The dosage effect of $\underline{M}^{st}$, when the dosage of the stippled allele is held constant at one dose ($\underline{R}^{st}$ $\underline{r}^{r}$ $\underline{r}^{r}$ kernels), is shown by the columns headed 1-1, 1-2 and 1-3. With each of the stippled alleles an increase in $\underline{M}^{st}$ dosage was attended by an increase in frequency of pigmented spots. $\underline{R}^{st}$-4 showed a linear increase in frequency of pigmented spots with increasing dosage of $\underline{M}^{st}$, while $\underline{R}^{st}$-1 and $\underline{R}^{st}$-2 showed a non-linear response to dosage of $\underline{M}^{st}$.

These data show that the three stippled alleles have distinctive phenotypic effects, and may be further differentiated by characteristic dosage effects, and response to increasing dosages of the specific stippled modifier.

Table 1. Mean number of pigmented spots per kernel, in a defined area, for the endosperm genotypes involving combinations of stippled alleles and the stippled modifier.

Stippled allele	Dosage of stippled and $\underline{M}^{st}$ (1)						
	1-0	2-0	3-0	1-1	1-2	1-3	2-1
R^{st}-1	6.3 ±0.17	20.3 ±2.36	37.9 ±1.44	15.4 ±0.86	48.5 ±2.94	47.2 ±1.60	61.6 ±4.08
R^{st}-2	0.008 ±0.08	6.2 ±0.43	7.7 ±1.64	5.5(2) ±0.80	27.8 ±0.20	34.4(3) ±1.37	41.6 ±2.86
R^{st}-4	0.3 ±0.04	0.9 ±0.15	4.4 ±0.29	9.3 ±0.91	15.3 ±0.99	20.7 ±2.51	17.8 ±1.21

(1) The first digit represents the number of stippled alleles in the triploid endosperm, the alternative being $\underline{r}^{r}$. The second digit represents the number of $\underline{M}^{st}$ elements, the alternative being $\underline{m}^{st}$.

(2) Constitution of these kernels was $\underline{R}^{st}$-2$\underline{M}^{st}$-2/$\underline{r}^{r}$/$\underline{r}^{r}$.

(3) Constitution of these kernels was $\underline{R}^{st}$-2$\underline{M}^{st}$-2/$\underline{r}^{r}\underline{M}^{st}$-1/$\underline{r}^{r}\underline{M}^{st}$-1, all other combinations involved the indicated stippled alleles with $\underline{M}^{st}$-1 (extracted from $\underline{R}^{st}$-1$\underline{M}^{st}$-1).

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3. Paramutability of r^r mutants from standard R^r.

The standard $\underline{R}^{r}$ allele, which was first observed to undergo paramutation in heterozygotes with $\underline{R}^{st}$, mutates most frequently to either of two types of alleles which are complementary in phenotype, $\underline{R}^{g}$ (colored aleurone and colorless, or green, seedlings) and $\underline{r}^{r}$ (colorless aleurone and red seedlings) (Brink; Quart. Rev. Biol. 35:120-137, 1960). Eight $\underline{R}^{g}$ mutants from standard $\underline{R}^{r}$ were found to be indistinguishable from the parent allele in aleurone pigmenting action and in paramutability in heterozygotes with $\underline{R}^{st}$. (Brink et al., Gen. 45:1297-1312; 1960). The analogous comparisons between the standard $\underline{R}^{r}$ allele and its derived

r^r mutants require the measurement of pigmentation in vegetative seedling tissues and are technically more difficult to make. A further criterion for paramutation at the R locus was suggested by the discovery that R^r and R^g alleles which have undergone paramutation in heterozygotes with R^{st} have also become weakly paramutagenic. (Brown and Brink; Gen. 45:1313-1316, 1960). Consequently, nine r^r mutant genes were tested for paramutagenic action following heterozygosity with R^{st}.

The paramutagenic action of each of the various alleles was tested, after two generations of heterozygosity with R^{st}, in heterozygotes with $R^g{}_2$, a mutant from standard R^r. The following crosses were made:

(1)	r^rR^{st}	x	$R^g{}_2R^g{}_2$
(2)	R^rR^{st}	x	$R^g{}_2R^g{}_2$
(3)	R^rr^r	x	$R^g{}_2R^g{}_2$
(4)	r^gr^g	x	$r^{r'}R^g{}_2$
(5)	r^gr^g	x	$r^rR^g{}_2$
(6)	r^gr^g	x	$R^{r'}R^g{}_2$
(7)	r^gr^g	x	$R^rR^g{}_2$

$R^{r'}$ and $r^{r'}$ genes (extracted from heterozygotes with R^{st}) and the corresponding control R^r and r^r genes (with no history of heterozygosity with R^{st}) were combined with $R^g{}_2$ in crosses (1) to (3). Crosses (4) to (7) are testcrosses of the resulting $r^{r'}R^g{}_2$, $r^rR^g{}_2$, $R^{r'}R^g{}_2$, and $R^rR^g{}_2$ progeny. A comparison of the aleurone phenotypes of the $R^gr^gr^g$ kernels from crosses (4) and (5) constitutes a test for paramutagenic action of the $r^{r'}$ alleles. A similar comparison between crosses (6) and (7) provides a measure of the paramutagenic action of $R^{r'}$ under comparable conditions.

Fifty $R^gr^gr^g$ kernels from each testcross ear were scored against a standard set of kernels defining seven pigmentation classes ranging from colorless (class 1) to self colored (class 7). The data obtained are summarized in Table 1. Each mean score entered in the table is derived from testcrosses of ten plants.

The mean scores entered in the bottom line of the table show that the pigmenting capacity of $R^g{}_2$ has been weakened in heterozygotes with $R^{r'}$. The difference between the scores for the $R^gr^gr^g$ testcross kernels from the two classes of staminate parents is significant at the .01 level of probability. There is no indication of a similar loss in pigmenting action of R^g following association with any of the $r^{r'}$ alleles, as shown in the remainder of the table. The mean scores for the $R^gr^gr^g$ testcross kernels from the $r^{r'}R^g$ staminate parents are actually higher than the scores of those from r^rR^g staminate parents for seven of the nine mutants. The difference is statistically significant (at the .05 level) only in the case of r^r 40. The basis for this apparent enhancement of R^g action is not clear at the present time, but a similar effect has been noted incidentally in Rr plants in other pedigrees not involving the R^{st} allele. An evaluation of the significance of the effect must await further study.

Table 1. Mean aleurone color scores for $R^g r^g r^g$ kernels from the crosses $r^g r^g$♀ x $r^{r'} R^g$♂ and $r^g r^g$♀ x $r^r R^g$♂. The bottom line gives the corresponding scores from the crosses $r^g r^g$♀ x $R^{r'} R^g$♂ and $r^g r^g$♀ x $R^r R^g$♂.

Allele Tested	♂ Testcross parent $r^r R^g$ (or $R^r R^g$)	$r^{r'} R^g$ (or $R^{r'} R^g$)	P*
r^r 30	5.54	5.49	>.5
r^r 31	5.73	5.67	>.5
r^r 32	5.54	5.68	.1>P>.05
r^r 33	5.45	5.55	.3>P>.2
r^r 34	5.41	5.54	.1>P>.05
r^r 37	5.56	5.77	.1>P>.05
r^r 38	5.64	5.80	.1>P>.05
r^r 39	5.67	5.74	>.5
r^r 40	5.49	5.73	.02>P>.01
R^r	5.29	5.02	.01>P>.001

*P is the probability of the null hypothesis by the t test.

It is clear from the data summarized in Table 1 that the r^r mutants, while heterozygous with R^{st} for two generations, have not acquired the capacity to induce paramutation of R^g to a more weakly pigmenting form, whereas the parent R^r allele has.[2] The mutational events by which the r^r alleles arose have, in each case, altered the capacity of the R locus to undergo paramutation in heterozygotes with R^{st}. The r^r mutants differ from the R^g mutants, both derived from standard R^r, in this respect.

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