

same chromosome, (ii) in this relation,  $R^{nj}$  determines the area competent to form pigment and (iii) formation of pigment within this area is dependent upon the action of  $R^{st}$ . (In ordinary  $R^{st}/R^{nj}$  heterozygotes, and also in  $R^{st}/R^{nj}/r\bar{g}$  trisomics, however, the full action of both alleles is expressed. That is, the crown region is solidly colored, and the remainder of the aleurone is spotted).

The new phenotype appeared on the ear of one plant among 138 offspring from an  $R^{st}/R^{nj}/r\bar{g}$  ♀ x  $R^f R^f$  ♂ mating. The remaining progeny were distributed among the six classes expected from such a trisomic ♀ x disomic ♂ cross. The plant in question was pollinated by  $r\bar{g}r\bar{g}$ . About 1/2 the resulting kernels were self-colored, as expected, and the rest (except 8) showed the new aleurone phenotype ( $R^{st:nj}$ ). Composition of the exceptional individual, therefore, was  $R^f/R^{st:nj}$ . Of 20 plants reared from  $R^{st:nj}/r\bar{g}$  seeds, and then pollinated by  $r\bar{g}r\bar{g}$ , 19 yielded  $R^{st:nj}$  and  $r\bar{g}$  kernels with about equal frequency, and 1 individual gave a 1:1 ratio for typical Navajo and colorless. Five of the 8 exceptional kernels on the original ear showed the Navajo phenotype, but the four plants obtained from these seeds bred as  $R^{st:nj}/r\bar{g}$  individuals. The other 3 exceptional kernels possessed comparatively few spots in the crown region. Progeny data suggest that they are probably the counterparts of "light stippled" which, as Ashman has shown, differs from stippled in a modifying factor normally situated about 6 crossover units distal to  $R$ , and widely distributed in non-stippled strains.

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## 2. Enhancement of $R^f$ action associated with reciprocal translocation T2-10a, involving a break in chromosome 10 proximal to the $R$ locus.

The following report is supplementary to that presented by Dr. Margaret Blackwood and the writer last year (MGC News Letter 33, pages 120-121, 1959).

1. As earlier observed, T2-10a  $R^f$  ( $TR^f$ ) gametes from  $TR^f/R^f$  plants have a lower pigment producing potential, on the average, than  $TR^f$  gametes from  $TR^f/r^f$  sibs. Testcross kernels from  $r\bar{g}r\bar{g}$  ♀ x  $TR^f/R^f$  matings nevertheless tend to give bimodal distributions for aleurone pigmentation. It has now been shown that the darker kernels from the latter mating, when subsequently grown out, yield a preponderance of semisterile, whereas the light kernels give a pronounced excess of fully fertile plants.

2. The effects of T2-10a on  $R^f$  action have been retested using the offspring from the mating  $R_4^B/r^f$  x  $TR^f/r^f$ . The  $R_4^B$  allele is a mutant from standard  $R^f$ , indistinguishable from the latter in aleurone pigment-producing action and in paramutability in heterozygotes with stippled. Employment of the  $R_4^B$  allele, carrying the green seedling marker, made it possible to identify definitively all eight classes of offspring from the  $R_4^B/r^f$  x  $TR^f/r^f$  cross, including the crossovers between T and the  $R$  locus. The results of testcrosses on  $r\bar{g}r\bar{g}$  ♀♀ of these 8 genotypes confirm the conclusions summarized in last year's News Letter. The points of particular interest are:

- $R^f$  pigment-producing action is enhanced when  $R^f$  is carried in coupling with T2-10a.
- Enhancement of pigment-producing action is retained for one generation at least after  $R^f$  is returned by crossing over from a T to a structurally normal chromosome.
- The pigment-producing action of  $R_4^B$  is not enhanced when in repulsion with T ( $TR^f/R_4^B$ ).
- The pigment-producing potential of  $TR^f$  gametes from  $TR^f/r^f$  plants is significantly higher than that of  $TR^f$  gametes from  $TR^f/R^f$  sibs. Likewise  $R^f$ , following return from a T chromosome to a structurally normal chromosome, has a higher pigment-producing potential in

$\underline{R}^f/\underline{r}^f$  than in  $\underline{R}^f/\underline{R}^f$  plants, at least in the generation immediately following that in which the crossovers occurred.

3. Additional tests show that the immediately resulting T2-10a  $\underline{R}^f/\underline{r}^f$  (crossover) offspring from  $\underline{T}^f/\underline{R}^f \times \underline{r}^f/\underline{r}^f$  matings, when testcrossed on  $\underline{r}^f/\underline{r}^f$  ♀♀, do not yield  $\underline{R}^f/\underline{r}^f$  kernels exhibiting enhanced aleurone pigmentation, in contrast to  $\underline{T}^f/\underline{r}^f$  plants from stock cultures in which T and  $\underline{R}^f$  have been in coupling for at least two generations. Whatever the basis of the action of the translocation on  $\underline{R}^f$  pigment-producing potential, therefore, there is a lag of at least one generation in expression of the phenomenon after the structural rearrangement is effected.

4. It was shown previously that  $\underline{R}^f$  carried by a T2-10a chromosome (stock culture) is relatively insensitive to paramutation in  $\underline{T}^f/\underline{R}^f$  heterozygotes. More recent experiments establish the additional fact that  $\underline{R}^f$  retains this insensitivity to paramutation in  $\underline{R}^f/\underline{R}^f$  individuals after return by crossing over from a T chromosome to a structurally normal chromosome, at least for one generation.

-- R. A. Brink

3. The effect on  $\underline{R}^f$  action of a reciprocal translocation (T9-10a) involving a break in chromosome 10 distal to the  $\underline{R}$  locus.

Several of the experiments made with T2-10a (and T4-10b) which involve chromosome 10 breaks proximal to the R locus (10L.53 and 10L.57) have recently been carried out with T9-10a also. The break in chromosome 10, according to Longley, is at 10L.92 in the latter case, and thus distal to the R locus (R is probably located at about .7). It is significant that the effects of T9-10a on  $\underline{R}^f$  action are closely parallel to those of T2-10a and T4-10b. In the T9-10a  $\underline{R}^f/\underline{r}^f$  (stock culture) combination,  $\underline{R}^f$ , for example, shows enhanced pigment-producing action, and also is relatively insensitive to paramutation in T9-10a  $\underline{R}^f/\underline{R}^f$  plants.

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4. The paramutagenic action of the marbled aleurone allele ( $\underline{R}^{mb}$ ).

Selection within the uniform W22 inbred line in which marbled was earlier incorporated yielded marbled sub-lines differing in paramutagenic competence. The capacity of  $\underline{R}^{mb}$  to alter standard  $\underline{R}^f$  in  $\underline{R}^f/\underline{R}^{mb}$  heterozygotes can be reduced by first passing the marbled allele through a heterozygote with stippled. Five independent self-colored mutants from marbled, on the other hand, retained the paramutagenicity of the parent  $\underline{R}^{mb}$  allele.

Paramutability of  $\underline{R}^f$  in heterozygotes with  $\underline{R}^{mb}$  was greatly reduced by placing  $\underline{R}^f$  in coupling with a large terminal heterochromatic knob. The return of  $\underline{R}^f$  from the knob-carrying chromosome to a normal chromosome, by crossing over, resulted in an increased sensitivity to paramutation in  $\underline{R}^f/\underline{R}^{mb}$  heterozygotes in the single case tested.

Attempts to change the amount of aleurone spotting in marbled plants by selection within the W22 inbred line resulted in the isolation of marbled families which differed not only in grade of marbling but also in rate of mutation to self-color. Marbled sub-lines which exhibited extensive aleurone pigmentation also showed high frequencies of germinally transmissible mutations to self-color. The