MOSAIC PERICARP IN MAIZE[1]

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INTRODUCTION

Mosaic pericarp is a coarse type of color variegation in the pericarp of maize. It is typical of variegations in that it is inconstant, exhibiting a high degree of variability in pattern, and giving rise to an inconstant dilute self-colored type (orange) and to stable colorless and self-red strains. In the present paper are described color and pattern variations that originated in pedigreed cultures and from a common source, but particular attention is given to the frequency of the occurrence of these variations and to the gene mechanism responsible for the change from one color or pattern to another.

PREVIOUS STUDY OF MOSAIC PERICARP

HAYES (1917) studied the mosaic pericarp patterns by making continuous selections of the various types for a number of years, and then crossing them with one another to determine their genetic relationships. The following genetic types were isolated: (1) self-red; (2) mosaic patterns ranging from ears in which nearly all of the seeds were heavily striated to ears in which only a few seeds showed red stripes; (3) dilute self-color

[1] This investigation was made in the Department of Field Crops, MISSOURI AGRICULTURAL EXPERIMENT STATION.

or orange (called very slight pattern by HAYES); and (4) colorless. It was found that the heavily striated ears tended to produce a progeny with more ears with a heavy pattern than was obtained in the progeny of the few-stripe ears, but the range of variation was not affected by continuous selection. The F_1 plants from the cross self-red×mosaic are reported as having had mosaic pericarp but more intense than the mosaic parent, and when such F_1 plants were self-pollinated F_2 progenies in the ratio of 1 typical mosaic:2 intense mosaic:1 self-red were produced. The cross self-red×pattern was found to give self-red ears in the F_1, and a ratio of 3 self-red : 1 pattern in the F_2 generation. The cross pattern×mosaic gave F_1 progenies with a greater range of variation than either parent and also a considerable percentage of bud-sport ears. From these results HAYES concluded that certain combinations produce germinal instability and that the factors for self-red, mosaic, very slight pattern (orange), and colorless, form a series of multiple allelomorphs.

MATERIAL AND METHOD

The strains of maize with mosaic pericarp that were used in the experiments reported were furnished by Doctor E. G. ANDERSON who obtained them from Doctor H. K. HAYES. All of the self-red strains that I had in my pedigreed cultures, as well as the self-red strain which was reported by HAYES as being recessive to mosaic, were used in the study of the relation of self-red to mosaic.

The material used for study was produced in a manner similar to that used in a study of the common calico type of variegation which was reported in a previous paper (EYSTER 1924). The variability in both color intensity and color pattern indicates that the gene concerned is inconstant. In order to study a particular variable gene it is necessary to have it associated with another gene which is stable and also allows the changes in the variable gene to come into expression. Accordingly, strains with mosaic pericarp and cob color were crossed with strains having colorless pericarp and red cob. This cross may be expressed factorially as follows: $MM \times WR$.[2]

The F_1 plants from the cross indicated above have mosaic pericarp and red cob and have the genetic constitution $\frac{MM}{WR}$. The F_1 plants, when backcrossed with strains having colorless pericarp and white cob, of the

[2] A single gene determines the development of pigment in both pericarp and glumes of the cob. For example, the gene *WR* produces colorless pericarp but red cob, while the gene *WW* causes both pericarp and cob glumes to be without pigment.

constitution $W\ W$, give progenies of two sorts as regards pericarp color, in approximately equal numbers: (1) plants with ears having colored cob glumes and pericarp, due to the gene MM in one of its allelomorphic forms as follows: mosaic cob and pericarp of the constitution $\frac{MM}{WW}$, self-red cob and pericarp of the constitution $\frac{RR}{WW}$, orange cob and pericarp of the constitution $\frac{OO}{WW}$; and (2) plants with ears having colorless pericarp and red cob, of the constitution $\frac{WR}{WW}$. The first group of ears has the gene for mosaic pericarp associated with a highly stable gene for colorless pericarp, so that any changes undergone by the variable gene for mosaic pericarp are expressed as color or pattern variations. The ears of the second group have the stable gene for colorless pericarp. Since the gene for mosaic pericarp is not involved, the ears were discarded. The red cob identifies the WR gene and makes it possible to eliminate it from the study.

The ears of the first group were separated into classes according to color intensity and color pattern of the pericarp. The ears of each class were then examined individually for color and pattern changes that extended over patches larger than a single kernel. Finally the kernels were shelled off the cob and the individual kernels separated into arbitrary classes according to their color intensity and color pattern.

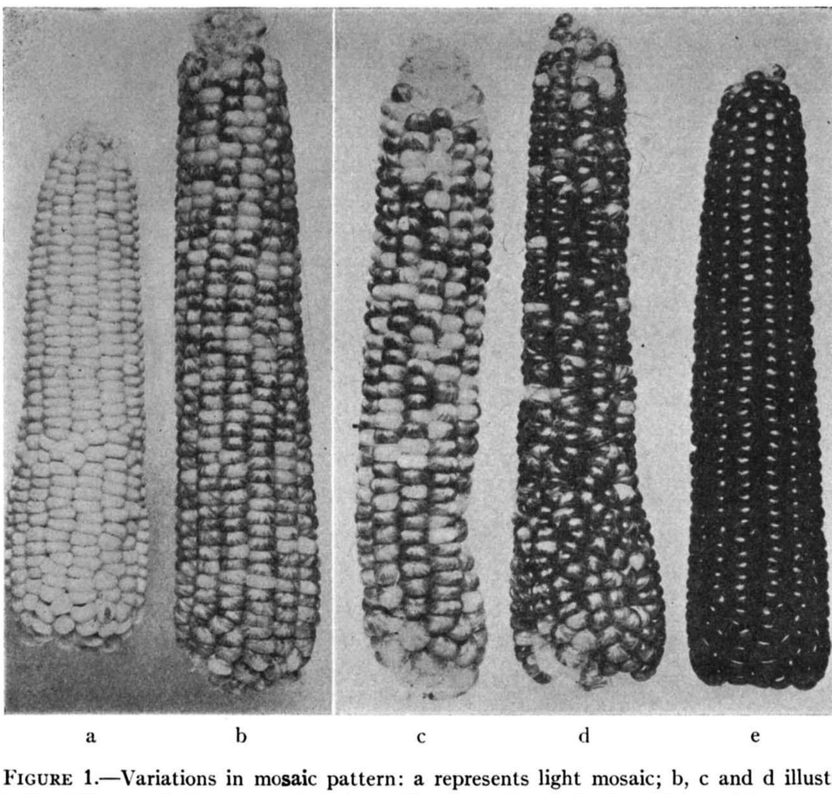
DESCRIPTION OF THE MOSAIC PATTERNS

The inconstancy of the mosaic patterns was described by HAYES (1917), who found that the mosaic strains give in their progeny a range of variability from ears with only a few seeds with deep-red stripes to ears in which nearly all of the seeds are quite heavily covered with red striations. Pattern changes in the progenies of self-fertilized mosaic strains may be due to the segregation of genes as well as to changes in the genes themselves. By crossing the mosaic strains with the colorless strains, as already described, it was possible to eliminate variations due to the segregation of genes for mosaic pericarp of different patterns. The pattern variations in mosaic strains that are heterozygous for colorless pericarp must be considered either different expressions of the same gene under different conditions, or distinct patterns due to some physical or chemical change in the gene itself.

The ears shown in figures 1 to 3 illustrate the more common pericarp variations that originated in pedigreed cultures from a single mosaic ear.

Ear a, figure 1, has a very light mosaic pattern, having only a few streaks of color on the entire ear. The ears b, c and d of figure 1 are typical of the heavier patterns, ranging from ears with fine streaks of red, more or less uniformly distributed, to ears in which nearly all of the seeds are heavily covered with bands of red. Ear e, figure 1, is from a self-red strain which originated from a heavy-mosaic type.

Frequently two or more patterns may appear on the same ear. Ear a, figure 2, has the light mosaic pattern over all of its surface except a large patch near the base, where the pattern is coarse mosaic. The ear b, figure 2, appears to have three distinct patterns: a fine rather uniform pattern

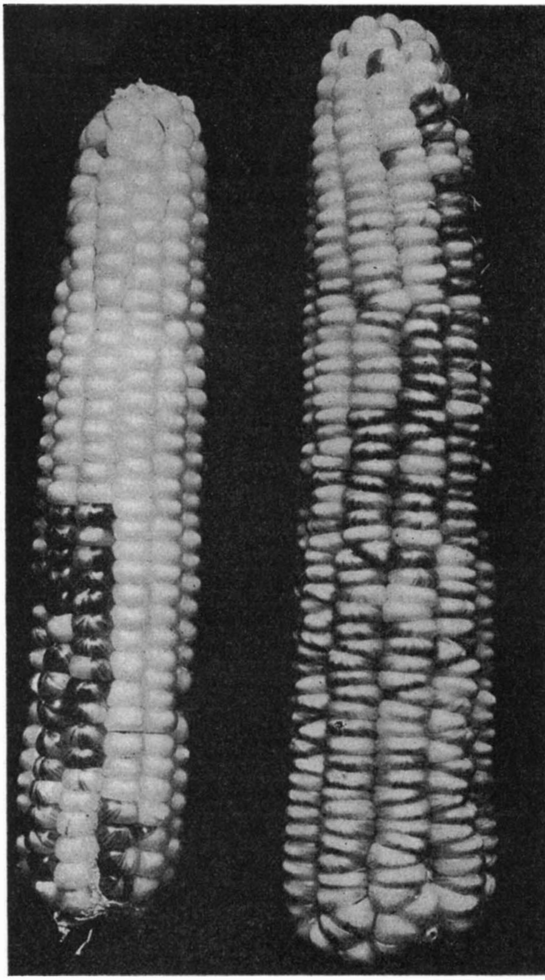


a b c d e

FIGURE 1.—Variations in mosaic pattern: a represents light mosaic; b, c and d illustrate heritable differences in heavy mosaic; e is a self-red ear of a strain that originated from mosaic.

(like that of ear b, figure 1) at the base, a heavy coarse pattern (like that of ear d, figure 1) on one side of the tip, and a light pattern (like that of ear a, figure 1) on the other side of the tip.

The ear illustrated in figure 3 has a dilute-red or orange-colored pericarp (called "very slight pattern" by HAYES). It is significant that a dilute-self-color or orange type should appear in the mosaic strains and resemble in all respects the orange type found in the variegated series described elsewhere (EYSTER 1924) and the lilac color of petals in *Hesperis matronalis*, which, according to DE VRIES (1910), occurs in the variegated strains.



a b

FIG. 2

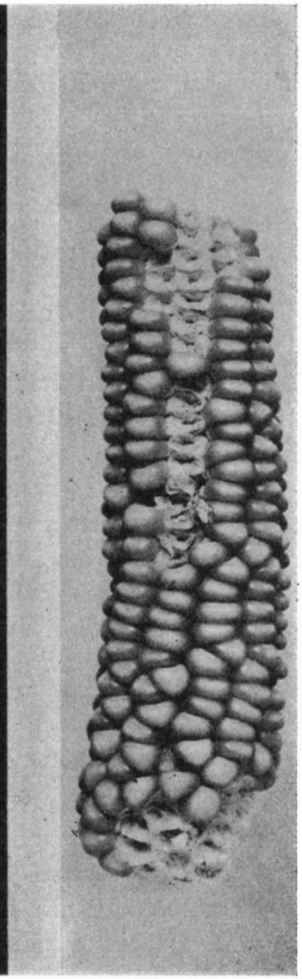


FIG. 3

FIGURE 2.—Ears with more than one genetic type of mosaic: a has light mosaic over most of its surface, but a large patch of heavy mosaic at the base; b has a fine mosaic pattern at the base, a light pattern on one side of the tip, and a heavy pattern on the other side of the tip.

FIGURE 3.—An ear with the dilute-red or orange type of pericarp.

INHERITANCE OF THE MOSAIC PATTERNS

By intercrossing the various color and pattern types which belong to the mosaic series, HAYES (1917) found them to be multiple allelomorphs.

Since all of the types have originated in the course of a few generations, and sometimes within a single generation, from a single parent plant, it is to be concluded, at least as a working hypothesis, that they represent diverse changes in a fundamental pericarp color gene. In connection with the preparation of suitable material for the study of the frequency and direction of color and pattern changes, intercrosses were made between most of the types, which showed the following genetic relationships:

Dominant	*Recessive*
Self-red	All other colors and patterns
Heavy mosaic	Light mosaic, orange, colorless
Light mosaic	Colorless
Orange	Colorless

So far as tests have been made, the results of the intercrosses agree with those reported by HAYES, with the important exception that self-red is not recessive to mosaic. Crosses were made between mosaic and a large number of self-red strains, including the self-red strain obtained from Doctor HAYES and reported by him as being recessive to mosaic, and in no case were the F_1 ears other than deep self-red. A large number of these F_1 plants were grown and many of them were backcrossed with a strain having colorless pericarp and white cob. The progenies from these backcrosses consisted of mosaic ears and self-red ears in approximately equal numbers, thus showing that the self-red F_1 ears were heterozygous for the mosaic pattern. The relation between orange and mosaic was not tested, but, according to HAYES, the orange type of pericarp is recessive to all the mosaic patterns.

Inasmuch as many of the ears that were classed as self-red by HAYES are recorded (HAYES 1917, table 1) as having produced some mosaic ears in their progenies when self-pollinated, it is possible that they were actually heavy mosaics. A cross between such a phenotypically red but genotypically deep-mosaic strain and a medium-mosaic strain would be expected to give the results observed by HAYES, namely, deeply striated F_1 ears intermediate in pattern as compared with the parent strains, and an F_2 progeny of 1 heavy mosaic (resembling self-red in appearance): 2 intermediate mosaic: 1 typical mosaic.

FREQUENCY OF COLOR AND PATTERN CHANGES

Mention has already been made of the common origin of the variations in color and pattern that have been described. These variations reproduce themselves in large measure, but change more or less frequently from one pattern or color to another.

Light mosaic

The very light mosaic (figure 1, ear a) is a very distinct pattern and is easily distinguishable from the more common heavy patterns.

A light-mosaic plant which was heterozygous for colorless pericarp and red cob was backcrossed with a plant having colorless pericarp and white cob, and produced a progeny, grown under pedigree number 3808, of 100 ears with colorless pericarp and red cob and 92 ears with mosaic pericarp. This is a close approximation to the 1:1 ratio expected. Of the mosaic ears 85 had the light pattern of the parent plant; one ear had three-fourths of its area changed to heavy mosaic; one ear was heavy mosaic over about one-eighth of its surface with the remainder of its surface medium mosaic; three ears had a medium-mosaic pattern; one ear had a patch of 34 kernels changed to medium mosaic, and one ear had a patch of 44 kernels changed to medium mosaic.

A similar progeny, grown under pedigree number 3807, yielded 120 mosaic ears. Of these 115 had the light pattern of the parent plant; three ears had more than half of their surface changed to medium mosaic; one ear had a patch of 12 kernels changed to medium mosaic; and one ear had a patch of six kernels changed to orange pericarp.

A summary of the changes from light mosaic to the heavy patterns as observed in four progenies is given in table 1.

TABLE 1

PEDIGREE	KERNELS LIGHT MOSAIC	CHANGES TO HEAVY PATTERNS, IN KERNELS					
		Band	¼	½	¾	1	>1
3807	29,237	0	0	0	0	0	4
3808	24,481	0	1	0	1	0	7
3811	5,438	1	0	0	0	2	0
4037	8,885	1	0	0	0	0	0
Total	68,041	2	1	0	1	2	11

The seventeen changes from light mosaic to heavy mosaic indicated in the above summary ranged in size from a small segment of a single kernel to patches covering an entire ear. As there were 68,041 with no change in pattern, the frequency of change from light to heavy mosaic may be said to be about one in 4000 kernels. The fact that most of the observed changes affected large areas would seem to indicate that they occur more frequently in early development than in the later stages.

Among the 68,041 light-mosaic kernels were also found 132 changes that appeared to be self-red, but only one of the changes was as large as one-half of a kernel, as may be seen in the following summary:

Unchanged (light mosaic)	68,041 kernels
Color changes to red	
Band (small segment)	127 kernels
One-fourth surface of a kernel	4 kernels
One-half surface of a kernel	1 kernel

This would be a frequency of change from light mosaic to red of one in a little more than 500 kernels. It must be admitted that while these color changes appear to be self-red they may in reality be heavy mosaic. So far as tests were made none of these changes was inherited, evidently due to the fact that only somatic tissue was affected.

Also among the 68,041 light-mosaic kernels were found 42 changes to dilute-red or orange pericarp, ranging in size from a narrow segment of a kernel to the entire surface of a kernel, as shown in the following summary:

Unchanged (light mosaic)	68,041
Changed to orange pericarp	
Band (small segment)	36
One-fourth surface of a kernel	3
One-half surface of a kernel	1
Three-fourths surface of a kernel	1
Entire kernel	1

According to these observations the frequency of change from light mosaic to orange is one in about 1620 kernels.

Heavy mosaic

The most striking characteristic of the more common mosaic types is the coarse, heavy pattern with a relatively large number of colorless kernels scattered over the ear. There is great variability in pattern depending upon the size and distribution of the colored segments. Some of the more common patterns are illustrated in figure 1, ears b, c and d.

TABLE 2

PEDIGREE	EARS WITH MOSAIC PATTERN			
	Heavy	Medium	Light medium	Light
1536	5	26	28	0
3799	19	27	3	2
4035	5	67	15	5
4109	14	75	10	5

The heavy mosaic patterns are extremely inconstant, as was shown by HAYES (1917). A progeny includes, in addition to the parental type, both

TABLE 3

PEDIGREE	TYPE	FREQUENCY OF CHANGE FROM HEAVY MOSAIC TO: Medium mosaic, Areas expressed in kernels									Light mosaic, Areas expressed in kernels								
		1/4	1/2	3/4	1	2	3	4	5	>5	1/4	1/2	3/4	1	2	3	4	5	>5
4031	1640	318	185	106	56	16	6	5	3	2	205	99	33	20	0	0	0	0	0
4035	3365	480	243	86	60	10	5	2	1	0	226	126	50	21	5	2	1	0	0
4109	1210	638	251	149	64	26	11	0	3	1	216	119	51	21	5	2	1	1	2
Total	6215	1436	679	341	180	52	22	7	7	3	647	344	134	62	10	4	2	1	2
Number per 1000	612.	141.5	67	33.5	18	5.1	2.2	.7	.7	.3	64	34	13	6.1	1.0	.4	.2	.1	.2

PEDIGREE	TYPE	FREQUENCY OF CHANGE FROM MEDIUM MOSAIC TO: Fine medium mosaic, Areas expressed in kernels									Light mosaic, Areas expressed in kernels								
		1/4	1/2	3/4	1	2	3	4	5	>5	1/4	1/2	3/4	1	2	3	4	5	>5
4035	4015	1077	561	187	230	16	5	1	0	0	536	412	147	112	6	1	2	0	5
4109	5257	2886	1364	653	484	102	40	28	16	44	1427	680	283	208	30	17	5	3	8
Total	9272	3963	1925	840	714	118	45	29	16	44	1963	1092	430	320	36	18	7	3	13
Number per 1000	444.	190.	92.	40.	34.	5.7	2.2	1.4	.8	2.1	94.	52.4	20.6	15.4	1.7	.9	.3	.2	.7

lighter and darker patterns, so as to produce a frequency distribution with the parental type as the modal class. Table 2 gives a summary of a number of progenies which had the mosaic gene associated with a gene for colorless pericarp.

An effort was made to determine with some degree of accuracy the frequency of changes in the heavy patterns. In table 3 are given the frequencies of changes from heavy mosaic to medium mosaic, heavy mosaic to light mosaic, medium mosaic to fine medium mosaic, and medium mosaic to light mosaic. The coarseness of pattern makes even an arbitrary classification extremely difficult, but high frequencies of change are apparent. The frequencies (taken from table 3) of such changes as affected a whole kernel or larger areas are given in table 4.

TABLE 4

PATTERN CHANGE	NUMBER OF CHANGES PER THOUSAND KERNELS EXAMINED
Heavy to medium.....	27
Heavy to light........	8
Medium to fine medium	46
Medium to light.......	19

These results indicate that the medium mosaic patterns change to lighter patterns about 1.9 times as frequently as does the heavy pattern studied. The extremely heavy pattern which approaches self-red in appearance changes to lighter patterns or colorless much less frequently than the heavy patterns included in this study. Just as the light-mosaic strains include a relatively large number of ears that appear colorless, the extremely heavy-mosaic types produce many ears that appear self-red. Apparently the frequency of change of self-red increases from light to the heavy patterns, while the changes to lighter patterns and colorless decrease as the patterns become more and more heavy.

The medium- and heavy-mosaic types were observed to change to dilute red or orange with the frequencies shown in table 5.

TABLE 5

PEDIGREE	MOSAIC KERNELS EXAMINED	ORANGE KERNELS OBSERVED
4031	2,702	0.5
4035	11,996	0
4109	13,242	1
Total	27,940	1.5

The frequency of change from heavy mosaic to orange, based on the above observations, is one in about 18,600 mosaic kernels.

Orange

Orange pericarp is a dilute self-color that has been observed to originate from the mosaic strains. The frequency of the change from mosaic to orange is summarized in table 6.

TABLE 6

MOSAIC PATTERN	NUMBER OF KERNELS EXAMINED	CHANGES TO ORANGE	CHANGES TO ORANGE PER THOUSAND KERNELS
Heavy...............	27,940	1.05	0.054
Light................	68,041	42	0.620

The color intensity of the orange kernels varies from whitish to red. The progeny ears of a number of orange strains heterozygous for colorless pericarp were separated into arbitrary color-intensity classes ranging from whitish (class A) to red (class F) with the results shown in table 7.

TABLE 7

PEDIGREE	INTENSITY OF ORANGE COLOR						EARS MOSAIC
	(WHITISH)					(RED)	
	A	B	C	D	E	F	
4026	3	9	14	24	13	5	1
4037	5	11	32	17	13	7	0
4124	11	19	31	14	4	2	0
4126	0	2	7	23	16	4	0

This fluctuating variability in color intensity is similar to that in the orange pericarp that originates from the calico type of variegation and to the lilac petal color in *Hesperis matronalis* to which reference has been made before.

Orange pericarp has been observed to change to mosaic and to what seems to be self-red, with the frequencies recorded in table 8, a summary of which is given in table 9. The changes from orange to mosaic and red are distinct and clear-cut, so that it was possible to get a good measure of the frequency of these changes. The frequency of change from orange to mosaic increases with color intensity up to class D, which has the highest frequency, 92.75 changes per thousand orange kernels examined. In the darker classes, E and F, the frequency of change from orange to mosaic

TABLE 8

PEDIGREE	TYPE	COLOR CHANGES TO										
		Mosaic								Red		
		Line	Band	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	2	Line	Band	$\frac{1}{8}$
Light A												
4026	532	18	7	..	..	1	(1 entire ear)			..	..	..
4037	1,358	60	..	..	1	..				..	..	..
4124	1,633	76	..	..	..	..				..	..	..
Total	3,523	154	7	..	1	1	..	..	..	..	..	..
B												
4037	2,709	66	10	..	..	..	..	..	..	..	..	..
4026	1,772	400	31	2	1	1	..	..	..	1	..	..
4124	3,543	218	6	..	..	..	..	..	..	..	..	..
4126	597	6	..	..	..	..	..	..	..	..	..	..
Total	8,621	690	47	2	1	1	..	..	..	1	..	..
C												
4026	2,789	458	46	3	1	2	..	1	..	8	2	..
4037	9,600	380	27	..	..	..	..	1	..	3	..	..
4124	6,683	262	8	..	..	..	..	..	..	1	..	..
4126	2,040	63	9	..	..	..	..	..	..	1	2	..
Total	21,112	1163	90	3	1	2	..	2	..	13	4	..
D												
4026	4,884	830	48	11	4	5	..	1	..	9	6	2
4037	4,732	535	5	2	2	..	..	1	..	4	1	..
4124	3,179	34	4	..	.	..	..	..	..	1	..	..
4126	5,409	311	51	4	6	4	2	4	..	3	2	1
Totals	18,204	1710	108	17	12	9	2	6	..	17	9	3
E												
4026	3,221	430	33	9	4	1	2	2	..	33	4	1
4037	3,972	71	7	2	1	..	1	1	..	5	1	..
4124	995	7	..	..	..	..	..	..	..	..	..	..
4126	3,963	175	38	2	2	1	1	1	..	1	1	..
Totals	12,151	683	78	13	7	2	4	4	..	39	6	1
Dark F												
4026	914	92	3	..	1	1	1	..	2	10	4	..
4037	1,965	29	6	..	..	1	..	..	..	11	4	..
4124	810	4	..	..	..	..	..	..	..	..	..	..
4126	1,190	13	7	..	..	..	..	..	..	4	1	..
Totals	4,879	138	16	..	1	2	1	..	2	25	9	0

decreases as the color intensity increases. Evidently there is a correlation between color intensity and gene stability.

TABLE 9

INTENSITY OF ORANGE	KERNELS UNCHANGED (ORANGE)	NUMBER OF CHANGES TO		NUMBER OF CHANGES PER THOUSAND KERNELS EXAMINED	
		Mosaic	Red	Mosaic	Red
A (whitish)	3,523	163	0	44.22	0.00
B	8,621	741	1	79.14	0.11
C	21,112	1216	17	54.42	0.76
D	18,204	1864	29	92.75	1.44
E	12,151	791	46	60.90	3.54
F (red)	4,870	160	34	31.62	6.71

The frequency of change from orange to red varies directly with color intensity of the orange, from 0.11 in class B to 6.71 in class F per thousand orange kernels.

Colorless

A colorless strain was found that originated in a pedigreed culture of a mosaic strain. Relatively large progenies of this strain have been grown for three generations and over a thousand ears have been examined, but no traces of color have been observed. It is to be concluded that this colorless strain has lost the instability of the mosaic strain from which it originated.

Self-red

A large number of what seemed to be self-red ears that originated from the mosaic strains have been tested, but practically all of them proved to be genotypically heavy mosaic.

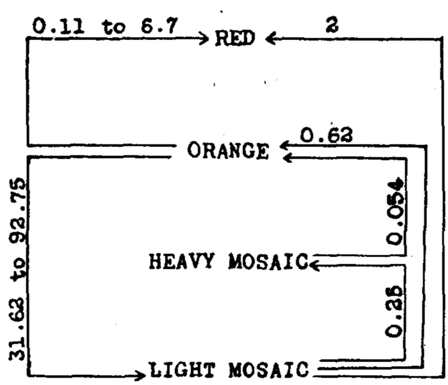


FIGURE 4.—A diagram to show the relative frequencies of pericarp color and pattern changes expressed in number of changes per thousand kernels.

At least one strain has been found (figure 1, e) that originated from mosaic, which, so far as tested, breeds true for the self-red color.

Summary of the color and pattern changes

The relative frequencies of the various color and pattern changes that have been described above are shown in the diagram in figure 4.

THE NATURE OF THE CHANGE FROM ORANGE TO MOSAIC

The character intermediate between the contrasting characters of the variegation, which is dilute red or orange in maize, is extremely interesting because of the light it throws on gene structure and the nature of variegation. In orange strains heterozygous for colorless pericarp the orange color

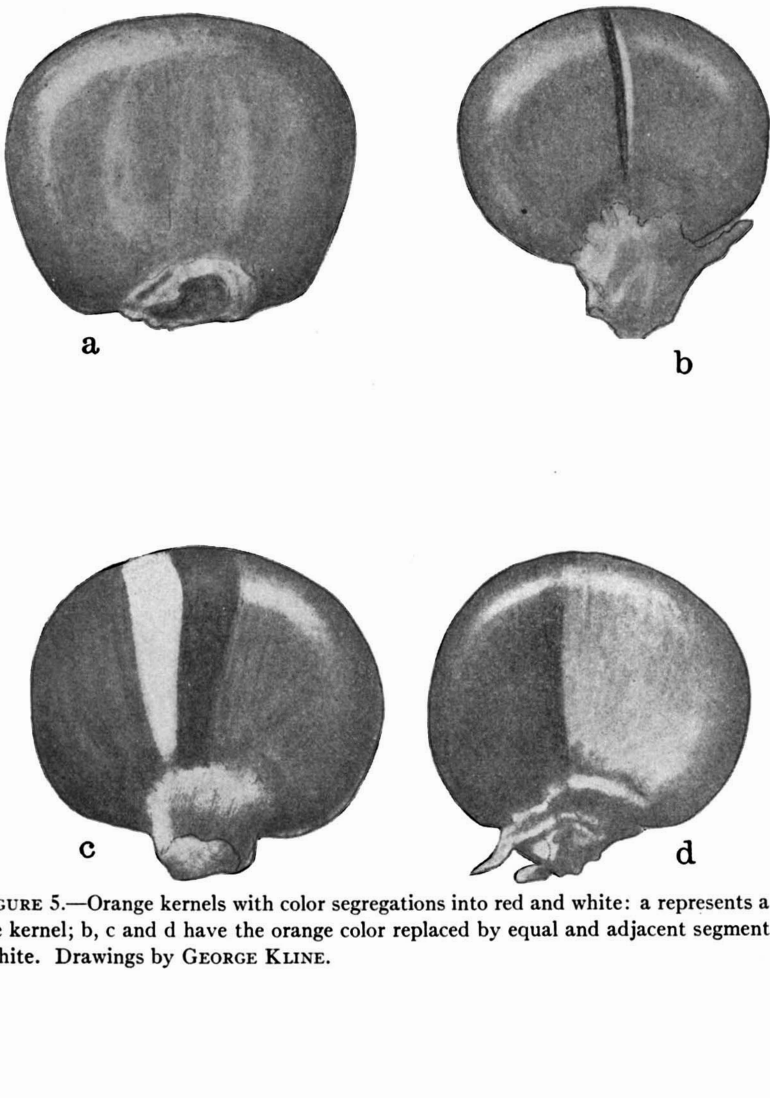


FIGURE 5.—Orange kernels with color segregations into red and white: a represents a typical orange kernel; b, c and d have the orange color replaced by equal and adjacent segments of red and white. Drawings by GEORGE KLINE.

breaks up into its component colors, red and white (colorless). In figure 5 are shown orange kernels with color segregation. Kernel a is a typical orange kernel with no color change. In kernel b, a small segment of the surface has the orange color replaced by a segment of red adjacent to an equally large segment of colorless pericarp. It is quite evident that the gene for orange pericarp was divided by a mitosis late in development in such a way that the pigment-producing and non-pigment-producing parts of the gene were separated in daughter cells. The red and white segments represent the cell progeny of the daughter cells with and without pigment-producing gene substances, respectively. The kernels c and d, figure 5, show similar color segregation, except that larger parts of the kernel are involved, evidently due to the breaking up of the orange gene at an earlier stage in development. Kernel d represents a gene change that occurred early enough to affect the entire kernel.

The kernels in figure 6 illustrate the breaking up of orange to form a mosaic. The color segregation in kernel a, figure 6, is similar to those in figure 5. In kernel b, figure 6, there are two segments in which the orange color was separated into its component colors, red and white, while the space between them is typically mosaic. This mosaic segment apparently was produced by the same mechanism that produced the large segments but represents a number of distinct segregations that occurred later in development. In kernel c, figure 6, the segregation of orange into red and white extends over more than half of the pericarp, while in ear d, figure 6, the orange color was completely broken up into red and white.

The color changes in kernels b and c in figure 5, and a and b in figure 6 were not inherited, due no doubt to the fact that the gene change occurred in cells which took no part in the development of the embryo sac. Kernels like c, figure 6, which have a large segment of the surface changed to mosaic, grow into plants which produce ears with orange or mosaic pericarp, depending upon whether or not the change affected the embryo sac, providing, of course, they were fertilized by a colorless strain. In general, the larger the color change the more likely it is that the effect has extended to the sporogenous cells and the change is inherited.

DISCUSSION

Like all variegations, mosaic pericarp is inconstant in the relative amounts and distribution of the contrasting characters of the variegation. Although all variegations are highly inconstant, a study of a number of different variegations has shown that they are constant in their inconstancy. The color and pattern variations that appear in the mosaic strain of maize are in all respects similar to those that occur in the calico type of variegation described by EMERSON (1913, 1917) and by EYSTER (1924), and to the color and pattern changes in a variegated strain of *Hesperis matronalis* as described by DE VRIES (1910). Some characteristics which are common to the three series of variegations mentioned above, as well as, probably, to all other variegations, are the following:

1. A variegation consists of contrasting characters segregated in the somatic tissue, and often also in the reproductive tissue.

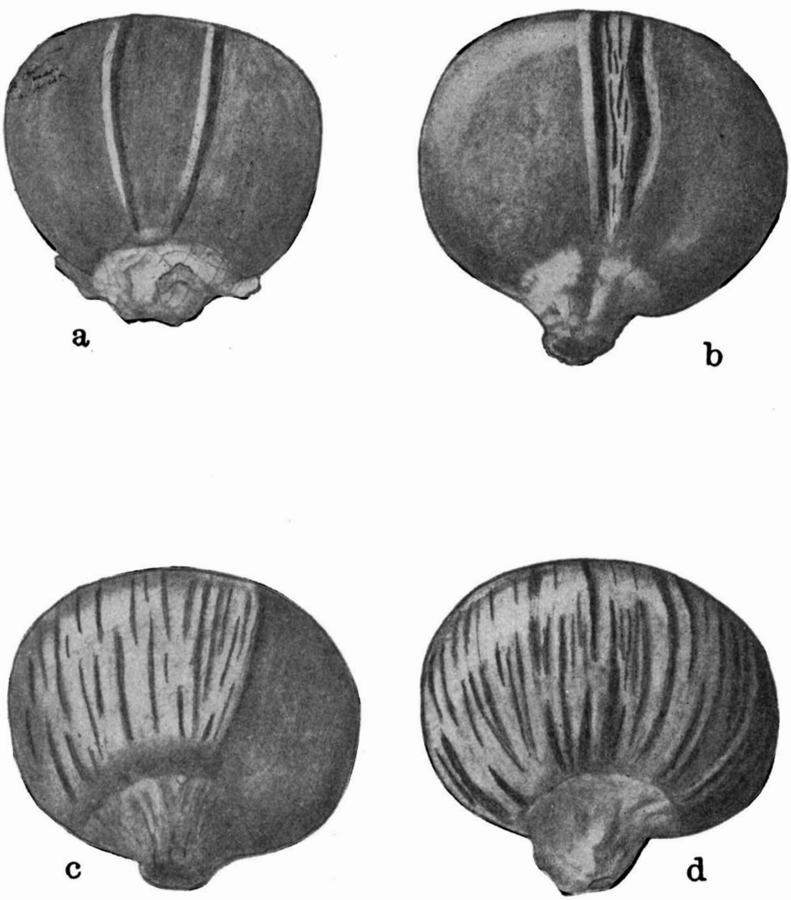


FIGURE 6.—Kernels which illustrate the breaking up of the orange color to form a mosaic: a represents a simple separation into red and white segments; b has two large color segregations and many smaller ones, so that part of the surface has the orange color broken up into a red-and-white mosaic; c has more than half of the orange surface broken up into red and white to form a typical mosaic; d has the orange completely broken up to form a mosaic. Drawings by GEORGE KLINE.

2. Variegations vary in pattern according to the relative amounts and distribution of the contrasting characters so as to form an intergrading series of patterns from one extreme to the other.

3. Color variegations give rise to an inconstant self-color which is intermediate between the contrasting characters of the variegation.

4. The intermediate self-color breaks up into the contrasting characters of which it is composed. The breaking up occurs in such a way as to make it probable that it is done by the mechanism of mitosis.

5. Variegations give rise to strains that breed true for one or the other of the contrasting characters. Such strains have lost the inconstancy peculiar to the variegated types.

If all variegations are fundamentally alike they should appear in a variety of patterns, give rise to an intermediate but inconstant type (like orange pericarp in maize), and produce constant types with only one or the other of the contrasting characters of the variegation (like the constant colorless and self-red strains that originate from the variegated strains in maize).

The color segregation in the pericarp of the orange kernels shown in figure 5 is such as to produce what are commonly known as sectorial chimeras. The replacement of the orange by equal and adjacent segments of red and white is good evidence that the mechanism of this color segregation is that of mitosis. So far as observations have been made, there appears to be little or no difference in color intensity in the homozygous orange strains as compared with orange strains heterozygous for colorless pericarp. Since one gene produces an orange pericarp not visibly different from that produced when two genes are present it is hardly likely that the somatic segregation of the orange to form adjacent segments of red and white is due to a non-disjunction of the chromosomes carrying the pericarp color gene. It is rather due to the non-disjunction of the contrasting particles within the gene.

The fact that the change from orange to mosaic is reversible and that this change involves the mechanism of mitosis would seem to indicate that the corresponding gene change is physical rather than chemical in nature. The gene for orange extends the pigment, though in reduced amount, throughout the pericarp tissue, while the gene for mosaic permits its contrasting elements to be segregated by mitosis. The relation of orange and mosaic is such as to suggest that their genes are fundamentally alike in content but have different structural arrangements so that they may be said to be isomeres. According to this view the change from orange to mosaic, or the reverse, would be the result of a structural rearrangement of the same gene elements. The fluctuating variability in the intensity of orange color and in mosaic pattern might be due to small differences in gene content which would result from slight irregularities in division or chance distribution of the gene substance in mitoses.

SUMMARY

Mosaic pericarp is a coarse type of variegation which has the inconstancy typical of variegations. A large number of mosaic patterns, an inconstant dilute-red or orange type, constant colorless, and constant red types originated in pedigreed cultures from a single parent plant. These variations are inherited and form a series of multiple allelomorphs with the following order of dominance: self-red, heavy-mosaic pattern, light-mosaic pattern, orange and colorless. The frequencies of the different color and pattern changes have been determined.

The color and pattern variations in mosaic are similar to those found in other variegations. Deductions have been made as to the mechanism of variegations and the nature of the gene.

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