

gametes was tested. The frequency of germinal changes to \underline{R}^{st} (light) in homozygous \underline{R}^{st} stocks was found to be only 0.3/1000, based on a population of 18,586 \underline{R}^{st} gametes.

The difference between the frequency of changes to \underline{R}^{st} (light) in \underline{R}^{st} heterozygotes with \underline{R}^R and \underline{r}^r and in \underline{R}^{st} homozygotes suggested that such changes are either 1) associated with heterozygosity, per se, at the \underline{R} locus, or 2) a product of crossing over between \underline{R}^{st} and a linked modifier carried on the \underline{R}^R and \underline{r}^r chromosomes.

A test was made using a proximal marker, golden (\underline{g}), and a distal marker, a terminal heterochromatic knob (\underline{K}), to test for the association of crossing over with changes of \underline{R}^{st} to \underline{R}^{st} (light). The following cross was made: $\underline{g} \underline{R}^G \underline{K}/\underline{G} \underline{R}^{st} \underline{k} \times \underline{g} \underline{r} \underline{k}$. \underline{R}^{st} (light) kernels were selected and planted; the resulting plants were scored for golden, and the ears were pollinated with \underline{rr} . \underline{K} was scored by making counts of the number of \underline{R}^{st} (light) and \underline{r} kernels on each ear to determine whether preferential segregation for \underline{R}^{st} (light) had occurred. The results from this test showed that changes to \underline{R}^{st} (light) were always associated with crossing over between \underline{R} and \underline{K} .

It is hypothesized that there is a locus about 5.7 crossover units distal to \underline{R} , the alleles of which modify the expression of \underline{R}^{st} . The modifier conditioning normal stippled expression was designated \underline{M}^{st} , and the one conditioning \underline{R}^{st} (light) expression was designated \underline{m}^{st} .

The \underline{R}^R and \underline{r}^r chromosomes in the first test carried \underline{m}^{st} , and the crosses made may now be diagrammed as follows: $\underline{R}^R \underline{m}^{st}/\underline{r}^r \underline{M}^{st} \times \underline{r}^r \underline{m}^{st}$. Crossing over produced an $\underline{R}^{st} \underline{m}^{st}$ chromosome which conditions \underline{R}^{st} (light). The complementary crossover class would be $\underline{R}^R \underline{M}^{st}$ in the $\underline{R}^R \underline{R}^{st}$ heterozygotes, and $\underline{r}^r \underline{M}^{st}$ in the $\underline{R}^{st} \underline{r}^r$ heterozygotes. Both of these complementary crossover classes have been identified, and they occur with the same frequency as \underline{R}^{st} (light).

The changes of \underline{R}^{st} to \underline{R}^{st} (light) in \underline{R}^{st} homozygotes cannot be ascribed to recombination between \underline{R}^{st} and a linked modifier. The few mutants obtained from these matings have been interpreted as mutations of \underline{M}^{st} to \underline{m}^{st} or transpositions of \underline{M}^{st} (see below).

R. B. Ashman

4. Transposability of \underline{M}^{st} , a modifier of stippled aleurone.

Numerous self-colored kernels were selected after the following cross: $\underline{R}^{st} \underline{r}^r \underline{g} \times \underline{r}^r \underline{R}^G \underline{g}$. These kernels were grown out to verify the presumed mutations of \underline{R}^{st} to self-color. The ears produced by the resulting plants were pollinated with $\underline{r}^r \underline{r}^r$. As observed in an earlier test, less than half of the phenotypically self-colored kernels gave self-colored (\underline{R}^{sc}) offspring. Fifty plants, in fact, grown from 64 self-colored kernels did not

give germinally transmissible \underline{R}^{sc} mutants, but segregated stippled and colorless kernels. Among these plants two were found which segregated $1/4 \underline{R}^{st}$, $1/4 \underline{R}^{st}$ (light), and $1/2 \underline{r}$, instead of the expected $1/2 \underline{R}^{st}$, and $1/2 \underline{r}$ kernels.

It has been shown that \underline{R}^{st} differs from \underline{R}^{st} (light) only in a modifier located about 5.7 crossover units distal to \underline{R} (see above). An explanation which satisfactorily accounts for the ratio observed on the ears from the two exceptional plants would assume that the linked modifier (\underline{M}^{st}) which conditions the \underline{R}^{st} phenotype is a transposable unit. On this basis it could be assumed that the \underline{R}^{st} (light) phenotype results from the absence of \underline{M}^{st} , and that in the two exceptional ears \underline{M}^{st} has shifted from its standard position, 5.7 crossover units distal to \underline{R} , to a new position which assort independently of \underline{R} . Verification of the transposition hypothesis requires progeny tests of the three classes of kernels on the ears from the two exceptional plants.

R. B. Ashman

5. Mutability of \underline{R}^{st} .

Tests were made of the mutability of \underline{R}^{st} and \underline{R}^{st} (light) in homozygous and in several heterozygous combinations.

\underline{R}^{st} and \underline{R}^{st} (light) in homozygotes were observed to mutate to self-color (\underline{R}^{sc}) at the respective rates of 17.0 and 19.9/10⁴ gametes tested. A total of 19,920 \underline{R}^{st} and 24,599 \underline{R}^{st} (light) gametes were scored. When \underline{R}^{st} and \underline{R}^{st} (light) were heterozygous with \underline{r}^r , they were observed to mutate to \underline{R}^{sc} at the respective rates of 4.9 and 4.3/10⁴ gametes tested. A total of 2,055 \underline{R}^{st} and 4,623 \underline{R}^{st} (light) gametes were scored from heterozygotes with \underline{r}^r . The basis for the difference in rate of mutation of \underline{R}^{st} and \underline{R}^{st} (light) to \underline{R}^{sc} in homozygotes and heterozygotes with \underline{r}^r is not yet known. Several somatic mutations of \underline{R}^{st} to \underline{R}^{sc} have been found, which indicates that mutations to \underline{R}^{sc} are probably not regularly associated with crossing over.

In \underline{R}^{st} (light) homozygotes, one mutation to colorless or near-colorless aleurone was found in 26,805 gametes tested. No mutations to colorless or near-colorless aleurone were found in \underline{R}^{st} homozygotes; 20,825 \underline{R}^{st} gametes were scored. Mutations to colorless or near-colorless aleurone with either red or green plant color were observed in both $\underline{R}^r \underline{R}^{st}$ and $\underline{R}^r \underline{R}^{st}$ (light) heterozygotes. It was assumed that mutants with green plant color came from stippled, and mutants with red plant color from \underline{R}^r . Based on this assumption, \underline{R}^{st} and \underline{R}^{st} (light) were observed to mutate to colorless or near-colorless aleurone in heterozygotes with \underline{R}^r at the respective rates of 5.4 and 4.2/10⁴ gametes tested. A total of 10,942 \underline{R}^{st} and 4,720 \underline{R}^{st} (light) gametes were scored. These data show that the frequency of mutations of \underline{R}^{st} and \underline{R}^{st} (light) to colorless or near-colorless is much greater when stippled is heterozygous with \underline{R}^r than when it is homozygous. The basis for this effect of homozygosity