

$a_1 \text{ sh}/a_1 \text{ m}^{(r)} \text{ Sh}$ , (non-variegated  $\text{Sh}$  x variegated  $\text{Sh}$ ) variegated and non-variegated non-shrunken ( $\text{Sh}$ ), and non-variegated shrunken ( $\text{sh}$ ) kernels were selected, and plants obtained from these were selfed in order to test the presence of  $w_{13}^m$ .

Three sets of progeny (1, 2 and 3) of three crosses.

|                            | progeny of $w_{13}^m$ | absent | present |
|----------------------------|-----------------------|--------|---------|
| variegated $\text{Sh}$     | 1                     | 5      | 17      |
|                            | 2                     | 2      | 19      |
|                            | 3                     | 0      | 13      |
| non-variegated $\text{Sh}$ | 1                     | 21     | 0       |
|                            | 2                     | 22     | 0       |
|                            | 3                     | 14     | 0       |
| non-variegated $\text{sh}$ | 1                     | 8      | 8       |
|                            | 2                     | 4      | 19      |
|                            | 3                     | 6      | 14      |

The data indicate that  $\text{En}$  is part of or closely linked to  $w_{13}^m$ . Most of the variegated  $\text{Sh}$  progeny are associated with  $w_{13}^m$ ; some, however, are without  $w_{13}^m$ . This indicates that  $\text{En}$  is separable from  $w_{13}^m$ , except that the same result could be obtained from the mutation of  $w_{13}^m$  to  $w_{13}$  (green). Distribution of progeny types in the non-variegated  $\text{Sh}$  class supports the indication of a close relationship between  $w_{13}^m$  and  $\text{En}$ . If  $\text{En}$  were separable from  $w_{13}^m$ ,  $w_{13}^m$  would be expected to occur in a ratio reciprocal to that of the variegated  $\text{sh}$  class. None were found. Results obtained and listed under the heading non-variegated  $\text{sh}$ , show linkage of  $w_{13}^m$  with  $a_1 \text{ sh}$ . The non- $w_{13}^m$  progeny arise from crossovers between  $\text{sh}$  and  $w_{13}^m$  which is near  $lg_2$ .  $\text{En}$  is either part of the  $w_{13}^m$  complex or it is closely linked to  $w_{13}^m$ . This relationship is now being tested further.

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1. Linkage studies involving the  $a_2$ - $bt_1$  region of chromosome five.

For the past several years we have undertaken a rather intensive crossover study of the region from  $a_2$ - $bt_1$  in

chromosome five. These studies have involved the loci  $a_2$ ,  $vp_2$ ,  $bm_1$  and  $bt_1$ . Plants of the constitution  $\frac{a_2}{vp_2} \frac{+}{+} \frac{+}{+} \frac{+}{a_2}$  were crossed to  $\frac{A_2}{A_2} \frac{+}{+} \frac{bm_1}{bm_1} \frac{bt_1}{bt_1}$  plants to produce  $F_1$  seeds of the genotypes  $\frac{A_2}{+} \frac{bm_1}{+} \frac{bt_1}{a_2} \frac{vp_2}{+}$  and  $\frac{A_2}{+} \frac{bm_1}{+} \frac{bt_1}{+} \frac{+}{+}$ . Also, plants of the constitution  $\frac{A_2}{+} \frac{+}{+} \frac{+}{A_2} \frac{vp_2}{+}$  were crossed to  $\frac{a_2}{a_2} \frac{+}{+} \frac{bm_1}{bm_1} \frac{bt_1}{bt_1}$  plants to produce  $\frac{a_2}{+} \frac{bm_1}{+} \frac{bt_1}{A_2} \frac{vp_2}{+}$  and  $\frac{a_2}{+} \frac{bm_1}{+} \frac{bt_1}{+} \frac{+}{A_2}$   $F_1$  seeds. The  $F_1$  plants were used as females in an isolation plot in which the male parents were  $\frac{a_2}{a_2} \frac{+}{+} \frac{bm_1}{bm_1} \frac{bt_1}{bt_1}$ . These testcross ears were then classified for crossovers in the  $a_2$ - $bt_1$  region. The number of rows on each testcross ear was determined and multiplied by the number of seeds per row to give an estimate of the total seeds per ear. Then the number of crossover seeds on each ear was determined. These crossover seeds were saved for further testing. The crossover data from these testcross ears are given in Table 1.

Table 1  
Summary of crossover data for the  $a_2$ - $bt_1$  region.

| Genotype of $F_1$  | Crossover classes |                 | Totals  | % C. O. |
|--|-------------------|-----------------|---------|---------|
|  | $\frac{A_2}{+}$   | $\frac{a_2}{+}$ |         |         |
| $\frac{A_2}{a_2} \frac{+}{(+ \text{ or } vp_2)} \frac{bm_1}{+} \frac{bt_1}{+}$ | 5,700             | 5,417           | 269,518 | 4.12%   |
|  | $\frac{a_2}{+}$   | $\frac{A_2}{+}$ |         |         |
| $\frac{a_2}{A_2} \frac{+}{(+ \text{ or } vp_2)} \frac{bm_1}{+} \frac{bt_1}{+}$ | 9,401             | 7,911           | 330,136 | 5.24%   |
|  | 15,101            | 13,328          | 599,654 | 5.05%   |

There is a consistent deficiency in the  $\underline{bt}_1$  class in these data. This perhaps is the result of abortive development of  $\underline{bt}_1$  seeds or the tendency of  $\underline{bt}_1$  seeds to mold, thus hindering their color classification.

In order to determine the  $\underline{vp}_2$  and  $\underline{bm}_1$  constitution of the non-purple crossovers from the two classes of testcross ears, plants from the non-purple crossover seeds were grown in an isolated plot, detasseled, and open pollinated by plants known to be heterozygous for  $\underline{vp}_2$ . The results of these crosses are given in Tables 2, 3 and 4.

Table 2  
 $\underline{vp}_2$  and  $\underline{bm}_1$  constitutions of non-purple crossovers from crosses of  $\underline{a}_2 \underline{a}_2 \underline{bt}_1 \underline{bt}_1$   $\times$   $\underline{a}_2 \underline{a}_2 \underline{+} \underline{+}$   
 $\underline{a}_2 (\underline{+} \text{ or } \underline{vp}_2) \underline{+} \underline{+}$   
 $\underline{bm}_1 \underline{bm}_1 \underline{bt}_1 \underline{bt}_1$ .

|  | Genotypes of crossovers                                      |   |  |  | Totals |
|--|--|---|--|--|--------|
|  | $\underline{a}_2 \underline{+} \underline{bm}_1$<br>Region 1 | $\underline{a}_2 \underline{vp}_2 \underline{bm}_1$<br>Region 2 | $\underline{a}_2 \underline{vp}_2 \underline{+}$<br>Region 3 | $\underline{a}_2 \underline{+} \underline{+}^{**}$ |        |
| Observed numbers   | 787  | 77  | 5  | 8  | 877    |
| Corrected value*   | 355  | 77  | 5  | 0  | 437    |
| % Corrected Data   | 81.2   | 17.6  | 1.1  |  |        |
| Total % C. O. for regions 1, 2 and 3 = .0505 (Total C. O. $\underline{a}_2$ - $\underline{bt}_1$ from Table 1) $\times$ line 3 | 4.10   | 0.89  | 0.06   |  |        |

\*This correction is necessary since only  $\frac{1}{2}$  of the  $F_1$  plants carried  $\underline{vp}_2$ . Thus, calculations are made on basis of that half that came from heterozygous  $\underline{vp}_2$  plants.

\*\*A crossover class involving region 3 of non- $\underline{vp}_2$   $F_1$  plants.

Table 3  
 $\underline{vp}_2$  and  $\underline{bm}_1$  constitutions of non-purple  $\underline{a}_2 \underline{a}_2 + \underline{bt}_1$  cross-  
 overs from crosses of  $\frac{\underline{a}_2}{\underline{A}_2} \frac{+}{(+ \text{ or } \underline{vp}_2)} \frac{\underline{bm}_1}{+} \frac{\underline{bt}_1}{+} \times \frac{\underline{a}_2}{\underline{a}_2} \frac{\underline{a}_2}{+} \frac{+}{+}$

$\underline{bm}_1 \underline{bm}_1 \underline{bt}_1 \underline{bt}_1$ .

| Genotypes of crossovers  |  |                                   |  |        |
|--|--|-----------------------------------|--|--------|
|  | $\underline{a}_2 \underline{vp}_2 +$<br>Region 1 | $\underline{a}_2 + +$<br>Region 2 | $\underline{a}_2 + \underline{bm}_1$<br>Region 3 | Totals |
| Observed numbers   | 505  | 430                               | 15   | 950    |
| Corrected values*  | 505  | 156                               | 12   | 673    |
| % Corrected Data   | 75.0   | 23.2                              | 1.8  |        |
| Total % C. O. for<br>regions 1, 2 and 3<br>= .0505 (Total<br>C. O. $\underline{a}_2 - \underline{bt}_1$ from<br>Table 1) $\times$ line 3 | 3.79   | 1.17                              | 0.09   |        |

\*This correction is necessary since only  $\frac{1}{2}$  of the  $F_1$  plants carried  $\underline{vp}_2$ . Thus, calculations are made on basis of that half that came from heterozygous  $\underline{vp}_2$  plants.

Table 4  
 Totals for C. O. regions 1, 2 and 3 ( $\underline{a}_2$  (1)  $\underline{vp}_2$  (2)  $\underline{bm}_1$   
 (3)  $\underline{bt}_1$ ).

|  | C. O.<br>Region 1 | C. O.<br>Region 2 | C. O.<br>Region 3 | Total |
|--|-------------------|-------------------|-------------------|-------|
| Sum of corrected<br>values from tables<br>2 and 3  | 860               | 233               | 17                | 1,110 |
| %  | 77.5              | 21.0              | 1.5               |       |
| Total % C. O. for<br>regions 1, 2 and<br>3 = .0505 (Total<br>C. O. $\underline{a}_2 - \underline{bt}_1$ from<br>Table 1) $\times$ line 2 | 3.91              | 1.06              | 0.08              |       |

The data used in making these calculations are based on selected crossover seeds from the  $a_2$ - $bt_1$  region, a distance of 5 crossover units. They are, therefore, equivalent of testing 22,200 (20 x 1,110) unselected gametes from 2 four point test crosses, and indicate the following linkage map:  $a_2$  - 3.91 -  $vp_2$  - 1.06 -  $bm_1$  - 0.08 -  $bt_1$ .

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## 2. Genetic and biochemical studies of $cl_1$ and its modifiers.

In the Maize Genetics Cooperation News Letter of 1963 (37:74-76) the results of allele tests were reported that suggested the dominant  $Cl_M^2$ ,  $Cl_M^3$ , and  $Cl_M^4$  modifiers of the albino seedling phenotype of the white endosperm-albino seedling mutant  $cl_1$  were allelic. Since then more extensive data have been collected and the dominant modifier  $Cl_M^5$  which was found in our genetic stocks was also tested for allelism. The data reported in Table 1 lends further support to the conclusion that all known modifiers of  $cl_1$  are allelic. Such modifiers seem to be rather widespread in corn lines. The original  $Cl_M^2$  and  $Cl_M^3$  modifiers were found in the inbreds T1 and C106 and  $Cl_M^4$  in inbred C131A. In crosses to transfer  $cl_1$  into the inbreds M14 and W22 they also were found to carry modifiers of  $cl_1$ . These modifiers are being tested for allelism with the others. The inbreds OH43 and N25 seem to be devoid of  $cl_1$  modifiers as do some, if not all, lines of Tama flint.

The modifier locus has not been determined as yet. Early attempts to locate it were hampered by the presence of modifiers in the series of translocations which were being used as linkage testers. However, we now have a series of waxy chromosome-nine translocations converted to M14 and this series has been crossed to  $cl_1$  devoid of modifiers. If the M14 modifier turns out to be allelic to the other modifiers, it is hoped that analysis of  $F_2$  progeny of this series of translocation crosses will reveal the location of the modifier locus.

Table 1  
Summary of data from allele tests of  $Cl_M^2$ ,  $Cl_M^3$ ,  $Cl_M^4$  and  $Cl_M^5$

| F <sub>1</sub> Cross |        |          |          | # F <sub>2</sub> seedlings | # albino | Conclusions |          |          |        |   |         |
|----------------------|--------|----------|----------|----------------------------|----------|-------------|----------|----------|--------|---|---------|
| $cl_p$               | $cl_p$ | $Cl_M^4$ | $Cl_M^4$ | x                          | $cl_1$   | $cl_1$      | $Cl_M^3$ | $Cl_M^3$ | 6119   | 0 | Allelic |
| $cl_1$               | $cl_1$ | $Cl_M^3$ | $Cl_M^3$ | x                          | W7716    | W7716       | $Cl_M^5$ | $Cl_M^5$ | 2842   | 0 | Allelic |
| $cl_1$               | $cl_1$ | $Cl_M^3$ | $Cl_M^3$ | x                          | $Cl_1$   | $cl_1$      | $Cl_M^2$ | $Cl_M^2$ | 13,571 | 0 | Allelic |
| $Cl_1$               | $cl_1$ | $Cl_M^2$ | $Cl_M^2$ | x                          | $cl_p$   | $cl_p$      | $Cl_M^4$ | $Cl_M^4$ | 9045   | 0 | Allelic |
| $cl_p$               | $cl_p$ | $Cl_M^4$ | $Cl_M^4$ | x                          | W7716    | W7716       | $Cl_M^5$ | $Cl_M^5$ | 1810   | 0 | Allelic |
| $Cl_1$               | $cl_1$ | $Cl_M^2$ | $Cl_M^2$ | x                          | W7716    | W7716       | $Cl_M^5$ | $Cl_M^5$ | 1724   | 0 | Allelic |