

1. Paramutation at the R locus in maize plants trisomic for chromosome 10.

A comparison was made of the aleurone phenotypes resulting from pollination of an $r\bar{e}r\bar{e}$ inbred strain (W23) with moderately inbred W22 sib plants of the following genotypes: $R^r r\bar{e}$ (control), $R^r R^{st}$ (disomic) and $R^r/R^{st}/r\bar{e}$ (trisomic). The object of the experiment was to test the hypothesis that paramutation of R^r to a weakly pigmenting allele, R^i , which was known from previous tests to occur in 100% of the cases in $R^r R^{st}$ plants, takes place at the zygotene stage of meiosis, when the R^r and R^{st} alleles are synapsed. The $r\bar{e}$ allele present in the $R^r r\bar{e}$ and $R^r/R^{st}/r\bar{e}$ male parents had earlier been shown to be non-paramutagenic. Assuming 2 by 2 pairing at zygotene at any given chromosome level (Newton and Darlington, 1929) only the R^r male gametes that carry R^r ex-conjugants from $R^r R^{st}$ zygotene pairings in $R^r/R^{st}/r\bar{e}$ trisomic plants should be paramutant, and the rest should be normal, if the hypothesis in question is valid. Not more than 50%, and perhaps as few as 33%, of the R^r gametes formed by $R^r/R^{st}/r\bar{e}$ trisomic plants should be paramutant on this basis. The average scores for aleurone pigmentation of the $R^r r\bar{e} r\bar{e}$ kernels, on an arbitrary scale of 0-40, for the three classes of matings was found to be as follows:

$r\bar{e}r\bar{e}\bar{e}$ ♀	x $R^r r\bar{e}$ ♂	39.23±0.16
"	x $R^r R^{st}$ (disomic) ♂	5.07±1.23
"	x $R^r/R^{st}/r\bar{e}$ (trisomic) ♂	6.37±1.13

Aside from a few seeds that could have resulted from pollen contamination, the $R^r r\bar{e} r\bar{e}$ kernels resulting from the application to $r\bar{e}r\bar{e}$ individuals of pollen from the trisomic $R^r/R^{st}/r\bar{e}$ plants, as well as from the disomic $R^r R^{st}$ individuals, were of the paramutant phenotype throughout. Thus the results do not support the hypothesis that R^r is changed to the paramutant form, R^i , in $R^r R^{st}$ plants, when the R^r and R^{st} alleles are conjugated at zygotene.

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2. "Enhancement" of R^r action associated with two reciprocal translocations involving breaks in chromosome 10 proximal to the R locus.

Evidence was obtained in 1957 indicating that the aleurone pigment-producing action of the standard R^r allele was significantly increased (from dark mottling to near-self-color, in single dose) if R^r was introduced into either the T2-10a or the T4-10b translocation. Both translocations involve breaks approximately 9 crossover units proximal to the R locus. Furthermore, it appeared from other tests that TR^r (read translocated R^r) was less paramutable in heterozygotes with the stippled allele (TR^r/R^{st}) than was R^r in ordinary $R^r R^{st}$ plants. More comprehensive experiments with

this material were carried out in 1958, the results of which may be summarized as follows:

(a) T2-10a \underline{R}^r and T4-10b \underline{R}^r are, in fact, significantly stronger in aleurone pigment-producing action than standard \underline{R}^r in a normal chromosome 10.

(b) On reincorporation into a normal chromosome 10 from a T chromosome, \underline{R}^r retains its enhanced pigment-producing action. This observation excludes an explanation of the phenomenon in terms of position effect of the conventional kind.

(c) Enhancement of \underline{R}^r action does not appear in the offspring of plants carrying a T chromosome bearing an \underline{r} (colorless aleurone) allele, with standard \underline{R}^r present in a normal chromosome 10 ($\underline{Tr}/\underline{R}^r$). Evidently the original change to enhanced \underline{R}^r action requires that \underline{R}^r be in coupling, not in repulsion, with T, in the translocation heterozygote.

(d) Testcrosses on \underline{rr} plants of $\underline{TR}^r/\underline{TR}^r$ homozygotes yield the same enhanced \underline{R}^r phenotype as results when pollen from $\underline{TR}^r/\underline{r}$ plants is used. Seemingly, "pairing stress" at meiosis is not a factor in the enhancement process.

(e) Partial reversion of the enhanced pigment-producing action of \underline{R}^r in a \underline{TR}^r chromosome toward the level of standard \underline{R}^r is found among the offspring of $\underline{TR}^r/\underline{R}^r$ plants.

(f) Paramutability of \underline{TR}^r in $\underline{TR}^r/\underline{R}^r$ heterozygotes (and also of \underline{R}^r extracted from a \underline{TR}^r chromosome) is markedly lower than that of standard \underline{R}^r in ordinary $\underline{R}^r/\underline{R}^r$ individuals.

(g) The partial reversion of enhanced \underline{R}^r toward standard \underline{R}^r , observed among the offspring of $\underline{TR}^r/\underline{R}^r$ plants, is paralleled by an increase in paramutability when an \underline{R}^r allele with this history is made heterozygous with stippled.

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3. Basis of the light stippled phenotype.

A few stippled aleurone kernels with a much reduced frequency of spotting were regularly observed in a series of matings of $\underline{R}^r/\underline{R}^r$ and $\underline{R}^r/\underline{r}$ with \underline{rgrg} . When such kernels were planted, and the resulting individuals were selfed, ears were formed that showed an \underline{rst} (light) phenotype. The frequency of such germinal changes to \underline{rst} (light) was found to be 58.7/1000 and 50.3/1000 \underline{R}^r gametes when tested in $\underline{R}^r/\underline{rst}$ and $\underline{R}^r/\underline{r}$ heterozygotes, respectively. A population of 13,084 \underline{R}^r