THE EFFECT OF ENVIRONMENT ON VARIEGATION PATTERNS IN MAIZE PERICARP[1]

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STATEMENT OF THE PROBLEM

EMERSON (1914, 1917) was the first to call attention to the remarkable series of multiple allelomorphs concerned with the development and distribution of color in maize pericarp. These allelomorphs include genes for self red, self orange, white-capped red, basal red, and colorless pericarp, associated with either self red or white cobs, and at least three types of variegated pericarp associated with similarly variegated cobs. The principal difference between these genes was thought to lie in their relative frequencies of mutation. It was suggested that the several types of variegated pericarp differ in frequency of factorial change by virtue of the fact that the change begins earlier in some types than in others.

HAYES (1917) made a study of a coarse type of variegation in maize, known as mosaic pericarp, with results quite similar to those found by EMERSON in the calico type of variegation. HAYES intercrossed the various

[1] This investigation was made in the Department of Field Crops, MISSOURI AGRICULTURAL EXPERIMENT STATION. The experiments were conducted at Sacaton, Arizona, under the supervision of C. J. KING, and at Chula Vista, California, under the supervision of C. G. MARSHALL, through the courtesy of the Office of Crop Acclimatization of the BUREAU of PLANT INDUSTRY.

allelomorphic types and concluded that certain combinations produce germinal instability.

EYSTER (1924) was able to demonstrate the suggestion made by EMERSON that the large series of multiple allelomorphs is evidence that a fundamental gene concerned in the development of pericarp and cob colors and color pattern has at one time or another mutated in diverse ways. A single self orange ear, in the course of a few generations in pedigreed cultures, gave rise to a large series of multiple allelomorphs, including strains of self orange varying in color intensity from whitish to deep red, self red, white-capped red, colorless and a relatively large number of distinct types of variegation, ranging in color pattern from ears that are almost colorless to ears that approach the self red ears in appearance.

It has also been found (EYSTER 1925) that the fundamental gene for mosaic pericarp changes in such a way as to give rise to pericarp and cob colors and color patterns which are in every respect parallel to those which occur in the calico type of variegation.

The detailed studies of both the calico and the mosaic series of multiple allelomorphs led the writer (loc. cit.) to the following general conclusions: (1) Self orange color is the expression of a gene which includes in its structure gene elements for red pericarp associated with gene elements for colorless pericarp, and (2) a variegation is produced when the contrasting gene elements become segregated by the mechanism of mitosis in the course of pericarp development.

The idea that a variegation is the result of the mitotic segregation of elements within the gene suggested the question as to the possible effects of different environmental conditions on the process. Accordingly, as a preliminary experiment, plantings from each of a number of variegated and self orange ears were made in localities which differ strikingly in such environmental conditions as might be expected to affect growth and development, and the present paper is a report of the results that have been found.

MATERIALS AND METHODS

The materials used in this experiment were prepared by crossing the plants having the pericarp color or pattern to be studied with a strain having colorless pericarp but red cob, and then back-crossing such F_1 plants with a strain having colorless pericarp and colorless cob, according to the method described elsewhere (EYSTER, 1924). The kernels of the variegated ears prepared in this manner were of two sorts as regards their genetic constitution, as follows: $\frac{W\ R}{W\ W}$ and $\frac{V\ V}{W\ W}$. Accordingly, approxi-

mately one-half of the plants produced ears with colorless pericarp and red cob, while the remainder of the plants produced ears with variegated pericarp and cob or some other allelomorphic type due to a genetic change in the *V V* gene. Likewise the kernels of the orange ears were of two sorts as regards their genetic constitution as follows: $\frac{W\ R}{W\ W}$ and $\frac{O\ O}{W\ W}$. In this case also, approximately one-half of the plants produced ears with colorless pericarp and red cob, while the remainder of the plants produced ears with orange pericarp and cob or an allelomorphic type due to a genetic change in the *O O* gene. By this method it was possible to identify the gene under study, regardless of what allelomorphic changes it may have undergone. In each case the ears with colorless pericarp and red cob, of the constitution $\frac{W\ R}{W\ W}$, were discarded.

It should be kept in mind that a single gene is responsible for the development and distribution of pigment in both pericarp and cob. The genes which have been referred to above are the following:

	Expression in	
Symbol	Pericarp	Cob
W R	Colorless	Red
W W	Colorless	Colorless
V V	Variegated	Variegated
O O	Orange	Orange

Eight variegated and two orange ears were used in the experiment. The kernels of each ear were removed from the cob separately and divided into three equal lots, one lot to be planted in each of the localities chosen for growing the plants.

LOCALITIES IN WHICH THE PLANTS WERE GROWN

One lot of the kernels from each ear was grown in each of the following localities: Columbia, Missouri; Chula Vista, California; and Sacaton, Arizona.

Columbia, Missouri was chosen, largely as a matter of convenience, as a location where the environmental factors might be considered best suited for the normal growth and development of maize. Due to unfavorable cultural conditions and unusual chinch-bug injury, very few ears were matured in this locality, though more than 2500 plants were grown. Such ears as were produced in each of the progenies were quite like those grown at Chula Vista, California.

The planting at Chula Vista, California was made early in June, and the matured ears were harvested OCTOBER 15, making a growing season of approximately four months. During this period the air temperature seldom exceeded 75 degrees *F* and the mean daily fluctuation was not much over 20 degrees *F*.[2] The soil temperature had a daily range of from 60 degrees *F* to 80 degrees *F* and was very uniform. The radiation is less than that of the corn belt region due to the high relative humidity.

The planting at Sacaton, Arizona was made July 11 and the ears were fully matured October 15, making a growing season of a little more than three months. The air temperature was quite variable, ranging from 60 degrees *F* at night to as much as 110 degrees *F* during the day. The soil temperature was more variable, changing with the irrigations. The atmosphere at Sacaton is typical southwestern desert air, with a low relative humidity and a high radiation.

The soils in which the plantings were made at Chula Vista and Sacaton are quite comparable, both being alkaline and somewhat impervious. Both crops were grown under irrigation. The water used in irrigation at Chula Vista was surface water stored during the winter from mountain streams, while the water used at Sacaton was taken from wells and was distinctly salty. Both plots were irrigated before water stress conditions developed so that soil moisture conditions can be considered as having been optimum.

The chief environmental difference between Chula Vista and Sacaton seems to have been the higher and more variable temperature and greater transpiration at Sacaton. As a consequence of this difference the season required to mature the pericarp at Sacaton was fully a month shorter than that required at Chula Vista.

THE EFFECT OF ENVIRONMENTAL DIFFERENCE ON THE VARIEGATION PATTERN

The variegated ears grown at Chula Vista, in a cool, moist climate, where the growing season was relatively long, developed a fairly coarse pattern of variegation in the form of splashes, bands, and larger segments of the surface of a kernel, while the remainder of the pericarp appeared perfectly colorless. Variegated ears of the same genetic constitution and taken from the same parent ear but grown at Sacaton, in a region with a hot, dry climate and a short growing season, developed a strikingly

[2] The writer is indebted to J. H. Kempton of the Office of Crop Acclimatization of the Bureau of Plant Industry for the detailed statements concerning the environmental conditions existing at Chula Vista, California, and at Sacaton, Arizona.

different variegation pattern. The variegation consists in a smaller number of red areas which cover one-fourth and larger parts of the surface of a kernel, but a larger number of smaller red areas in the form of splashes,

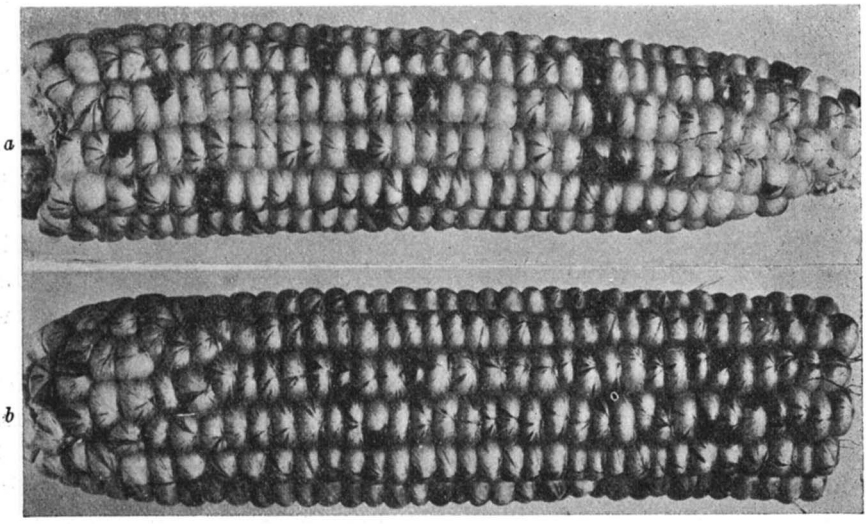

FIGURE 1.—Typical ears showing the variegation patterns of ears of the same strain grown under different environmental conditions. (*a*) Pattern which developed under Chula Vista conditions. (*b*) Pattern which developed under Sacaton conditions.

lines, and bands. The general surface of the kernels, not occupied by the red markings of the variegation is not colorless in the Arizona-grown ears as in the California-grown ears, but has a more or less distinct washed-out-

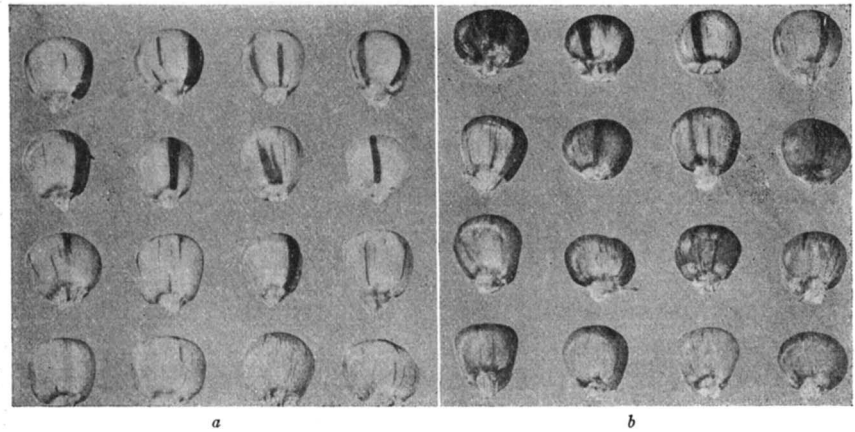

FIGURE 2.—(*a*) Representative kernels from ear shown in Fig. 1 a. (*b*) Representative kernels from ear shown in Fig. 1 b.

red color. Accordingly, all of the Arizona-grown variegations consist of relatively small areas of red on a washed-out-red background. The difference in the variegation pattern under the conditions of these two environ-

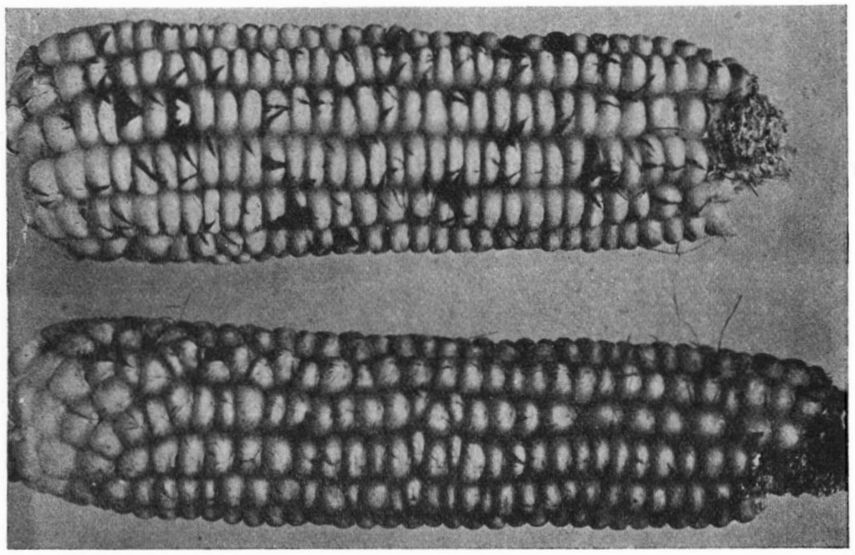

FIGURE 3.—Typical ears showing the variegation patterns of ears of a second strain grown under different environmental conditions. (*a*) Pattern which developed under Chula Vista conditions. (*b*) Pattern which developed under Sacaton conditions.

ments was consistent in all of the plantings that were made, as may be seen from the accompanying illustrations.

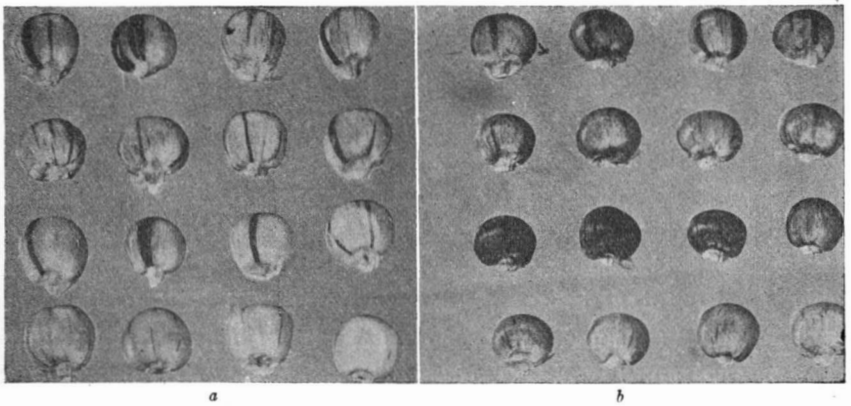

FIGURE 4.—(*a*) Representative kernels from ear shown in Fig. 3 *a*. (*b*) Representative kernels from ear shown in Fig. 3 *b*.

Kernels taken from the same parent ear were grown at Sacaton under number 2986 and at Chula Vista under number 2997. The ear shown in figure 1*a* illustrates the variegation pattern typical of the ears grown at Chula Vista, and ear figure 1*b* is representative of the ears grown at

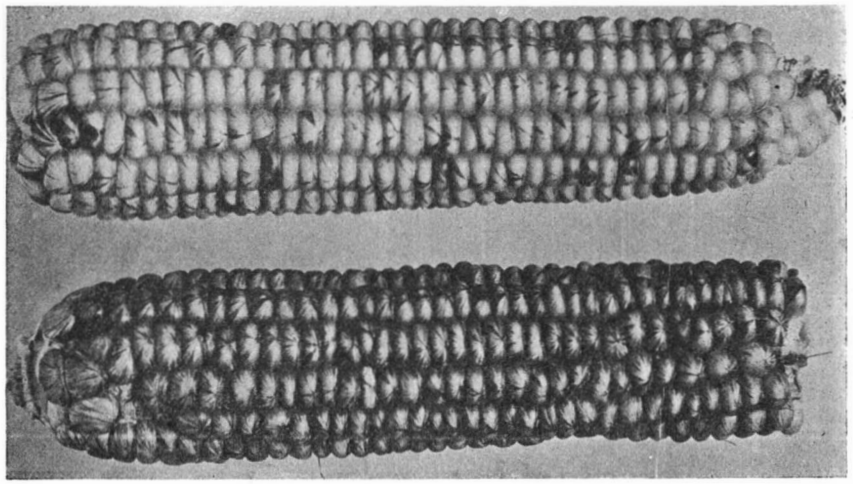

FIGURE 5.—Typical ears showing the variegation patterns of ears of a third strain grown under different environmental conditions. (*a*) Pattern which developed under Chula Vista conditions. (*b*) Pattern which developed under Sacaton conditions.

Sacaton. A comparison of typical kernels taken from these ears is shown in figure 2. The kernels grown at Chula Vista are shown in figure 2*a*, and those grown at Sacaton in figure 2*b*. The pattern differences which have already been described are apparent in these illustrations.

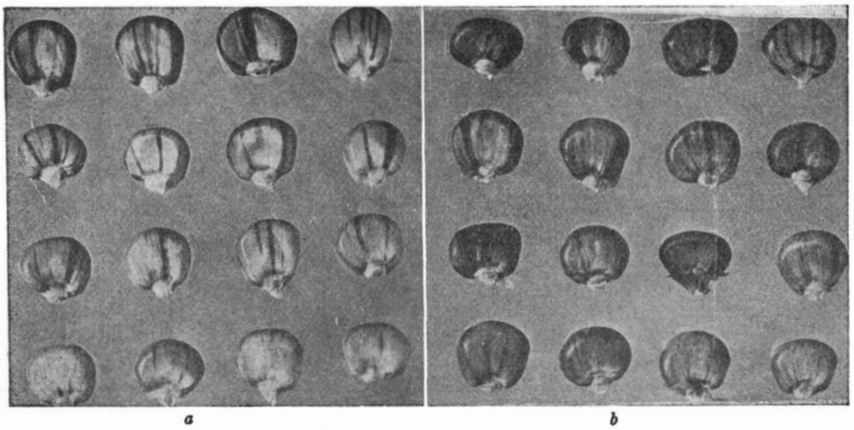

FIGURE 6.—(*a*) Representative kernels from ear shown in Fig. 5 *a*. (*b*) Representative kernels from ear shown in Fig. 5 *b*.

Kernels taken from a second variegated ear were grown at Chula Vista under number 2998 and at Sacaton under number 2987, and a typical ear from each planting is shown in figure 3. Typical kernels from these ears are illustrated in figure 4. The relatively large areas of red on a colorless background are characteristic features of the California-grown ears, and are in striking contrast with the fine markings and residual color in the pericarp of the Arizona-grown ears.

From a third variegated ear a planting was made at Chula Vista under number 2992 and at Sacaton under number 2982, and a representative ear from each planting is shown in figure 5. Representative kernels from each of these ears are illustrated in figure 6. Again the variegation patterns are strikingly different. Similar differences were found also in each of the other plantings that were made in connection with this experiment.

FREQUENCY OF OCCURRENCE OF SELF RED AREAS IN VARIEGATIONS UNDER THE CONDITIONS OF THE DIFFERENT LOCALITIES

The variegated ears were first studied for areas of red extending over more than a single kernel. The kernels were then shelled off the ear and studied individually and classified according to the size of the largest red area on each kernel.

California-grown Ears

From five to ten percent of the variegated ears grown in this locality had an exceedingly light pattern, while the remainder of the ears were like those shown in the illustrations above. The ears were separated into those which had the very light pattern and those which had the medium pattern like the parent ears before the data on the number and size of the red areas were taken.

A summary of the red areas found on the ears with the extremely light variegation pattern is given in table 1.

TABLE 1

PEDIGREE	VARIEGATED KERNELS	CHANGES TO RED IN KERNELS				
		$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	>1
2997	2163	3	2	0	0	0
2998	1710	2	5	1	0	0
2990	2604	15	6	1	0	0
2992	203	7	3	1	1	0
2993	1126	3	4	2	1	0
2995	1178	3	2	0	0	0
Total	9584	33	22	5	2	0
percent	99.36	0.34	0.23	0.05	0.02	0.00

Two red areas were as large as a single kernel, but none were found that were larger than this. Less than one percent of the kernels had red areas that were as large as one-fourth of the surface of a single kernel.

The data on the number and size of the red areas that occurred on the more heavily variegated California-grown ears are given in table 2.

TABLE 2

PEDIGREE	VARIEGATED KERNELS	CHANGES TO RED IN KERNELS				
		¼	½	¾	1	>1
2997	8654	150	40	25	13	1
2998	6848	118	40	24	6	4
2990	10418	270	62	20	3	2
2992	5898	227	64	40	21	3
2993	4491	189	60	45	20	5
2995	6555	216	105	48	23	4
Total	42864	1170	371	202	86	19
percent	95.87	2.62	0.83	0.45	0.20	0.04

Nineteen red areas extended over more than a single kernel, and 4.13 percent of all the kernels had red areas that covered one-fourth the surface of a single kernel or larger areas.

Arizona-grown Ears

The variegated ears grown in Arizona did not include a single ear with the extremely light pattern found among the California-grown ears. The patterns were all fundamentally like those shown in the illustrations which have already been described, with variations in the number and size of the red areas and in the amount of residual color in the general pericarp.

A summary of the red areas that occurred on the variegated ears grown in Arizona is given in table 3.

Comparison of the Occurrence of Red Areas in California-and Arizona-grown Variegations

It should be kept in mind that the California-grown variegations were of two distinct patterns: (1) a medium heavy pattern, similar to that of the parent ear, and (2) an extremely light pattern. The variegations grown in Arizona were of one general type and consisted of many relatively fine red markings on a reddish background. A comparison in the frequency of the occurrence of red markings which covered one-fourth of a kernel and larger

areas in the heavy variegations grown in the two localities is shown in table 4.

In every planting that was made and studied there were more self red areas covering one-fourth of a kernel or larger areas in the California-grown variegations than in the corresponding variegations grown in Arizona. The differences range from 0.07 ± 0.17 to 2.56 ±0.27. In four of

TABLE 3

PEDIGREE	VARIEGATED KERNELS	CHANGES TO RED IN KERNELS				
		¼	½	¾	1	>1
2986	9254	96	21	16	18	1
2987	9624	154	51	39	19	0
2980	12211	143	60	22	5	1
2982	6215	107	58	19	16	0
2983	7123	246	105	41	37	4
2985	4500	92	43	16	13	0
Total	48927	838	338	153	108	6
Percent	97.14	1.66	0.67	0.30	0.22	0.01

TABLE 4

PEDIGREE.		CHANGES TO RED COVERING ¼ KERNEL AND LARGER AREAS, IN PERCENT.		DIFFERENCE
California	Arizona	California	Arizona	
2997	2986	2.58± .11	1.62± .09	0.96± .14
2998	2987	2.73± .13	2.66± .11	0.07± .17
2990	2980	3.31± .12	1.86± .08	1.45± .14
2992	2982	5.68± .20	3.12± .18	2.56± .27
2993	2983	6.63± .24	5.73± .18	0.90± .30
2995	2985	5.73± .19	3.52± .18	2.21± .26
Average		4.14±0.07	2.86±0.05	1.28± .086

the six plantings, the differences are from seven to a little more than ten times their probable errors and are doubtless significant. A total comparison of the six plantings shows that the percent of self red areas covering one-fourth or more of the surface of a kernel was 4.14 ± 0.07 under the California conditions and 2.86 ± 0.05 under the Arizona conditions. This is a difference of 1.28 ± 0.086. This difference is approximately 14.5 times as large as its probable error.

The objection might be made that by excluding the very light-patterned ears of the California-grown material an unfair comparison is made. Consequently in table 5 is given a summary of all the California-grown variegations, including the extremely light variegated ears, in comparison with the Arizona-grown variegations.

TABLE 5

PEDIGREE		CHANGES TO RED COVERING ¼ KERNEL AND LARGER AREAS, IN PERCENT.		DIFFERENCE
California	Arizona	California	Arizona	
2997	2986	2.12±0.09	1.62±0.09	0.50±0.13
2998	2987	2.30±0.11	2.66±0.11	−0.36±0.15
2990	2980	2.83±0.09	1.86±0.08	0.97±0.12
2992	2982	5.67±0.19	3.12±0.18	2.55±0.26
2993	2983	5.53±0.20	5.73±0.18	−0.20±0.27
2995	2985	4.59±0.15	3.52±0.18	1.07±0.23
Average		3.51±0.05	2.86±0.05	0.65±0.07

Again in four of the six plantings the California-grown kernels had a larger percent of kernels with red areas that covered one-fourth or more of the surface of a kernel. The differences in percent range from four to nearly ten times their probable errors, even when the extremely light variegated ears of the California-grown plants are included. The differences in families 2998–2987 and 2993–2983 are in favor of the Arizona-grown ears but are not significant.

When the extremely light and heavy variegations of the California-grown kernels are considered together, the self red areas amount to 3.51 ± 0.05 percent, as compared with 2.86 ± 0.05 percent in the Arizona-grown variegations. This is a difference of 0.65 ± 0.07 . This difference is a little more than nine times its probable error.

The result of this comparison is that the California-grown kernels have more red markings that cover one-fourth the surface of a kernel and larger areas than the Arizona-grown variegations.

VARIEGATED AREAS ON SELF ORANGE KERNELS

Orange kernels, of the genetic constitution that has already been indicated, were taken from the same ear and divided into three lots, one of which was planted in Missouri under number 2974, the second lot was planted in Arizona under number 2984, and the third lot was planted in California under number 2994. The number of ears that were produced

from the planting in Missouri was too small for further study. The ears of the Arizona and California plantings varied from whitish to deep orange or red, and the orange pericarp changed to variegation and self red in the manner described previously (EYSTER, 1925). No color changes were larger than the surface of a single kernel.

The kernels were removed from the ears and classified according to the presence and size of variegated areas as given in table 6.

TABLE 6

	CHANGES TO VARIEGATION.			TOTAL
	Orange kernels	Band to ¼ kernel	¼ to entire kernel	
California grown	14462	1492	153	16107
Arizona grown	14412	1252	90	15754

The relative frequencies of the changes from self orange to variegated pericarp in the California-and Arizona-grown ears may be seen more clearly from the comparison expressed in percent of the total number of kernels given in table 7.

TABLE 7

	PERCENT OF TOTAL KERNELS			TOTAL
	Orange kernels	Changes to Variegation		
		Band to ¼ kernel	¼ to 1 kernel	
California grown	89.79	9.26±0.16	0.95±0.05	10.21±0.16
Arizona grown	91.48	7.95±0.15	0.57±0.04	8.52±0.16
Difference	−1.69	1.31±0.22	0.38±0.06	1.69±0.23

The variegations which covered from a band to one-fourth of the surface of a kernel occurred 1.31 ± 0.22 percent more frequently in the pericarp of the California-grown ears. This difference is about six times its probable error. The variegations that extended over as much as one-fourth the surface of a kernel and larger areas could be recorded accurately, and it was found that the California-grown ears had 0.38 ± 0.06 percent more of these larger areas than the Arizona-grown ears. This difference is a little more than six times its probable error.

This comparison indicates that changes in pericarp color from orange to variegation occurred more frequently under the California conditions.

RED AREAS ON SELF ORANGE KERNELS

A record was also made of the color changes from orange to self red which covered a longitudinal band of the surface of a kernel and larger areas. No red area was found that extended over more than a single kernel. A summary of the red areas which occurred on orange pericarp is given in table 8.

TABLE 8

	CHANGES TO SELF RED			TOTAL
	Orange kernels	Band to ¼ kernel	¼ to entire kernel	
California grown	15059	934	114	16107
Arizona grown	15361	342	51	15754

A comparison of the frequency of occurrence of red areas in orange pericarp between the California-grown and Arizona-grown ears, expressed in percent of the total number of kernels observed, is given in table 9.

TABLE 9

	PERCENT OF TOTAL KERNELS			TOTAL
	Orange kernels	Changes to Self Red.		
		Band to ¼ kernel	¼ to 1 kernel	
California grown	93.56	5.80±0.12	0.71±0.04	6.51±0.13
Arizona grown	97.50	2.18±0.08	0.32±0.03	2.50±0.09
Difference	−3.94	3.62±0.14	0.39±0.05	4.01±0.16

The red areas which covered from a longitudinal band to one-fourth of the surface of a kernel occurred 3.62 ± 0.14 percent more frequently in the pericarp of the California-grown ears. This difference is a little more than twenty-five times its probable error. The red areas which extended over areas larger than one-fourth of the surface of a single kernel occurred 0.39 ± 0.05 percent more frequently under the California conditions. This difference is approximately eight times its probable error.

From these data it is to be concluded that the changes in pericarp color from orange to red occurred more frequently under the California conditions as compared with the conditions in Arizona.

DISCUSSION

In previous studies on variegation, especially those mentioned in an early part of this paper, results were reported which suggest that a variegation is caused by the segregation of contrasting substances in the same gene. The size of a color change is large or small depending upon whether the necessary segregation within the variegation gene occurs earlier or later in development. As was pointed out by EMERSON, the probability of pericarp color changes effecting the germ-plasm and thus becoming genetic increases as they extend over larger segments of the surface of a kernel. The higher percents of color changes extending over one-fourth of the surface of a kernel and larger areas in the variegated and self-orange strains grown in California, as compared with the same strains grown in Arizona, indicate that genetic changes occurred more frequently under the California conditions. Since the genetic constitution of the several strains grown in the two localities were identical, it must be concluded that the observed differences in the frequency of genetic changes were due to the differences in the environmental conditions of the two localities.

Although the Arizona-grown variegations have fewer red markings that extend over relatively large areas, they appear to have more total color than the California-grown variegations. This suggests that the minimum amount of the pigment-producing component of the variegation gene necessary to cause pigment to develop in the pericarp may vary under different environmental conditions. According to this view, some of the segments which become pigmented in Arizona remain colorless in California.

These preliminary studies indicate rather definitely that environmental factors not only may modify the expression of a character in the soma, but may also have a direct influence on the germ-plasm.

SUMMARY

1. Strains of maize with variegated pericarp and strains with orange pericarp were grown under strikingly different environmental conditions as a preliminary study of the relation of environmental factors on the somatic expression and genetic changes of these pericarp color patterns.

2. Each strain was grown at Chula Vista, California and at Sacaton, Arizona. The chief environmental difference between these two localities seems to have been the higher and more variable temperature and greater transpiration at Sacaton. As a consequence of this difference the season required to mature the pericarp at Sacaton was fully a month shorter than that required at Chula Vista.

3. Eight variegated strains were grown at each of these localities, and in every case there was a definite and consistent difference in the variegation pattern.

4. The California-grown variegations consistently had more red markings covering one-fourth the surface of a kernel and larger areas than the Arizona-grown variegations. The significance of this difference is that under the California conditions more of the color changes extended into the germ-plasm and thus became genetic.

5. Changes from orange to variegation, and from orange to red also occurred more frequently under the California conditions.

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