

Clowes (1967) has shown that in rapidly dividing cap initials of corn, G_1 is telescoped such that DNA synthesis can start as early as telophase. In our case the short cell cycle indicates that most cells of the root tip were rapidly dividing, leading to an overlap of the S period with the end of telophase, and thus, effectively eliminating G_1 .

Literature Cited

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1. Effects of ionizing irradiation on paramutation at the R locus in maize.
 - A. Effects of X-irradiation on pigmenting potential of standard R^r and paramutants from standard R^r

Standard R^rR^r seeds and pollen from R^rR^r plants were irradiated with 10,000r and 1,200r, respectively, following which testcrosses were made on r^gr^g plants. The data obtained by evaluating the one dose $R^rR^r r^gr^g$ aleurone of the testcross ears indicated that these treatments produced no effect on the pigmenting potential of R^r . On the other hand, the pigmenting potential of strongly repressed $R^{r''}$ alleles (passed through heterozygotes with the R^{st} allele for three generations) was partially restored, and to different levels, after X-irradiation of seeds (10,000r) and pollen (1,400r). Complete restoration, however, occurred only rarely. The frequencies of detectable changes were 21 per cent for treated seeds and 12 per cent for treated pollen. Other paramutant alleles at different levels of repression were tested by the same methods; all gave a response similar to that of the $R^{r''}$ alleles. Further tests showed that the X-ray-induced increases in pigmentation were heritable, and that all the paramutant alleles whose pigmenting ability had been increased by X-irradiation were still paramutable. The high frequency of X-ray-induced changes support the suggestion (Brink 1964) that there is a component at or near the R locus responsible for repression, and that this component, rather than the R structural gene itself, is involved in the response to irradiation. That the increases in paramutant pigmenting ability were to different levels also supports the postulate that more than one unit of the genetic component is involved in repression.

B. Effects of X-irradiation on the paramutability of standard \underline{R}^r

Homozygous $\underline{R}^r \underline{R}^r$ seeds and pollen from $\underline{R}^r \underline{R}^r$ homozygotes were X-irradiated with 10,000r and 1,200r, respectively, and then used as staminate parents in crosses with unirradiated $\underline{R}^{st} \underline{R}^{st}$ plants. The paramutability of the irradiated \underline{R}^r alleles was then measured by testcrossing the $\underline{R}^r \underline{R}^{st}$ heterozygotes on $\underline{r}^g \underline{r}^g$ plants. The \underline{R}^r alleles showed no detectable changes in paramutability after seed X-irradiation. On the other hand, the data showed a highly significant reduction in the paramutability of \underline{R}^r alleles in 28 per cent of the plants resulting from pollen treatments. This result is similar to that reported by Linden (1963) in a study with gamma rays. There was no case, however, in which paramutability was completely lost after X-irradiation. The frequency of changes induced was far higher than that characteristic of mutation in general, which suggests that irradiation leads to inactivation of the component conditioning paramutability rather than to an induced gene mutation at the \underline{R} locus. That paramutability was reduced but never lost suggests that more than one unit of the repressor component is responsible for paramutability, and that this component is closely associated with the \underline{R} structural gene.

C. Effects of X-irradiation on the paramutagenicity or \underline{R}^{st} , \underline{R}^{sc} , and $\underline{r}^r(I)$

The paramutagenic alleles tested were first crossed to standard $\underline{R} \underline{R}$ homozygotes used as females, and the heterozygotes thus obtained were then testcrossed on $\underline{r}^g \underline{r}^g$ plants. The pigmentation of the testcross paramutants was examined for changes in the paramutagenicity of the tested alleles. \underline{R}^{st} showed no detectable changes in paramutagenicity after X-irradiation of $\underline{R}^{st} \underline{R}^{st}$ seeds with 10,000r. Pollen from seven $\underline{R}^{st} \underline{R}^{st}$ plants was also irradiated. Forty-nine per cent of the treated pollen grains from one plant were significantly reduced in potential paramutagenic action. Nine \underline{R}^{sc} alleles (mutant derivatives of the \underline{R}^{st} allele having different levels of paramutagenicity) were generally found to be insensitive to X-irradiation at the seed stage (14,000r). The alleles derived from two of the 68 irradiated seeds were exceptional, however, and showed an increase in paramutagenicity. Two paramutagenic $\underline{r}^r(I)$ alleles (isolated from the testcross progeny of $\underline{R}^r \underline{R}^{st}$ heterozygotes) were also studied. Paramutation of \underline{R}^g was reduced in $\underline{R}^g / \underline{r}^r(I)_5$ heterozygotes when the strongly paramutagenic $\underline{r}^r(I)_5$ allele was X-irradiated at the seed stage with 14,000r. Such a reduction did not occur, however, in \underline{R}^g heterozygotes carrying the irradiated weakly paramutagenic $\underline{r}^r(I)_3$ allele. Sensitivity to X-irradiation and direction of induced changes in paramutagenicity appears to vary among different paramutagenic alleles.

These results are similar to Linden's findings, which showed that the paramutagenicity of \underline{R}^{st} and \underline{R}^{mb} was reduced in some cases and enhanced in others after gamma-irradiation. The new findings support the interpretation that a paramutagenic allele involves more than one component. The variability of the effects of irradiation on paramutagenicity of paramutagenic alleles suggests that the chromosomal component responsible for paramutagenic action is not equivalent to the component responsible for paramutability, which is consistently and uniformly affected by irradiation. Since the effect of irradiation on paramutagenicity can be either

reduction or enhancement, it is assumed that an inactivation mechanism is not the principal factor involved. It may be that the X-ray-induced changes in paramutagenic properties have the same characteristics as the changes produced by a number of other genetic factors known to influence the level of R action (e.g., Rst or r).

D. Effects of X- and gamma-irradiation on paramutation of standard R^r in heterozygotes with different paramutagenic alleles

Paramutation of R^r was significantly reduced in R^rRst heterozygotes after direct X-irradiation of R^rRst seeds with 8,000r and 10,000r. Aleurone pigmentation was examined in paramutants extracted from testcrosses of treated and control R^rRst heterozygotes made on rgrg plants. Thirty-three per cent of the testcross ears in the 8,000r treatment group and 16 per cent of the testcross ears in the 10,000r treatment group were darker than their respective control ears. Similar results were obtained in R^rR^{sc}₁₂₃ and R^g/r^r(I)₄ seed treatments, although in the latter case treatment induced only small changes. A further test showed that the Rst alleles of the very dark testcross ears derived from treated R^rRst seeds retained the same level of paramutagenic action as the control; and it has already been noted that R^r allele showed no detectable changes in paramutability when treated at the seed stage with 10,000r. Therefore, the dark R^r paramutants induced by treating R^rRst seeds were due either to derepression of the repressed R^r allele, which implies that paramutation has proceeded to a significant extent before seed germination, or to an impairment of the process of paramutation, which indicates that paramutation also occurs during plant development, or to both factors.

Irradiation of plants, rather than seeds or pollen, was another approach used in investigating whether paramutation occurs during vegetative growth. R^rRst plants responded to X-irradiation with different changes in R^r pigmentation action at different growth stages. The data demonstrated that the plants were relatively more sensitive to irradiation during the earlier stages of development than during the later stages close to, and during, meiosis. However, it was not determined whether paramutation proceeds evenly in the cells of the developing R^rRst tassel until the separation of R^r and Rst at meiosis, or whether paramutation proceeds more rapidly in the early stages of tassel development. Data obtained from gamma-irradiation of plants also indicated that R^rRst plants were more sensitive to treatment before meiosis than during meiosis.

This experiment also showed that plants heterozygous for R^r and different paramutagenic alleles, Rst, R^{sc}₁₃₂, and R^{sc}₁₁₀, responded to X-irradiation with bidirectional changes, that is to either an enhanced or a reduced level of paramutation. All three different heterozygotes showed induced repression in the level of R^r pigmentation ability when irradiation was applied between 19 and 21 days of plant growth. On the other hand, R^rRst plants treated at 33 days of growth and 41 days of growth produced R^r paramutants with increased pigmentation. That less pigmented and more highly pigmented R^r paramutants were produced by irradiating plants is additional proof that paramutation can occur during tassel development.

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