

that of the parent allele finds a parallel in McWhirter's earlier observation that many, but not all, self-colored mutants from ordinary \underline{R}^{st} are still strongly paramutagenic in $\underline{R}^r \underline{R}^{st}$ heterozygotes.

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2. A phenotypic comparison of three stippled alleles.

Three stippled alleles (\underline{R}^{st}) have been compared on the basis of aleurone-pigmenting effects, dosage effects, and interaction with the stippled modifier, \underline{M}^{st} .

The stippled alleles were:

\underline{R}^{st-1} -- from Wisconsin genetic stocks,

\underline{R}^{st-2} -- from Maize Co-op. stocks,

\underline{R}^{st-4} -- a "mutant" originally found heterozygous with \underline{R}^{sc80} (a self-coloured mutant) in an exceptional plant in the progeny derived by self-pollination of a plant of $\underline{R}^{sc80} \underline{R}^r$ genotype. There is circumstantial evidence for origin of \underline{R}^{st-4} by mutation of \underline{R}^{sc80} , but recurrence of the mutation was not obtained.

The stippled alleles were incorporated in W22 inbred background, and matings were made among stocks carrying \underline{R}^{st} , $\underline{R}^{st}\underline{M}^{st}$, $\underline{r}^r\underline{M}^{st}$ and \underline{r}^r , to obtain the endosperm genotypes required. The data reported are from the matings which enable an analysis of the dosage effect of the stippled alleles in absence of the modifier, and the dosage effect of the stippled modifier when stippled is held constant at 1 dose.

The number of pigmented spots, in an area enclosed by a 10 x 10 reticule grid at 30x magnification, on the abgerminal face of the kernel was measured. This area was approximately 6 mms². The mean scores reported are based on 125 kernels (25 from each of five ears) for each endosperm genotype with the exception of combinations 1-1 and 1-3 for \underline{R}^{st-4} . The latter means were based on 100 kernels (25 kernels from each of four ears).

The first three columns of the table show the aleurone-pigmenting effect and dosage response of the three stippled alleles, in the absence of the stippled modifier. The three stippled alleles differ markedly in the frequency of self-coloured spots at each of the dosages 1-0, 2-0 and 3-0. \underline{R}^{st-1} produced a linear increase in frequency of pigmented spots with increasing dosage. \underline{R}^{st-2} and \underline{R}^{st-4} were non-linear in dosage effect. $\underline{R}^{st-2} \underline{r}^r \underline{r}^r$ kernels (combination 1-0) were essentially colourless, only one of 125 kernels examined had a pigmented aleurone spot.

The interaction of \underline{M}^{st} with the stippled alleles is shown by the comparison of the columns headed 1-0 with 1-1, and 2-0 with 2-1 for each of the \underline{R}^{st} alleles. Substitution of \underline{M}^{st} for \underline{m}^{st} resulted in marked increases in the frequency of pigmented spots. Interaction with \underline{M}^{st} may be held to be an objective criterion for distinguishing stippled alleles, and all three alleles showed the interaction. The distinctive effects of each of the stippled alleles are maintained in these combinations, however, as is shown by cross comparison between \underline{R}^{st} alleles.

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
\underline{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
\underline{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
\underline{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 \underline{r}^r mutants from standard \underline{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 pigmentation 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