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THE FREQUENCY OF SOMATIC MUTATION IN VARIEGATED PERICARP OF MAIZE¹

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Some years ago (EMERSON 1922) the writer announced that in F_2 of certain crosses of variegated with colorless pericarp in maize the heterozygous individuals changed to self color more frequently than did the homozygous individuals of the same cultures.² No "explanation" of this phenomenon was then apparent, but later results, though still far from affording an adequate solution of the problem, have furnished at least a working hypothesis. The original unpublished paper, with minor modifications, is given below, under the heading, "Somatic mutations in heterozygous and in homozygous variegated pericarp."

In this earlier paper, variations in variegated pericarp were referred to as mutations, and it is still permissible so to designate them if the term mutation is used in a generic sense to mean any heritable change. It is even appropriate still to term these variations "gene mutations" for the genes certainly undergo changes. Since the advent of hypotheses of gene elements,³ (EYSTER 1924, 1925, 1928) it has become apparent that the gene changes in variegated pericarp may be due merely to a sorting out of genomeres and that these changes are, therefore, possibly of quite a different nature from "ordinary" gene mutations. The writer does not care at present either to commit himself to the idea of gene elements or to reject it. He, therefore, uses the term gene mutation in the sense indicated above with no implication concerning the nature of the changes undergone by the variegation gene.

SOMATIC MUTATIONS IN HETEROZYGOUS AND IN HOMOZYGOUS VARIEGATED PERICARP

In earlier papers (EMERSON 1914, 1917), it has been shown that in races of maize with variegated⁴ pericarp there occur somatic mutations from the

¹ Paper No. 160. Department of Plant Breeding, CORNELL UNIVERSITY, Ithaca, N. Y.

² This statement was based on data given in an unpublished paper presented before the Joint Genetics Section of the BOTANICAL SOCIETY OF AMERICA and the AMERICAN SOCIETY OF ZOOLOGISTS at the Toronto meeting, December 28, 1921.

³ Such a hypothesis was suggested by CORRENS (1919). A somewhat different one was proposed independently by E. G. ANDERSON and M. DEMEREC in an unpublished paper presented before the Joint Genetics Sections at Toronto in 1921. Later, EYSTER outlined in detail a similar hypothesis.

recessive variegated type to the dominant self colored type. The areas affected vary from a minute part of a single seed to an entire ear or to all the ears of a plant. Two types of somatic mutations of different appearance, but presumably of the same fundamental nature, have been recognized. One, the dark-crown type, is not inherited, while the other, the self colored type, has an even chance of being inherited.⁵ Non-mutated areas remain colorless. Fundamentally, therefore, variegated races differ from white ones in that they mutate somatically to the self colored condition with considerable frequency while white races, so far as observed, do not so mutate. Likewise light and dark variegated races differ from each other mainly in the frequency of their somatic mutation.

Since the gene for white does not mutate, either when duplex WW ,⁶ or simplex, WV , and since a single mutation affects only one of the duplex genes, VV , in homozygous variegated maize, it should follow, as pointed out in an earlier paper (EMERSON 1917), that somatic mutation will occur about twice as frequently in homozygous, VV , as in heterozygous, VW , material. This expectation is based on the assumption that the mutability of the variegation gene is uninfluenced by its allelomorph mate or by anything associated with it.

Variegated maize pericarp is unusually favorable for a comparison of the relative mutability of homozygous and of heterozygous material. The change to self color occurs with a frequency that makes quantitative studies readily possible. The self-color mutation is dominant to variegation. Obviously this is essential to the study, for otherwise the mutation could not be expressed in homozygous variegated material. The existence of a third allelomorph that is recessive to variegation, such as white, is equally essential for otherwise heterozygous variegation would be masked by the dominant self color associated with it. A further feature of the maize material, which, if not essential, is at least of great advantage, is the possibility of distinguishing homozygous from heterozygous variegated ears without the necessity of making progeny tests. The variegated strains used in these investigations have variegated cobs as well as variegated kernels. When such strains are crossed with ones having white kernels and

⁴ The writer has dealt only with the so-called "calico" variegation, not with a somewhat different type known as "mosaic" (HAYES 1917, EYSTER 1925).

⁵ The writer had assumed that the dark-crown type is epidermal and the self colored type sub-epidermal in origin, but RANDOLPH (1926) has shown this assumption to be incorrect particularly with respect to the coloration at the crown of the kernel.

⁶ The factor pair for pericarp color is usually designated by the symbols P p and the several allelomorphs by superscripts. For the sake of simplicity the latter alone are here used, P being omitted. For an account of the allelomorphs of the pericarp gene, see ANDERSON (1924).

red cobs, the F_1 ears have variegated kernels and red cobs. In F_2 there occur three types in the relation of one with white kernels and red cobs, two with variegated kernels and red cobs, and one with variegated kernels and variegated cobs. The variegated ears with red cobs are always heterozygous, VW , while those with variegated cobs are homozygous, VV , for pericarp color.

The procedure suggested by the considerations noted above was followed in the tests to be reported here. Strains of maize with variegated pericarp and cobs were crossed with red cobbled whites and the F_1 plants were self-pollinated. The variegated ears of each F_2 progeny were first separated into two lots, one with self red and the other with variegated cobs. Each lot was then classified into color grades from very light variegation, grade 1, in which most kernels are white, only a few showing narrow red stripes, to very dark variegation, grade 7, in which most kernels show numerous fine red stripes. Next, each ear was examined separately, the approximate total number of kernels noted, and the numbers of self colored and partly self colored kernels determined. In these determinations, narrow red stripes were disregarded, no kernel being classed as partly self colored unless it had a broad self colored stripe involving perhaps one tenth of the area of the kernel. Each group of self colored kernels was noted separately and the number of kernels in it recorded. The same procedure was followed in noting dark-crown variations except that no account was taken of changes affecting less than an entire kernel.⁷

In all, fourteen F_2 progenies with 570 ears and approximately 240,000 kernels were examined. The number of groups of self colored and partly self colored kernels of homozygous, VV , and of heterozygous, VW , ears are recorded in table 1. The data are expressed as numbers of groups (mutations) per 1000 kernels and are so arranged that class centers for number of kernels per group are doubled for each succeeding class. The first class includes all kernels from about one tenth to almost entirely self colored.

It is clear from the data given in table 1, that, contrary to expectation, heterozygous variegated pericarp, VW , instead of mutating about one half as frequently as homozygous, VV , material, actually mutated more frequently. This is particularly noticeable for mutations affecting a single kernel or less. On the whole the single variegation gene of heterozygous ears mutated 1.42 times as frequently as the two variegated genes of homozygous ears.

⁷ For making most of these counts, the writer is indebted to M. DEMEREC and FRED DENNIS.

TABLE 1
Number of self-color mutations per 1000 kernels in homozygous and in heterozygous variegated ears.

GENOTYPE	CLASS CENTERS FOR NUMBER OF KERNELS AFFECTED											TOTAL
	1/2	1	2	4	8	16	32	64	128	256	512	
VV	17.16	3.93	1.23	.543	.095	.027	.014	..	.014	..	.014	23.03
VW	24.13	5.95	1.97	.501	.085	.036	.006	.006	.018	.024	.012	32.74
Ratio VW:VV	1.41	1.51	1.60	.92	.89	1.33	.43	..	1.29	..	.86	1.42

TABLE 2
Number of dark-crown mutations per 1000 kernels in homozygous and in heterozygous variegated ears.

GENOTYPE	CLASS CENTERS FOR NUMBER OF KERNELS AFFECTED											TOTAL
	1	2	4	8	16	32	64	128	256	512		
VV	3.85	.86	.543	.162	.095	.014	.014	.014	.014	.014	..	5.57
VW	4.78	1.11	.851	.296	.163	.066	.006	.018	.012	.012	.054	7.36
Ratio VW:VV	1.24	1.29	1.57	1.83	1.72	4.71	.43	1.29	.86	1.32

Data obtained from counts of dark-crown kernels of the same F_2 progenies are given in table 2.

Mutations resulting in dark-crown kernels occurred on the whole 1.32 times as frequently in heterozygous as in homozygous material, the difference being practically the same as was found for self-color mutations. There seems, therefore, no escape from the conclusion that the single variegation gene of VW material had a mutability of about 2.7 times that of either one of the two variegation genes of VV material.

The differences noted above are even more strikingly shown when light variegated strains alone are considered. Of the fourteen F_2 progenies from which the records given in tables 1 and 2 were obtained, five came from crosses of red cobbed whites with light variegated types of maize. They included 259 ears and approximately 114,000 kernels. The data from these progenies are given in table 3.

In these light variegated strains, as seen from table 3, self-colored mutations occurred about 3 times and dark-crown mutations 2.3 times as frequently in heterozygous as in homozygous ears, an average of 2.64 times as frequently in the one as in the other lot. This, the writer is inclined to believe, can mean nothing other than that the single variegation gene of VW ears had a mutability of more than five times that of either one of the two variegation genes in VV ears.

In the nine F_2 progenies from crosses of dark variegated strains with red cobbed whites, the number of somatic mutations of both the self-colored and the dark-crown types together was 1.1 times as great in heterozygous as in homozygous ears. Even here the mutability of the one V gene of VW ears must, it would seem, have been at least twice as great as that of either one of the two V genes in VV ears.

So far no account has been taken of the somatic mutations that occur so late in development that they result merely in narrow streaks of red. The relatively great frequency of occurrence of these fine red stripes makes it difficult if not impossible to count them. (See ANDERSON and EYSTER 1928) They were, however, evaluated fairly accurately as noted earlier in this account, by classifying the F_2 ears into color grades from very light, grade 1, to very dark, grade 7, the several grades being dependent largely on the relative number of fine red stripes on the seeds. A total of 368 ears, one ear per plant, from seven of the F_2 progenies, were thus graded. A summary of the data is given in table 4.

The mean color grade of the heterozygous ears was 1.27 grade higher than that of the homozygous ears, a difference of over twelve times its probable error. Calculated by PEARSON'S (1908) formula for comparing

TABLE 3
Number of self-color and dark-crown mutations per 1000 kernels in homozygous and in heterozygous light variegated types of maize.

GENOTYPE	CLASS CENTERS FOR NUMBER OF KERNELS AFFECTED										TOTAL				
	1/2	1	2	4	8	16	32	64	128	256		512			
SELF-COLOR MUTATIONS															
VV	7.65	1.06	.287	.086029	9.11
VW	21.31	4.78	.629	.390	.063	.038013	27.24
Ratio VW:VV	2.79	4.51	2.19	4.53	2.99
DARK-CROWN MUTATIONS															
VV	..	1.67	.316	.201	2.19
VW	..	3.22	.893	.578	.176	.038	.050	..	.025	.013025	5.02
Ratio VW:VV	..	1.93	2.83	2.88	2.29

two independent distributions, $\chi^2=67.59$. Such a value of χ^2 , where $n'=7$, leaves no doubt that the two distributions in question are significantly different.⁸ It follows, therefore, that the difference in frequency of somatic mutation between *VV* and *VW* material is much the same when determined by color grades based on fine red stripes as when determined from the number of groups of self colored and dark-crown kernels.

TABLE 4

Number of ears of various color grades in homozygous and in heterozygous variegated maize.

GENOTYPE	VARIATION GRADES							TOTAL	MEAN GRADE
	1	2	3	4	5	6	7		
<i>VV</i>	7	37	19	24	17	4	..	108	3.18
<i>VW</i>	..	29	48	39	73	64	7	260	4.45
Difference	1.27
Ratio <i>VW</i> : <i>VV</i>	1.40

What appears to be behavior similar to that noted above for maize was reported by CORRENS (1903) for *Mirabilis*. Pink, yellow, and pale yellow flowered races of *Mirabilis* were crossed with what was at the time regarded as a white flowered race. The F_1 plants had strongly variegated flowers, about one third of them showing some wholly self colored flowers and a few having entire branches with such flowers. Later (CORRENS 1904) it was observed that the supposedly white flowered race used in these crosses produced a few flowers with minute red streaks. Evidently it was an extremely light variegated type. No variegated flowers were observed in any of the pink or yellow races with which it was crossed nor were any such seen in the progenies of intercrosses between these pink and yellow races. CORRENS interpreted these results as due to the interaction of factors brought into the cross from the two parents, factors that were wholly latent in the pink and yellow races and almost wholly so in the so-called white race. It appears, therefore, that the mutability of the gene for

⁸ One is perhaps not warranted in using the probable error as calculated by the usual formula $0.6745s/\sqrt{n}$ from arrays so unlike a normal frequency distribution as these are. Pearson's

formula, $\chi^2 = S_1 \left\{ \frac{NN' \left\{ \frac{f_p}{N} - \frac{f_p'}{N'} \right\}^2}{f_p + f_p'} \right\}$, has been used in place of or together with the formula

for the probable error of the mean in determining the probable significance of differences between the frequency distributions reported in this paper.

variegated flowers in *Mirabilis* is increased in crosses with non-variegated races much as is the gene for variegated pericarp in maize.

It seems unlikely that the behavior noted in maize can be explained by the assumption of an interaction of independently inherited modifying factors furnished by the two parents. If the mutability of the variegation gene is influenced in any such way, it should be possible to find crosses that would not produce the effects so far observed. To explain thus the behavior noted in maize, the postulated modifying factor must be the allelomorph of the variegation gene or some factor or factors linked with it. It must be remembered in this connection that in maize the comparison was made between homozygous and heterozygous ears of the same F_2 progenies grown from self pollinated F_1 heterozygotes—a circumstance that would afford abundant opportunity for recombinations of independently inherited modifying factors.

DIFFERENTIAL EFFECTS OF VARIOUS WHITE RACES ON THE MUTABILITY OF THE VARIEGATION GENE IN CROSSES

The suggestion offered in the last paragraph of the earlier paper, as quoted above, that, if the mutability of the variegation gene is influenced by factors carried by the white parent of heterozygous ears, it should be possible to find white strains which would have no such effect in crosses, has been tested in later studies.

In 1923 several white races of maize were crossed with pollen of three individuals of a culture of variegated maize. The white races were selected from diverse types, such as dent, flint, flour, and sweet varieties or crosses. The three plants, from which pollen was used in the crosses, were homozygous for variegation, VV , but were F_2 's of a cross between a very light variegated type and a dark variegated type. In order to be sure that the pollen used on the several white races was as uniform as possible, one day's production of pollen from each variegated plant was divided and applied at once to the silks of the several white races. Pollen of these three variegated plants was used also on other variegated cultures, which were segregating, producing white, homozygous variegated and heterozygous variegated ears. Finally, each of the three pollen parents of these crosses was selfed.

F_1 progenies of these crosses and progenies from the self pollinations were grown in 1924 and duplicate cultures of some of them in 1927.

Since the earlier work had indicated that differences in frequency of mutation could be determined with fair accuracy by grading the ears into classes from very light variegated, grade 1, or no variegation, grade 0, to very dark variegated, grade 7, and since this method is much less labori-

ous than the counting of self colored kernels (compare tables 1 and 4), the grading method alone was used in the later work. Extreme accuracy is not claimed for this method. In fact, it is likely that most any sample of ears would be graded somewhat differently at different times. To test this the writer reclassified three lots of ears one month after they had been graded the first time, and without referring to the earlier records. The results are given in table 5.

TABLE 5
Comparison of independent classifications of identical lots of variegated ears.

CULTURE	CLASSIFICATION	DISTRIBUTION OF EARS OF THE SEVERAL VARIEGATION GRADES							TOTAL NUMBER OF EARS	MEAN GRADE
		1	2	3	4	5	6	7		
1	First			21	18	10	8	3	60	4.23
	Second			21	20	8	8	3	60	4.20
2	First				8	9	19	13	49	5.76
	Second				9	8	23	9	49	5.65
3	First	106	35	4					145	1.30
	Second	97	44	4					145	1.36

As might well be expected there was less close agreement between the grading of lots grown and classified in 1924 and the duplicate lots grown in 1927. Since, fortunately, the 1924 lots had been preserved and were re-examined immediately after the 1927 lots had been classified, relatively little of the observed difference between the two lots as finally recorded is to be ascribed to personal errors in grading. The differences, as will be shown later, were not greater than might be expected from small random samples of the same lots.

The results obtained from the 1924 cultures, together with those from such duplicates as were grown in 1927, are given in table 6.

Although there are differences in the frequency distribution of variegation grades between duplicate cultures grown in 1924 and 1927, on the whole the differences are surprisingly small. In no case is the difference in mean grade between the two lots as much as three times its probable error, and in only one case does it approach closely that magnitude. And in no case were the frequency distributions significantly different as determined by PEARSON'S (1908) formula. Duplicate cultures may, therefore, be combined and treated as one lot.

A strikingly different situation from the above is presented by the fre-

TABLE 6

Number of individuals of various grades of variegation in F₁ of crosses of variegated maize with white races from diverse sources.

PARENT CULTURE NUMBERS		F ₁ PROGENY									
VARIEGATED	WHITE	YEAR GROWN	VARIATION GRADES							TOTAL	MEAN GRADE
			1	2	3	4	5	6	7		
13358-3	..	1924	17	15	2	17	24			32	1.47
	13363-2	1924		1	7	40	36			44	4.45
		1927		1	7	40	36	1		85	4.34
	13369-3	1924			2	18	5			25	4.12
		1927			4	62	6			72	4.03
	13371-1	1924			3	23	2			28	3.96
	13372-1	1924			12	16	3	1		32	3.78
13367-1	1924		1		11	46			58	3.76	
13366-1 -5	1924				10	23	1		34	3.74	
	1924				16	32	2		50	3.72	
13358-5	..	1924	7	6	6	1		2	22	2.41	
	13363-3	1924									
		1927			7	7	7			21	4.00
	13369-4	1924	2	5	8	3	5	4	7	34	4.29
		1927	6	8	11	7	5	9	6	52	3.92
	13371-2	1924		5	11	21	12	3	52	3.94	
	13372-2	1924		3	10		11		24	3.79	
13367-2	1924		3	10	14	5	1	33	3.73		
13366-2	1924		5	16	13	8		42	3.57		
13358-6	..	1924			7	3	1	5	16	4.25	
	13363-1	1924					7	7	11	27	5.30
		1927					8	9	19	49	5.76
	13372-5	1924		1	2	6	13	2	24	4.54	
13367-4	1924		1	4	10	19	3	38	4.58		

quency distributions and mean grades of the several F₁ progenies of either variegated parent crossed with the different white types. For ready comparison the mean grades of all crosses are summarized in table 7.

TABLE 7
Mean grades of variegation in F₁ of crosses between homozygous variegated plants and different white races of maize.

SEED PARENTS	VARIEGATED POLLIN PARENTS		
	13358-3	13358-5	13358-6
13358-3 -5 -6	1.47	2.34	4.28
13363-2 -3 -1	4.38	4.17	5.59
13369-3 -4	4.05	4.07	
13371-1 -2	3.96	3.74	
13372-1 -2 -5	3.78	3.79	4.54
13367-1 -2 -4	3.76	3.73	4.58
13366-1 -5 -2	3.74 3.72	3.57	

Plant 3 (culture 13358) produced a very light variegated ear, grade 1, and its progeny from selfing had a mean grade of 1.47. When this plant was crossed onto a plant of culture 13363, the mean grade of its F₁ progeny was 4.38. Crosses with other white varieties gave lower F₁ grades, the differences in some cases, however, not being statistically significant. The lowest F₁ grades of the crosses with pure colorless varieties was 3.74 and 3.72 for two crosses on plants of culture 13366. The difference in mean grade between the crosses with 13363 and 13366 is 0.65, which is more than ten times the probable error of the difference. The frequency distributions

of these two cultures are so unlike that χ^2 calculated from them has a value of 72.6.

Similar differences are shown between the F_1 grades of crosses of the other two variegated plants, individuals 5 and 6 of culture 13358. Plant 5 had an ear of slightly darker variegation, grade 2, than plant 3 and its progeny from selfing was of correspondingly higher grade, 2.34. Plant 6 was medium variegated, grade 5, and its progeny from selfing had a mean grade of 4.28. The progeny grades of crosses of these two variegated plants with the several white varieties show the same trend as exhibited by the crosses of variegated plant 3. Thus the progeny of a cross of plant 5 on 13363 had a mean grade of 4.17 while a cross of plant 5 on 13366 produced a progeny of mean grade 3.57. These facts strengthen materially the conclusion that different colorless varieties influence differently the mutability of the variegation gene in crosses.

In addition to the crosses with white varieties of diverse types discussed above, the same three variegated plants of culture 13358 were crossed on seven plants grown from seed of a self pollinated variegated plant, which was heterozygous for variegation because of an earlier cross with a red cobbled white. The selfed ear from which these seven plants were grown had a red cob and was light variegated, grade 2. None of the seven plants used as seed parents of the crosses with the three homozygous variegated plants of culture 13358 was selfed so that what their progenies would have been is unknown. The grade of variegation of each of the seven crossed ears, however, was noted, and these grades are given in table 8, together with the detailed results of the crosses.

Before a discussion of these results is given, the origin of the stock, culture 13360, in which the seven crossed ears were produced may well be noted. This stock came from a long line of pedigree breeding tracing back in some ancestral lines for 18 generations of cross and self pollinations. No less than three distinct variegated strains and 15 white strains were combined in its ancestry. In the near ancestry of 13360 there were two generations from selfing of homozygous plants all of low grade variegation, as follows. Culture 9318 had a mean grade of 2.0. From a selfed ear of grade 1 of this lot, there was grown culture 10057, the mean grade of which was 1.0. A selfed ear of this lot of grade 0 (one on which no grain with any red stripe could be found) produced culture 11311 with a mean grade of 0.82. An ear of grade 1 of this lot pollinated by a homozygous red cobbled white of complex ancestry produced culture 12152 with a mean variegation grade of 4.25. A selfed ear of grade 2 of this lot produced culture 13360. Two of the seven ears of 13360 that were crossed by one or other

of the three variegated plants of 13358 were homozygous red cobbed whites, one was a homozygous variegated cobbed variegate, and four were heterozygous red cobbed variegates.

The F_1 progenies of these seven crosses are given in table 8, together

TABLE 8

Number of individuals of various grades of variegation in F_1 of crosses of homozygous variegated plants with the progeny of a heterozygous variegated plant.

POLLEN PARENT CULTURE NUMBER	SEED PARENT			F ₁ PROGENY											TOTAL	MEAN GRADE
	CULTURE NUMBER	GENO- TYPE	GRADE	GENO- TYPE	YEAR GROWN	VARIATION GRADE										
						0	1	2	3	4	5	6	7			
13358-3	Selfed	VV	1	VV	1924		17	15							32	1.47
	13360-8	WW	0	VW	1924		7	17	18	8					50	2.54
					1927		17	20	36	10				83	2.47	
	-3	VW	1	VW VV	1924	1	6	30	1	1					39	1.87
					1924	1	33	5	1	1				41	1.22	
	-4	VW	1	VW	1924	1	31	14		1					47	1.34
1927						32	31	3					66	1.56		
			VV	1924	1	49	1							51	1.00	
				1927		74	4	1						79	1.08	
13358-5	Selfed	VV	2	VV	1924		7	6	6	1		2		22	2.41	
					1927		33	25	23	7	5	3		96	2.32	
	13360-10	WW	0	VW	1924	1		5	12	8	9	1		36	3.58	
	-7	VW	3	VW	1924		4	4	6	12	1	2		29	3.28	
					1927		11	7	7	13	3		4	45	3.13	
			VV	1924	1	2	4	8	3	1			19	2.68		
				1927		15	10	6	3	4	3	1	42	2.62		
-5	VV	1	VV	1924	2	13	13	3		1			32	1.66		
13358-6	Selfed	VV	5	VV	1924				7	3	1	5		16	4.25	
					1927			1	3	5	4	3		16	4.31	
	13360-13	VW	3	VW	1924	1	1		5	17	5	5		34	4.09	
					1927	2	1	9	8	19	6	11	8	64	4.23	
			VV	1924		6	6	6	7	5	1		31	3.06		
				1927		4	18	11	7	11	8		59	3.46		

with the grades of the progenies of the selfed pollen parents of the crosses.

Here, again, there are no statistically significant differences in mean grade between the duplicate cultures grown in 1924 and 1927. The mean grades of all these progenies, with duplicate cultures combined, are summarized in table 9.

TABLE 9

Mean grades of variegation in F₁ of crosses between homozygous variegated plants and the progeny of a heterozygous variegated plant.

CULTURE NUMBER	SEED PARENTS			VARIEGATED POLLEN PARENTS		
	GRADE	GENOTYPE	♀ GAMETE	13358-3	13358-5	13358-6
13358-3	1	VV	V	1.47		
-5	2	VV	V		2.34	
-6	5	VV	V			4.28
13360-8	0	WW	W	2.50		
-10	0	WW	W		3.58	
-5	1	VV	V		1.66	
-3	1	VW	W V	1.87 1.22		
-4	1	VW	W V	1.47 1.05		
-7	3	VW	W V		3.19 2.64	
-13	3	VW	W V			r. 18 3.32

The two red cobbled white plants, 8 and 10, of culture 13360 when crossed by homozygous variegated plants gave progenies with a higher mean grade of variegation than did the self pollinated pollen parents of these crosses. But the mean grades of these crosses were materially lower than crosses of the same pollen parents on any of the white races as recorded in tables 6 and 7. It is perhaps a plausible suggestion that the very low grade variegation of the near ancestors of these two whites had in some way lessened their ability to increase the mutability of the variegation gene of the low grade pollen parents.

A single homozygous very light variegated, grade 1, plant 5, of culture 13360, crossed by plant 5 of culture 13358 produced an F₁ with a mean grade of variegation of 1.66. The pollen parent of this cross had a varie-

gation grade of 2 and its progeny from selfing a mean grade of 2.34. Evidently this very low grade seed parent was able to reduce the grade of variegation of the pollen parent.

Two heterozygous (red cobbed) variegated plants, 3 and 4, of culture 13360 crossed by plant 3 of culture 13358 gave progenies that were not far different in grade from the progeny of the selfed pollen parent. The fact that these two heterozygous variegated plants had red cobs made it possible to separate their F_1 progenies into two lots, one with red cobs and the other with variegated cobs. The variegated cobbed lots must have carried the variegation genes of the heterozygous seed parents and have been homozygous variegated, VV . Likewise the red cobbed lots must have carried the white genes of the heterozygous seed parents and therefore must themselves have been heterozygous, VW . The two heterozygous seed parents had very light variegated ears, grade 1, and the pollen parent also a light variegated ear, grade 1. The progeny of the selfed pollen parent had a mean grade of 1.47. The mean grades of the homozygous ears (variegated cobs) of the F_1 progenies were 1.22 and 1.05. Apparently the very low grade variegation genes of the seed parents, or something carried in the same chromosome with them, reduced, or certainly did not increase, the mutability of the variegation gene of the pollen parent.

The heterozygous ears (red cobbed) of these same F_1 cultures had mean grades of 1.87 and 1.47 respectively. The first of these mean grades is significantly higher than that of the selfed progeny of the pollen parent, 1.47; the second is identical with it. These heterozygous progenies are to be regarded as quite the equivalent of F_1 progenies of pure white races crossed by variegated plants since pure white races could have been readily established from the seed parents had they been selfed. Evidently, therefore, potential white types have been found which do not increase the grade of variegation in crosses above that of the variegated parent.

Another heterozygous variegated ear of culture 13360, individual 7, was crossed by plant 5 of culture 13358. In this cross the mean grade of the homozygous ears was somewhat, though not significantly, higher than that of the pollen parent's selfed progeny. Here the grade of the ears of the seed parent was 3. The heterozygous ears of this cross had a mean grade of 3.19 which is significantly higher than that of the pollen parent's selfed progeny, 2.34.

Finally, a heterozygous plant, 13, of culture 13360, with an ear of grade 3, crossed by plant 6 of culture 13358, gave an F_1 progeny the homozygous variegated ears of which were of significantly lower grade, 3.32, than those of the pollen parent's selfed progeny, 4.28. The heterozygous

ears of the same F_1 culture were of slightly, though not significantly, lower grade, 4.18, than that of the pollen parent's selfed progeny. Here again is involved a potential white strain which did not raise the grade of variegation of a cross above that of the variegated parent.

It must be remembered in this connection, that the assumption on which this study was based is that a homozygous variegated ear, being duplex for the variegation gene, VV , should have a much higher grade of variegation than one heterozygous for the same gene and therefore simplex for variegation, VW . From this standpoint, no white race, or potential white race, has been found that does not increase materially the grade of variegation in crosses, over that expected.

RECIPROCAL CROSSES OF VARIEGATED AND OF VARIEGATED AND WHITE PARENTS

The writer is quite unable—perhaps from lack of sufficiently keen imagination—to see how the mere fact of heterozygosity could account for the results here reported. Without the disturbing effects of other genes, heterozygotes normally exhibit complete dominance of one allelomorph over the other, or various degrees of partial dominance, or even no dominance, resulting in an almost exactly intermediate condition. Heterozygotes exhibiting characters unlike those of either parent or parental characters in an intensified form, so far as they have been carefully analyzed, have been shown to have received from one or both parents modifying or complementary genes which were responsible for the unexpected results. Variegation, however, though a wide-spread phenomenon, at least in the plant kingdom, may well be unlike “ordinary” characters, as indeed the gene-element hypothesis would have us believe.

It is conceivable that an effect ascribed to heterozygosity might be due to a peculiar reaction of chromosomes or genes of the sperm with the strange cytoplasm of the egg. It should be mentioned in this connection that culture 13360, which gave such strikingly different results from those obtained from various white strains crossed by the same variegated plants, was closely related to culture 13358 which furnished the pollen parents of all these crosses. As has been noted, culture 13360 was an F_2 of a cross of a red cobbled white with a plant of an inbred strain of very low grade variegation, 11311-5. Culture 13358 was an F_2 of a cross of the same low grade variegated plant, 11311-5, with a plant of an inbred strain of high grade variegation. It might be argued, therefore, that the cytoplasm of culture 13360 was not very different from that to which the chromosomes of culture 13358 were accustomed.

Reciprocal crosses should throw some light on such a problem as this. Detailed records of grades of variegation of reciprocal crosses are given in table 10.

TABLE 10
Number of individuals of various grades of variegation in F₁ of reciprocal crosses.

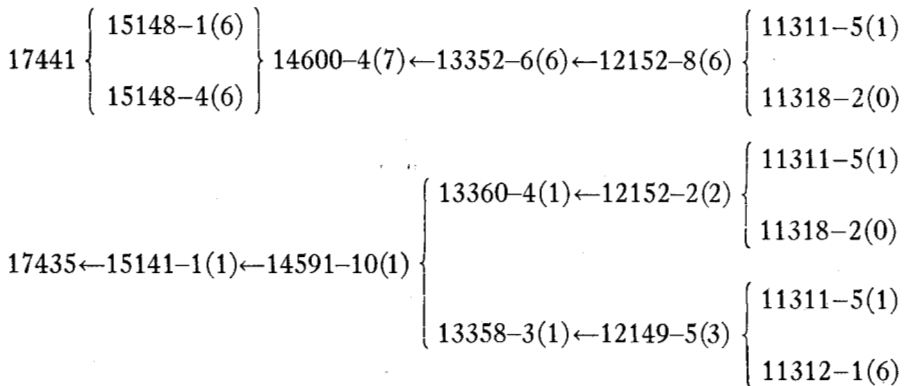
SEED PARENT		POLLEN PARENT				F ₁ PROGENY						MEAN GRADE	
CULTURE NUMBER	GENO-TYPE	GRADE	CULTURE NUMBER	GENO-TYPE	GRADE	VARIEGATION GRADES							TOTAL
						1	2	3	4	5	6		
11311-5	VV	1	11312-1	VV	6		15	9	7	5	2	38	3.21
11312-1	VV	6	11311-6	VV	1		10	12	7	5	1	35	3.29
17434-15	WW	0	17435-1	VV	1	1	21	42	16			80	2.91
17435-1	VV	1	17434-15	WW	0		7	17	6			30	2.97
17435-1	VV	1	17441-2	VV	6		6	14	25	13	2	60	3.85
17441-2	VV	6	17435-1	VV	1		2	13	47	20	2	84	4.08
17435-5	VV	1	17441-7	VV	6	1	6	10	9	5		31	3.35
17441-7	VV	6	17435-5	VV	1		7	15	5	7		34	3.35
17820-2	VV	1	17826-3	WW	0		1	2	31	6	1	41	4.10
17826-3	WW	0	17820-2	VV	1				36	7		43	4.16

Of the five pairs of reciprocal crosses, records of which are given in table 10, there is no appreciable difference between the two members of any pair either in distribution of grades or in mean grades. Of the first pair, culture 11312 is represented by plant 1 in both the direct and the reciprocal crosses, but culture 11311 is represented by plant 5 in one cross and plant 6 in the other. In all other cases the same individuals are involved in the reciprocal crosses. Culture 11311 came from two generations of selfing and selection for low grade variegation and its mean grade was 0.82. Culture 11312 came from four generations of selfing and selection for high grade variegation and its mean grade was 4.52. The two cultures were relatively unrelated, having only five common ancestors in sixteen generations, the nearest common ancestor being ten generations removed.

The parents of the next pair recorded in table 10 were, so far as known, quite unrelated. Culture 17435 traces back five generations to culture 11311, while culture 17434 was obtained from Dr. LINDSTROM of Ames, Iowa. The plant of the latter culture used in the crosses was a heterozygous

red cobbled white from a cross of a red cobbled white with a variegated strain, out-crossed with a white cobbled white.

The next two pairs of reciprocal crosses shown in table 10 involved culture 17435, used in the above cross, and culture 17441. Both were homozygous variegated and closely related to each other and to the parents of the first pair of reciprocals of table 10. One of the lines, however, had been selected for high grade and the other for low grade variegation, as indicated by the grade numbers in parentheses after the culture numbers in the pedigree chart below.



Culture 17441 had a mean grade of variegation of 5.75 and culture 17435 a mean grade of 1.00. Although both cultures were of so nearly the same ancestry, they differed markedly, not only in variegation grade, but in other respects, the plants of culture 17441 having only single stalks with one ear, while those of culture 17435 were tillered and had from three to five ears per plant.

The last pair of reciprocals compared in table 10 involve quite unrelated stocks. Culture 17820 was the progeny of 17435-1 of the pedigree chart given above. Its mean grade of variegation was 1.09. Culture 17826 was a red cobbled white strain which had been inbred by selfing for seven generations.

The results given in table 10, involving unrelated cultures as well as somewhat closely related ones, and including reciprocal crosses between homozygous variegates of very different grade as well as between variegates and whites, indicate clearly that reciprocal crosses are practically identical with respect to grades of variegation. This would seem to indicate that the reaction of sperm chromosomes to unaccustomed cytoplasm is not a factor of importance in influencing the mutability of the variegation gene in crosses.

THE HYPOTHESIS OF MODIFYING GENES

In the writer's opinion the most plausible interpretation of the results reported in this paper is that a gene, or perhaps more than one, at a locus other than that of the variegation gene and its allelomorphs but in the same chromosome, influences the mutability of the variegation gene, *V*. Such a modifying gene, if any exists, can not have its locus in a non-homologous chromosome, for then the chances for reassortment between chromosomes is such that in an F_2 culture the heterozygous ears, *VW*, should not have a higher grade of variegation than the homozygous ones, *VV*, as in fact they do have (table 4).

If an allelomorph of the variegation gene, such as *W-W*, white cobbed white, or *W-R*, red cobbed white, is itself responsible in crosses for the increase in intensity of variegation over that of the variegated parent, the change in the effect of this white gene from association with a low grade variegation gene, as in culture 13360, discussed above, must, it would seem, be ascribed to a direct contamination of one allelomorph by another. This is, perhaps, not beyond the bounds of possibility if the variegation gene is not a simple unit but rather composed of distinct gene elements, which might conceivably be transferred from one allelomorph to the other at synapsis. But the writer is wholly unable to devise a consistent working hypothesis to account for his results on any such assumption.

On the assumption that there exists a gene, or perhaps more than one, linked with the variegation gene and capable of modifying its mutability, results such as those derived from culture 13360 are readily interpreted on the basis of ordinary crossing over. This hypothesis of modifying genes is, at the present stage of our knowledge, not without value, for it should be possible, unless such genes are too numerous, to demonstrate its correctness or incorrectness. This the writer is, of course, attempting to do by introducing into certain variegated stocks other well known genes of the linkage group to which the variegation gene and its allelomorphs belong. That other genes modify the behavior of a mutable gene in *Drosophila virilis* has been demonstrated by DEMEREC (1928).

It is difficult for the writer to think of variegation in terms of dominance and recessiveness of variegation genes of high or low grade. His conception of the difference between low grade and high grade variegation is merely that, in the one case, mutations from white to red occur less frequently than in the other. Or, if the hypothesis of gene elements is preferred, it is a matter of the relative rapidity of the sorting out of gene elements, dependent in turn probably on the particular combination of gene

elements originally present. It is doubtless conceivable, though in the writer's opinion hardly probable, that the presence in a somatic cell of a frequently changing (high grade variegation) gene could activate its less frequently changing (low grade) allelomorph, for, in that case, one must suppose also that a white gene, though mutating rarely if at all, can none the less activate its low grade variegation mate. If, however, rate of mutation of the gene, or of sorting out of its elements, is influenced by a distinct gene which can be carried in a non-variegated race, this gene of a white race might be at least partially dominant over its allelomorph from a low grade variegation stock and thereby raise the variegation grade in crosses of low grade variegation with white.

The data in table 10 may have some bearing on the question of dominance either of the variegation gene itself or of an associated gene that influences the rate of change of the variegation gene. Unfortunately none of the individual plants that were used in the reciprocal crosses reported in table 10 was selfed, so that what its progeny would have been can not be known. But the mean grades of the cultures in which these plants occurred afford some basis of comparison. The fact that the parents of the progenies concerned were from stocks that had been selfed for from two to four generations should make the results more trustworthy than they would otherwise be. The relevant data are given in table 11.

TABLE 11

Comparison of mean grades of variegation of parents and their F_1 progeny in crosses between homozygous variegated plants.

CULTURES	GRADES OF PARENT PLANTS	MEAN GRADES OF PROGENY		
		Observed	Average	Difference
11311	1	0.82	2.67	0.58
11312	6	4.52		
11311-5×11312-1	1×6	3.21	3.25	
11312-1×11311-6	6×1	3.29		
17435-1×17441-2	1×6	3.85	3.96	0.59
17441-2×17435-1	6×1	4.08		
17435	1	1.00	3.37	
17441	6	5.75		
17435-5×17441-7	1×6	3.35	3.35	
17441-7×17435-5	6×1	3.35		

In one of the comparisons of table 11, the F_1 ears had a mean grade of variegation almost exactly the same as the average of the mean grades of the parent cultures. In the other two comparisons, the mean grades of the progenies were somewhat, probably significantly, higher than the averages of the mean grades of the parent cultures. Since, however, one pair of parent cultures, 17435 and 17441, is involved in two of the comparisons, and since the two pairs of F_1 progenies of crosses of different individuals of these two parent cultures differ as greatly from one another as either one does from the average of the parent cultures, the data give little support to the assumption that either a high grade or a low grade variegation gene is even partially dominant to the other. If there is any tendency toward dominance, it is the higher grade variegation which shows it. This is not in agreement with EYSTER'S (1928) proposed explanation to account for increased variability of the variegation gene in crosses with white.

Speculation as to how the two variegation genes act to produce the intermediate grade observed in F_1 of crosses of high grade with low grade stocks would be useless if it were not possible to undertake an investigation of the problem.

The observed results should be produced if each allelomorph influences its mate directly so that the two become approximately equal in mutability. A more plausible suggestion is that the postulated modifying genes interact to induce an approximately equal mutability of the two variegation genes intermediate between their original variabilities. If so, however, each of the two variegation genes must presumably return to its original state later when removed from the influence of its unlike mate or of the modifying factor associated with its mate, for there is marked segregation in grade of variegation in F_2 of crosses of low grade with high grade stocks. Now that the writer has found in maize collected in the Andes Mountains of South America what he had looked for in vain for many years in North America, a homozygous variegated race with red cobs, it should be possible to identify in F_2 and later generations of crosses of unlike variegated races the particular variegation genes present in any individual, just as it has been possible in the past to do this in crosses of variegated with red cobbed white races. But such a study must await the synthesis of a stock that combines with variegated pericarp and dominant red cob the closely linked recessive tassel seed 2.

There is the further possibility that the same intermediate grade of variegation in F_1 and similar segregation in F_2 of crosses of low grade by high grade variegated races might result if the low grade gene and its high

grade mate maintain their original variabilities uninfluenced by their respective allelomorphs or by any modifying genes associated with them. Thus, in a cross combining a grade 1 gene with a grade 6 one, $V_1 V_6$, if each gene mutates, or its elements assort, at its original rate, the resulting grade of variegation should be intermediate between the grades of the parent stocks, $V_1 V_1$ and $V_6 V_6$.

Certain data presented in one of the writer's earlier papers (EMERSON 1917), were interpreted as indicating that, in a cross of unlike variegated races, the two variegation genes retain their characteristic mutability. A cross of a very light variegated strain with a medium dark variegated one produced F_1 ears which were recorded as medium variegated. Thirty of these F_1 ears were pollinated by pure white races. From variegated kernels of these ears, 582 plants were grown. Their ears were divided on the basis of intensity of variegation into two approximately equal lots recorded as medium variegated and light variegated. From the same thirty parent ears, there were planted all the kernels that were self colored or partly (more than one tenth) self colored, and these produced 165 plants. The variegated ears of these plants were classified by the same standards used in classifying the ears from variegated kernels. The results are given in table 12.

TABLE 12

Percentage of self colored, medium variegated, and light variegated ears in the progeny of self colored, partly self colored, and variegated seeds of variegated ears pollinated by white races.

TYPE OF SEEDS PLANTED	PERCENTAGE OF PROGENY		
	Self colored	Medium variegated	Light variegated
Variegated	..	48.97	51.03
Less than half self colored	11.76	36.77	51.47
More than half self colored	29.63	12.96	57.41
Self colored	37.21	..	62.79

The important feature of these records is that, as the percentage of self colored ears in the progeny increased, the percentage of medium variegated ears decreased. From this it was concluded that "in these F_1 plants the factor for medium variegation mutates much more frequently than the factor for very light variegation— $V_m V_l$ ordinarily becomes (by mutation) SV_l rather than $V_m S$."

In so far as these early records can be regarded as trustworthy—in the more recent work there have not been encountered cultures which could

be classified into two sharply separated groups—they suggest that variegation genes of F_1 crosses of low grade with high grade races maintain more or less their normal mutability. But if mutation of a low grade variegation gene is not accelerated either directly by its high grade mate or by modifying genes associated with it, it is difficult to see how a white gene or its associated modifier could influence the mutability of a similar variegation gene in crosses of low grade variegation with white. The material now for the first time available should make possible a more satisfactory analysis of these problems.

SUMMARY

In this paper, which deals with the so-called "calico" type of variegated maize pericarp, it has been shown that:

1. Mutations from variegation to self color occur more frequently in the heterozygous, VW , than in the homozygous, VV , segregates from crosses of variegated, VV , with white, WW .
2. Different white races influence differently the mutability of the variegation gene in crosses of variegated with white.
3. White stocks recovered as segregates from heterozygous variegated stocks of low grade increase the mutability of the variegation gene in crosses less than do the white races tested.
4. Reciprocal crosses of variegated with white and of low with high grade variegation are not significantly different in grade.
5. Dominance of neither low grade nor high grade variegation in crosses of the two types has been demonstrated, the grade of F_1 being intermediate between the parental grades.

These facts are thought by the writer to be best interpreted by the assumption that there exist modifying genes linked with the variegation gene, which influence the mutability of the latter.

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