

This pigment-enhancing "side-effect" of stippled tends, of course, to vitiate the present test for a cytoplasmic component in the \underline{R} paramutation system. If a cytoplasmic element that depresses \underline{R} aleurone pigmentation is present in the \underline{r}^r segregates from $\underline{R}^{st}\underline{r}^r$ ♀♀, its effect is exceeded by the oppositely directed inter-kernel action of stippled.

R. A. Brink

2. Relative paramutagenic capacities of the paramutant forms of \underline{R}^E mutants derived from the standard \underline{R}^r allele.

It has been found that the standard \underline{R}^r allele and its \underline{R}^E mutant derivatives not only become heritably reduced in pigmenting action when passed through a heterozygote with the stippled (\underline{R}^{st}) allele but that they also acquire the capacity to promote a similar, though smaller, reduction in pigmenting action when combined with other paramutable genes (Brown and Brink, Genetics 45:1313-1316, 1960). The data reported here indicate that ten \underline{R}^E alleles independently derived by mutation from standard \underline{R}^r are indistinguishable from one another with regard to the level of paramutagenic activity acquired in heterozygotes with \underline{R}^{st} .

Pollen from each of twelve $\underline{R}^r\underline{R}^r$ plants was applied to silks of $\underline{R}^E\underline{R}^{st}$ plants representing the ten \underline{R}^E alleles. Progeny from a total of 111 successful pollinations of this type were grown in the following season, and two randomly selected $\underline{R}^r\underline{R}^E$ plants from each family were testcrossed to $\underline{r}^r\underline{r}^E$ pistillate parents. In this way, \underline{R}^E genes derived from nine to twelve $\underline{R}^E\underline{R}^{st}$ plants in the case of each \underline{R}^E allele were combined with standard \underline{R}^r genes from a common source. Differences in paramutagenic competence among the paramutant forms of the various \underline{R}^E alleles should be reflected in this test as differences in the level of pigmenting action of \underline{R}^r genes in the corresponding groups of $\underline{R}^r\underline{R}^E$ plants.

Forty-two $\underline{R}^r\underline{r}^E\underline{r}^E$ kernels from each $\underline{r}^E\underline{r}^E$ ♀ x $\underline{R}^r\underline{R}^E$ ♂ test mating were scored against a standard set of kernels defining seven pigmentation classes. The mean $\underline{R}^r\underline{r}^E\underline{r}^E$ scores from testcrosses of two $\underline{R}^r\underline{R}^E$ plants from each of the 111 $\underline{R}^E\underline{R}^{st}$ x $\underline{R}^r\underline{R}^r$ matings are shown in Table 1.

An analysis of variance performed on the data in Table 1 revealed no differences among the mean scores attributable to the \underline{R}^E alleles involved in the respective pedigrees ($F = .751$, $P > .1$). The overall mean $\underline{R}^r\underline{r}^E\underline{r}^E$ scores from testcrosses of $\underline{R}^r\underline{R}^E$ plants involving individual \underline{R}^E alleles are all within the range 5.21 to 5.34. These results show that the ten \underline{R}^E mutants from standard \underline{R}^r are indistinguishable from one another with regard to the level of paramutagenic action acquired in heterozygotes with \underline{R}^{st} .

Table 1

Mean scores for $\underline{R}^1\underline{R}^2\underline{r}^3$ kernels from testcrosses to $\underline{r}^4\underline{r}^5$ pistillate parents of $\underline{R}^1\underline{R}^2$ offspring of $\underline{R}^1\underline{R}^2$ ♀ x $\underline{R}^1\underline{R}^2$ ♂ matings. Each entry represents the pooled tests of two $\underline{R}^1\underline{R}^2$ plants.

$\underline{R}^1\underline{R}^2$ ♂ parent no.	\underline{R}^3 allele number									
	1	2	3	4	5	6	7	8	9	10
1	5.10	5.26	5.29	5.48	5.38	5.50	5.57	---	5.28	5.01
2	4.73	5.26	5.32	5.32	5.01	5.32	5.27	5.32	5.07	5.18
3	5.43	5.32	5.11	5.30	4.98	5.25	5.48	5.41	5.18	5.19
4	5.35	5.28	5.12	5.29	5.41	5.00	5.27	5.20	5.53	5.43
5	5.34	5.07	4.87	5.43	5.16	5.37	5.11	5.02	5.22	5.43
6	5.31	5.12	5.43	---	5.49	5.22	5.43	5.11	5.84	4.99
7	5.24	5.41	5.31	5.40	5.41	5.32	5.29	5.36	5.08	5.08
8	5.42	5.31	5.40	---	---	5.29	5.20	5.31	5.03	4.81
9	5.20	5.46	5.26	5.10	5.19	5.48	---	5.30	5.27	5.68
10	5.55	5.63	5.03	5.17	5.28	5.29	5.44	5.19	5.45	5.08
11	5.29	---	4.92	5.43	---	5.38	---	5.51	5.10	5.40
12	5.24	5.28	5.42	5.06	4.97	---	---	5.10	5.43	---
Mean	5.27	5.31	5.21	5.30	5.23	5.31	5.34	5.26	5.29	5.21

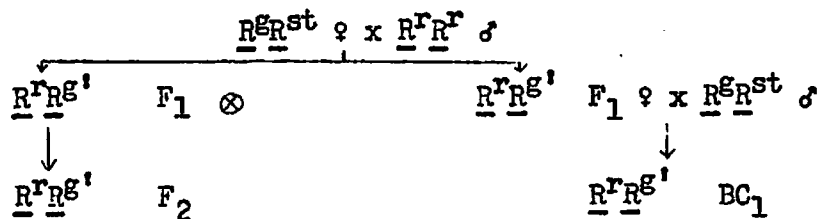
Previous studies (Brink, Brown, Kermicle and Weyers; Genetics 45:1297-1312, 1960) established that the pigmenting capacities of R^I and eight of its R^E mutant derivatives are reduced to a similar extent in heterozygotes with R^{st} . Testcrosses to $r^E r^E$ pistillate parents of $R^I R^{st}$ and $R^E R^{st}$ sib progeny from $R^I R^E \times R^{st} R^{st}$ matings have confirmed that the R^I and R^E alleles are equally sensitive to the paramutagenic stimulus of R^{st} when measured in terms of aleurone pigmenting action. The present test does not provide for an assessment of the relative paramutagenic potencies of paramutant R^I and paramutant R^E . The observation that ten R^E mutants of independent origin do not differ in level of paramutagenic action acquired in heterozygotes with R^{st} , however, agrees with the conclusion, implied by the results of tests of $R^I R^{st}$ and $R^E R^{st}$ plants, that the mutational events underlying the origin of the R^E alleles involved in these studies have not altered the chromosomal elements concerned with paramutation.

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3. Progressive secondary paramutation.

The reduction in the pigmenting action of paramutable R alleles which is induced by paramutant R^I genes is slight when compared with that incited by R^{st} (Brown and Brink, Genetics 45:1313-1316). Tests of $R^I R^E$ and $R^I R^E$ plants in F_1 , F_2 , and backcross 1 generations, which are described here, reveal that the extent of impairment in the pigmenting action of R^E or R^I is cumulative when the paramutant allele acts in two successive sporophytic generations.

$R^I R^E$ staminate testcross parents were produced according to the following mating plan:



Four lines, each containing a different R^E allele, were established from single $R^E R^{st}$? x $R^I R^I$? pollinations. A single $R^I R^E$? offspring from each $R^E R^{st}$ x $R^I R^I$ mating was selfed to produce $R^I R^E$? F_2 plants, and another was crossed to $R^E R^{st}$? to produce $R^I R^E$? backcross 1 (BC_1) plants. The two $R^E R^{st}$? plants in each pedigree were sibs grown from the same parental ear.