distal to the knob while Gl is proximal. The location of Lg with respect to the knob is uncertain as yet. Four types of F₁ plants are expected although not with equal frequencies inasmuch as both the abnormal 10 and K 3L chromosomes undergo preferential segregation. In a total of 50 F₁ plants which were studied cytologically for the presence or absence of the abnormal 10 and K 3L chromosomes, and from which backcross progenies were obtained, there were 25 plants

heterozygous for abnormal 10 and K 3L, 10 heterozygous for abnormal 10 but homozygous for k 3L, 11 homozygous for normal 10 but heterozygous K 3L, and 4 which were homozygous normal 10 and knobless 3. The following backcross data were obtained using the F₁ plants as the egg parent:

| | (0) | (0) | (1) | (1) | (2) | (2) | (1-2) | (1-2) | Total |
|------------------------|------|-----|-----|------|-----|-----|-------|-------|-------|
| | G1 | gl | G1 | gl | G1 | gl | G1 | gl | |
| | Lg | lg | lg | Lg | Lg | lg | lg | Lg | |
| | A | a | a | A | a | A | A | a | |
| abn 10/N 10; K 3L/k 3L | 2529 | 871 | 663 | 2060 | 859 | 474 | 309 | 662 | 8427 |
| abn 10/N 10; k 3L/k 3L | 730 | 656 | 425 | 465 | 471 | 493 | 210 | 178 | 3628 |
| N 10/N 10; K 3L/k 3L | 954 | 870 | 514 | 525 | 274 | 326 | 121 | 143 | 3727 |
| N 10/N 10; k 3L/k 3L | 286 | 259 | 122 | 118 | 174 | 159 | 67 | 38 | 1223 |

Analysis of these data gave the results shown below:

| | % G1 | % Lg | % A | Recombination | | |
|------------------------|---------|---------|--------|---------------|------|-------|
| | | | | G1-Lg | Lg-A | Total |
| abn 10/N 10; K 3L/k 3L | 51.7 | 72.5 | 63.6 | 43.9 | 27.3 | 71.2 |
| abn 10/N 10; k 3L/k 3L | 50.6 | 50.8 | 52.3 | 35.2 | 37.3 | 72.5 |
| N 10/N 10; K 3L/k 3L | 50.0 | 50.9 | 51.7 | 35.0 | 23.2 | 58.2 |
| N 10/N 10; k 3L/k 3L | 53.1 | 50.4 | 51.5 | 28.2 | 35.8 | 64.0 |

One of the unusual features of these data is the increase in crossing over found in plants heterozygous for abnormal 10. The average total recombination for the G1-Lg-A regions in the two classes carrying abnormal 10 is 72 percent while it is 61 percent in the two classes homozygous for normal 10. Another point of interest is the reduction in crossing over in the Lg-A region when the knob is heterozygous. The average value for this region in the two classes homozygous for knobless chromosomes 3 is 36.5 percent and only 25.2 percent in the two classes heterozygous for the knob. It is obviously desirable to ascertain the location of the Lg₂ locus with respect to the knob; no accurate placement is possible at this time but the Lg locus most likely lies proximal to the knob. Another matter of some importance is that the decrease in recombination in the Lg-A region found in plants heterozygous for the knob is accompanied by an increase in the G1-Lg region. Comparing first the two classes each heterozygous for abnormal 10 but differing in that one is heterozygous for K 3L while the other is homozygous for k 3L, we find a decrease in the Lg-A region and an increase in the G1-Lg region in K 3L/k 3L plants as compared to k 3L/k 3L. The total amount of recombination is essentially equal. A comparison of the data from N 10/N 10 K 3L/k 3L and N 10/N 10 k 3L/k 3L plants also indicates a decrease in the Lg-A region in K 3L heterozygotes as compared to homozygous k 3L plants and an increased amount of recombination in the G1-Lg

region in the K 3L heterozygotes. It should be stressed that these crossover data come from sibling plants.

Studies are underway to see if the increase in crossing over in the long arm of 3 found in abnormal 10 heterozygotes will also occur in other chromosomes and to determine what the frequency of crossing over will be in homozygous abnormal 10 plants.

Preferential segregation for the chromosome 3 markers occurred in only one of the four F₁ classes--namely the class heterozygous for both abnormal 10 and K 3L. Plants heterozygous for abnormal 10 and homozygous k 3L exhibited random segregation for genes in 3L as did plants in the two classes homozygous for normal 10. Before discussing the varying extent of preferential segregation for the G₁, L_g and A loci, it is necessary to consider what is known of the cytological locations of these loci. Studies with In 3a show that G₁ is proximal to position 0.4 and Dempsey (1955 News Letter) has shown that it is distal to point 0.1. There are approximately 20 crossover units between G₁ and the centromere. The L_g locus cannot be accurately assigned at this time. It is known to be distal to point 0.4 and probably lies proximal to the knob (0.6) but this conclusion is not soundly based. The distal-most locus A is situated in the segment delimited by positions 0.8 and 0.9; it lies therefore beyond the knob.

The low degree of preferential segregation for the G₁ allele is understandable on the hypothesis that preferential segregation takes place only when crossing over occurs resulting in anaphase I dyads having one knobbed chromatid with the G₁ allele and one knobless chromatid with the g₁ allele. Heterozygous dyads of this type arise from tetrads with single exchanges between the centromere and g₁ and from all kinds of double exchanges where one exchange is in the centromere-g₁ region and the second exchange is between the knob and A. All other double exchanges with one crossover to the left of g₁ give random segregation for the g₁ locus.

The high degree of preferential segregation for the L_g allele is expected since there is more opportunity for the appropriate crossovers which lead to heteromorphic dyads and hence to preferential segregation. If the order is centromere (1) G₁ (2) L_g (3) K (4) A, singles in regions 1 and 2, 3-strand doubles in 1-2, and all doubles in 1-4 and in 2-4 lead to preferential segregation for L_g. Preferential segregation for the A allele comes from singles in 1, 2, and 3, from 3-strand doubles in 1-2, from 3-strand doubles in 1-3 and from 3-strand doubles in 2-3. The higher degree of preferential segregation for the L_g allele as compared to the A allele is due to the frequent occurrence of double exchanges in regions 2 and 4 which lead to preferential segregation for L_g but not for A.

In the 1955 News Letter we presented data showing preferential segregation for the knobbed chromosome 9 in heteromorphic bivalents

in plants both homozygous and heterozygous for abnormal 10. Additional data have since been obtained which are in agreement with this conclusion. It now appears, however, that preferential segregation for the knobbed 9 is higher in plants homozygous for abnormal 10 than in heterozygous plants. The following data have been obtained using the wd character which is always associated with a knobless 9 since it is due to a deficiency for the tip of 9S.

| | | | | |
|--------------------------------|---------------------------------|-------|-------|-------|
| N 10/N 10; K Wd/k wd | 1629 Wd: 1618 wd (control data) | | | |
| | Wd Wx | wd Wx | Wd wx | wd wx |
| abn 10/N 10; K Wd Wx/k wd wx | 3676 | 1504 | 2198 | 2546 |
| | (59.2% Wd and 52.2% Wx) | | | |
| abn 10/abn 10; K Wd Wx/k wd wx | 967 | 225 | 591 | 430 |
| | (69.8% Wd and 53.9% Wx) | | | |

An unusual situation was encountered when plants of abnormal 10/normal 10; K 8L j/k 8L J constitution were used as the egg parent in backcrosses. Since the knobbed chromosome 8 carried the j allele it was anticipated that preferential segregation would occur for the j allele which is situated in the distal portion of 8L not too far removed from the knob. The data are listed below:

| | | | | |
|-----------------------|------------|------------|------------|--------|
| <u>G J</u> | <u>g j</u> | <u>g J</u> | <u>G j</u> | |
| 1936 | 518 | 682 | 138 | = 3274 |
| 59.1% | 15.8% | 20.8% | 4.2% | |
| (63.3% G and 79.9% J) | | | | |

The high percentage of functioning megaspores apparently carrying the J allele was wholly unexpected and disturbing since the J allele was carried by the knobless chromosome 8. Indeed, the frequency of the j class should have been much higher than that of the J class. This finding, which was contrary to the data obtained with other heteromorphic chromosome pairs, could be explained if the abnormal 10 chromosome carried a dominant suppressor of j. Stocks carrying abnormal 10 are known in which the j phenotype is suppressed. Thus many plants of the J phenotype actually were homozygous for the j allele whose action was inhibited by a dominant suppressor of j in the distal portion of the long arm of abnormal 10. Approximately 70 percent of the functioning megaspores had abnormal 10 with the suppressor. Therefore 70 percent of the backcross progeny would be phenotypically J even if all chromosomes 8 in the basal megaspores possessed the j allele.

M. M. Rhoades
Ellen Dempsey