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 rfrgs inbred strain (W23) with moderately inbred W22 sib plants of the following genotypes: R<sup>fr</sup>/RS<sup>fr</sup> (control), R<sup>fr</sup>/R<sup>st</sup>/RS<sup>fr</sup> (disomic) and R<sup>fr</sup>/R<sup>st</sup>/R<sup>st</sup> (trisomic). The object of the experiment was to test the hypothesis that paramutation of R<sup>fr</sup> to a weakly pigmenting allele, R<sup>fr</sup>'<sup>l</sup>, which was known from previous tests to occur in 100% of the cases in R<sup>fr</sup>/R<sup>st</sup> plants, takes place at the zygote stage of meiosis, when the R<sup>fr</sup> and R<sup>st</sup> alleles are synapsed. The r<sup>fr</sup> allele present in the R<sup>fr</sup>/R<sup>st</sup> and R<sup>fr</sup>/R<sup>st</sup>/R<sup>st</sup> male parents had earlier been shown to be non-paramutagenic. Assuming 2 by 2 pairing at zygote at any given chromosome level (Newton and Darlington, 1929) only the R<sup>fr</sup> male gametes that carry R<sup>fr</sup> ex-conjugants from R<sup>fr</sup>-R<sup>st</sup> zygote pairing in R<sup>fr</sup>/R<sup>st</sup>/R<sup>st</sup> 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<sup>fr</sup> gametes formed by R<sup>fr</sup>/R<sup>st</sup>/R<sup>st</sup> trisomic plants should be paramutant on this basis. The average scores for aleurone pigmentation of the R<sup>fr</sup>/rfrgs kernels, on an arbitrary scale of 0-40, for the three classes of matings was found to be as follows:

\[
\begin{align*}
\text{rfrgs} \times \text{rfrgs} & : 39.23 \pm 0.16 \\
\text{"} \times \text{rfrgs} & : 5.07 \pm 0.23 \\
\text{"} \times \text{rfrst} & : 6.37 \pm 0.13
\end{align*}
\]

Aside from a few seeds that could have resulted from pollen contamination, the R<sup>fr</sup>/rfrgs kernels resulting from the application to rfrgs individuals of pollen from the trisomic R<sup>fr</sup>/R<sup>st</sup>/R<sup>st</sup> plants, as well as from the disomic R<sup>fr</sup>/R<sup>st</sup> individuals, were of the paramutant phenotype throughout. Thus the results do not support the hypothesis that R<sup>fr</sup> is changed to the paramutant form, R<sup>fr</sup>'<sup>l</sup>, in R<sup>fr</sup>-R<sup>st</sup> plants, when the R<sup>fr</sup> and R<sup>st</sup> alleles are conjugated at zygote.

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2. **"Enhancement" of R<sup>fr</sup> 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<sup>fr</sup> allele was significantly increased (from dark mottling to near-self-color, in single dose) if R<sup>fr</sup> was introduced into either the T2-10a or the Th-10b translocation. Both translocations involve breaks approximately 9 crossover units proximal to the R locus. Furthermore, it appeared from other tests that TH<sup>fr</sup> (read translocated R<sup>fr</sup>) was less paramutagenic in heterozygotes with the stippled allele (TH<sup>fr</sup>/R<sup>st</sup>) than was R<sup>fr</sup> in ordinary R<sup>fr</sup>-R<sup>st</sup> plants. More comprehensive experiments with
this material were carried out in 1958, the results of which may be summarized as follows:

(a) T2-10a $R^F$ and Th-10b $R^F$ are, in fact, significantly stronger in aleurone pigment-producing action than standard $R^F$ in a normal chromosome 10.

(b) On reincorporation into a normal chromosome 10 from a $T$ chromosome, $R^F$ 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 $R^F$ action does not appear in the offspring of plants carrying a $T$ chromosome bearing an $r$ (colorless aleurone) allele, with standard $R^F$ present in a normal chromosome 10 ($Tr/R^F$). Evidently, the original change to enhanced $R^F$ action requires that $R^F$ be in coupling, not in repulsion, with $T$, in the translocation heterozygote.

(d) Testcrosses on $rr$ plants of $TrF/TrF$ homozygotes yield the same enhanced $R^F$ phenotype as results when pollen from $Tr^F/r$ 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 $R^F$ in a $Tr^F$ chromosome toward the level of standard $R^F$ is found among the offspring of $Tr^F/R^F$ plants.

(f) Paramutability of $Tr^F$ in $Tr^F/Rst$ heterozygotes (and also of $R^F$ extracted from a $Tr^F$ chromosome) is markedly lower than that of standard $R^F$ in ordinary $Rst^F$ individuals.

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

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A few stippled aleurone kernels with a much reduced frequency of spotting were regularly observed in a series of matings of $R^F Rst$ and $Rst^F rSge$. When such kernels were planted, and the resulting individuals were selfed, ears were formed that showed an $Rst^-$ (light) phenotype. The frequency of such germinal changes to $Rst^-$ (light) was found to be $58.7/1000$ and $50.3/1000$ $Rst$ gametes when tested in $Rst Rst$ and $Rst^F Rst^F$ heterozygotes, respectively. A population of $13,088$ $Rst^-$