PARAMUTAGENIC ACTION OF PARAMUTANT R^r AND R^g ALLELES IN MAIZE[1]

DOUGLAS F. BROWN AND R. ALEXANDER BRINK

Department of Genetics, University of Wisconsin, Madison, Wisconsin

Received July 8, 1960

THE present article is concerned with an aspect of paramutation that was first noted during the study of the locus dependence of the paramutant R^r phenotype (BRINK, BROWN, KERMICLE and WEYERS 1960). It was observed that, in R^rR^{st} plants, the R^r allele not only paramutated to a weakly pigmenting form but also it, in turn, acquired the capacity to promote paramutation. The change in R expression which may be induced by such a paramutant allele ($R^{r'}$ or $R^{g'}$) is small relative to that regularly effected by R^{st} in R^rR^{st} individuals, and will be referred to as secondary paramutation.

MATERIALS AND METHODS

The reader is referred to a previous paper (BRINK, BROWN, KERMICLE and WEYERS 1960) for a description of the materials and methods used in this investigation.

Measurement of the paramutagenic action of a paramutant allele requires that the paramutant and nonparamutant factors be distinguishable among the offspring of a heterozygote by a criterion independent of paramutation. This requirement is met in $R^{r'}R^g$ and $R^rR^{g'}$ plants by the contrasting seedling color effects of the R^r (red) and R^g (green) alleles.

The data which provide evidence for secondary paramutation were obtained from the following four testcrosses:

(1) r^gr^g ♀ × $R^{r'}R^g$ ♂. The staminate parent in this cross was derived from the mating, R^rR^{st} × stock R^gr^g.

(2) r^gr^g ♀ × R^rR^g ♂. The staminate parent used in this control mating was derived from the cross, stock R^rR^r × stock R^gr^g.

These two testcrosses permit a test for paramutagenicity of $R^{r'}$. If secondary paramutation of R^g occurs in $R^{r'}R^g$ plants, then the $R^gr^gr^g$ kernels resulting from testcross (1) should be more lightly pigmented than those from testcross (2).

(3) r^gr^g ♀ × $R^{g'}R^r$ ♂. The staminate parent was the offspring of the mating, R^gR^{st} × stock R^rR^r.

(4) r^gr^g ♀ × stock R^rR^r ♂.

Matings (3) and (4) permit a test for the paramutagenicity of $R^{g'}$ in $R^rR^{g'}$ plants. In this case, secondary paramutation would be evidenced by a reduced

[1] Paper No. 794 from the Department of Genetics, College of Agriculture, University of Wisconsin.

Second Printing 1969 / University of Texas Printing Division, Austin

pigmentation of the $R^rr^gr^g$ kernels from testcross (3) as compared with the standard phenotype from testcross (4).

Testcrosses (1), (2) and (3) were carried out with each of eight R^g mutants from the R^r allele. Since these mutants and standard R^r previously were found to be alike in both aleurone pigmenting capacity and paramutagenicity (BRINK, BROWN, KERMICLE and WEYERS 1960), the results of these crosses represent, in effect, eight independent tests for paramutagenicity of $R^{r'}$ and $R^{g'}$.

EXPERIMENTAL RESULTS

The aleurone color scores of $R^gr^gr^g$ kernels from testcrosses (1) and (2) for each of the eight R^g mutants are summarized in Table 1. The first line of each pair of frequency distributions contains the aleurone color data for kernels carrying the R^g factor in question extracted from heterozygotes with standard R^r; the second line contains the comparable data for kernels carrying the corresponding R^g allele extracted from heterozygotes with paramutant $R^{r'}$. The difference between the values for each pair of frequency distributions constitutes a measure of secondary paramutation in the heterozygotes containing $R^{r'}$. The $R^gr^gr^g$ kernels from test-

TABLE 1

Frequency distributions and means of aleurone color scores for $R^gr^gr^g$ *kernels on testcross ears from* r^gr^g ♀ × $R^{r'}R^g$ ♂ *(ex.* $R^rR^{st} \times R^gr^g$*) matings in comparison with those of* $R^gr^gr^g$ *kernels from* r^gr^g ♀ × R^rR^g ♂ *(ex.* $R^rR^r \times R^gr^g$*) control matings*

Parentage of staminate testcross parent	No. of plants tested	Distribution of color scores for $R^gr^gr^g$ kernels only							Mean score for $R^gr^gr^g$ kernels
		1	2	3	4	5	6	7	
$R^rR^r \times R^gr^g_1$	4	..	..	..	5	84	77	2	5.45
$R^rR^{st} \times R^gr^g_1$	10	1	8	9	251	123	28	..	4.36
$R^rR^r \times R^gr^g_3$	4	..	..	..	..	51	116	1	5.70
$R^rR^{st} \times R^gr^g_3$	10	6	1	3	107	214	89	..	4.88
$R^rR^r \times R^gr^g_4$	4	..	..	..	4	72	91	1	5.53
$R^rR^{st} \times R^gr^g_4$	10	6	..	3	104	249	57	1	4.82
$R^rR^r \times R^gr^g_5$	4	..	..	..	27	99	42	..	5.09
$R^rR^{st} \times R^gr^g_5$	10	8	8	33	266	91	14	..	4.11
$R^rR^r \times R^gr^g_6$	4	..	..	..	6	81	81	..	5.45
$R^rR^{st} \times R^gr^g_6$	10	1	1	2	99	244	73	..	4.91
$R^rR^r \times R^gr^g_7$	4	..	..	..	..	80	87	1	5.53
$R^rR^{st} \times R^gr^g_7$	10	1	1	4	129	225	60	..	4.80
$R^rR^r \times R^gr^g_8$	4	..	..	..	..	56	108	4	5.69
$R^rR^{st} \times R^gr^g_8$	10	1	10	3	186	183	37	..	4.55
$R^rR^r \times R^g{}_{10}r^g$	4	..	..	..	5	95	68	..	5.38
$R^rR^{st} \times R^g{}_{10}r^g$	10	2	..	2	79	238	99	..	5.02

crosses of $R^{r'}R^{g}$ plants are significantly lower in aleurone color score than those from testcrosses of $R^{r}R^{g}$ plants in each case. The average difference between the mean scores of the two classes is 0.80 of a class interval.

Table 2 contains the aleurone color data for $R^{r}r^{g}r^{g}$ kernels derived from testcrosses (3) and (4). The first line of the table shows the distribution of scores characteristic of standard R^{r} in single dose. The remaining distributions in the table represent the aleurone phenotypes of kernels carrying R^{r} genes extracted from heterozygotes with the eight respective $R^{g'}$ alleles. The difference between the mean score for control $R^{r}r^{g}r^{g}$ kernels from $R^{r}R^{r}$ staminate parents and the mean score for the $R^{r}r^{g}r^{g}$ kernels from each of the $R^{r}R^{g'}$ staminate parents is a measure of secondary paramutation in the respective $R^{r}R^{g'}$ heterozygotes. These differences, given in the last column of the table, are statistically significant in each case.

A direct comparison of magnitude of change in pigmenting capacity of the R^{g} alleles induced by $R^{r'}$, as shown in Table 1, and that of R^{r} induced by the $R^{g'}$ alleles, as summarized in Table 2, cannot be made because the two sets of data were not acquired in the same year and slightly different sets of standards were used in scoring the testcross kernels. These facts probably account for the seemingly greater change in R expression due to secondary paramutation shown in Table 1 than in Table 2.

DISCUSSION

The above results demonstrate that a standard R^{r} or R^{g} allele becomes weakened in pigmenting action when passed through a heterozygote carrying a paramutant R factor. The change in pigmenting action of R^{g} induced by $R^{r'}$ is small when compared to that induced by R^{st}. This relation is illustrated by the data in Table 3.

TABLE 2

Frequency distributions and means of aleurone color scores for $R^{r}r^{g}r^{g}$ *kernels on testcross ears from* $r^{g}r^{g}$ ♀ × $R^{r}R^{g'}$ ♂ (*ex.* $R^{g}R^{st}$ × $R^{r}R^{r}$) *matings in comparison with those of* $R^{r}r^{g}r^{g}$ *kernels from the control matings* $r^{g}r^{g}$ ♀ × *standard* $R^{r}R^{r}$ ♂

Staminate testcross parent	No. of plants tested	Distribution of color scores for $R^{r}r^{g}r^{g}$ kernels only							Mean score for $R^{r}r^{g}r^{g}$ kernels	D†
		1	2	3	4	5	6	7		
$R^{r}R^{r}$	12	..	..	..	2	62	437	..	5.88	...
$R^{r}R^{g'}_{1}$	13	2	..	1	25	156	404	..	5.63	0.25*
$R^{r}R^{g'}_{3}$	15	2	3	4	60	240	321	..	5.38	0.50*
$R^{r}R^{g'}_{4}$	14	2	2	1	40	195	348	..	5.50	0.38*
$R^{r}R^{g'}_{5}$	15	..	5	9	33	203	380	..	5.50	0.38*
$R^{r}R^{g'}_{6}$	15	2	..	..	22	205	400	1	5.59	0.29*
$R^{r}R^{g'}_{7}$	15	3	..	..	26	187	413	1	5.60	0.28*
$R^{r}R^{g'}_{8}$	15	3	..	..	22	173	432	..	5.63	0.25*
$R^{r}R^{g'}_{10}$	13	1	1	4	23	145	372	..	5.61	0.27*

* Significant at the .05 level of probability by Tukey's test.

† D=mean score for control $R^{r}r^{g}r^{g}$ kernels from $R^{r}R^{r}$ staminate parents minus the mean score for $R^{r}r^{g}r^{g}$ kernels from $R^{r}R^{g'}$ staminate parents.

TABLE 3

Mean scores for $R^g r^g r^g$ *kernels only from testcrosses of* $R^g R^r$, $R^g R^{r'}$ *and* $R^g R^{st}$ *plants*

R^g allele (1)	Staminate testcross parent		
	$R^g R^r$ (2)	$R^g R^{r'}$ (3)	$R^g R^{st}$ (4)
R^g_1	5.45	4.36	2.20
R^g_3	5.70	4.88	2.58
R^g_4	5.53	4.82	3.07
R^g_5	5.09	4.11	1.82
R^g_6	5.45	4.91	2.66
R^g_7	5.53	4.80	2.46
R^g_8	5.69	4.55	2.20
R^g_{10}	5.38	5.02	2.52

In Table 3, the results of three kinds of testcrosses are summarized. The figures in columns 2 and 3 have been brought forward from Table 1, and are the average aleurone color scores for $R^g r^g r^g$ kernels from testcrosses of $R^g R^r$ and $R^g R^{r'}$ plants, respectively. The scores in column 2 represent the level of pigmenting action of the R^g alleles in standard form. Those in column 3 represent the level of pigmenting action of R^g alleles that have been opposed to $R^{r'}$ and, therefore, have undergone secondary paramutation. The figures in the last column were obtained from results of $R^g R^{st}$ testcrosses which have been presented in a previous paper (BRINK, BROWN, KERMICLE and WEYERS 1960). The scores in this column represent the level of expression of the R^g alleles which have undergone primary paramutation in heterozygotes with R^{st}. A comparison of the figures in columns 2, 3 and 4 of Table 3 for each R^g allele shows that $R^{r'}$ is only weakly paramutagenic relative to R^{st}.

It is equally clear from the values in Table 2 that the change in pigmenting action of R^r induced by the $R^{g'}$ alleles is also small relative to that induced by R^{st}.

SUMMARY

Data are presented which show that paramutant R^r and R^g alleles derived from heterozygotes containing the R^{st} factor are themselves weakly paramutagenic.

ACKNOWLEDGMENTS

The study was aided by grants from the Research Committee of the Graduate School, University of Wisconsin, of funds supplied by the Wisconsin Alumni Research Foundation, and by grants from the National Science Foundation.

LITERATURE CITED

BRINK, R. A., D. F. BROWN, J. KERMICLE, and W. H. WEYERS, 1960 Locus dependence of the paramutant *R* phenotype in maize. Genetics **45**: 1297–1312.