A GENETIC ANALYSIS OF VARIEGATION[1]*

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Received April 10, 1924

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INTRODUCTION

Variegations refer to the presence of contrasting characters in the somatic tissues of individual plants and animals. They have been found

* The GALTON AND MENDEL MEMORIAL FUND has contributed toward the colored plate accompanying this article.

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

in the higher animals, affecting coat color, and in many species of plants, affecting flower color, seed-coat color, the distribution of the chloroplastid pigments, and, less frequently, morphological characters, as the decompounding of leaf parts. Every variegation has two or more different types around and between which it varies, but to which it is limited. Variegated pericarp of maize fluctuates between colorless and red with all possible patterns, ranging from fine to coarse, and from light to heavy. Leaves variegated for the chloroplastid pigments fluctuate between green and white, or green and yellow, with a large number of intergrading patterns. In several species of ferns compounding of the fronds occurs in patches of all sizes. The variety consists of individuals with compound fronds, individuals with typical fronds, and individuals with all possible combinations of typical and compounded pinnae.

Wherever they occur, variegations are fundamentally alike in their inconstancy, giving rise more or less frequently to individuals with only one of the contrasting characters of the variegation, with a series of intergrading individuals extending from one extreme to the other. The more extreme variations, as for example a red kernel on a variegated ear of maize or a branch with colorless leaves on a variegated plant, have been variously called sports, bud-sports, mutations, somatic mutations, and the like. Since the same kind of variability is common to all variegations, in plants as well as in animals, there must be some fundamental cause for it. The present paper is concerned with a genetic interpretation of the inconstancy peculiar to variegated plants and animals.

Variegations in pericarp color of maize furnish excellent material for a genetic analysis because of the many different variegation patterns, the high frequencies of color and pattern changes, and the ease with which an abundance of suitable material may be obtained.

PREVIOUS STUDIES OF VARIEGATION

De Vries (1905) was among the first to call attention to the inconstancy so common in variegated plants. He studied a variety of Antirrhinum with variegated flower color, in which he found a continuous range of variation from narrow- to broad-striped forms. These types, the narrow-striped less frequently than the broad-striped, gave rise to occasional self-red individuals. De Vries (1910) also studied a variety of *Hesperis matronalis* L. which varied in flower color from whitish to violet and gave rise more or less frequently to variegations. The occurrence and behavior of these flower-color variations seem to be exactly

like the color and pattern variations in orange pericarp as described in this paper. Of the color variations in Hesperis DE VRIES says:

"A glance at a large bed reveals the general distribution of color. At once the pale flowers are seen to be in the majority, whereas the whitish on the one hand and the lilac on the other are obviously rarer. The violet stand out conspicuously because they are not connected with the rest by any gradations. Except for this the variation is so continuous that it is almost impossible to express it in numbers. I have tried to arrange the plants in groups and to count the numbers of each group. And I give the numbers obtained in this way, only with the object of conveying to the reader the general impression which a bed makes on the observer, for it is inevitable that the limits between the groups should be somewhat arbitrary. . . ."

"For the purposes of these color valuations I picked a flowering cluster, if possible the terminal one, from each of the plants on a bed, brought them to my house and sorted them there. I made the following more or less clearly defined groups:

W. Whitish, always without stripes.
- W_1. Almost white; buds and withering petals almost white.
- W_2. White suffused with lilac; not darker when withering.
- W_3. Very pale lilac; buds lilac; only slightly darker when withering.

L. Lilac, sometimes striped or spotted.
- L_1. Definitely lilac, although pale; darker than W_3.
- L_2. Lilac; half as dark as V.

V. Violet, the color of the typical species."

The observations of DE VRIES indicate that the seed from the whitish-flowered plants give rise to progenies that are prevailingly whitish-flowered, but a few plants with lilac flowers and still fewer plants with violet flowers are produced. The seeds of the lilac-flowered plants produced plants with whitish flowers, plants with lilac flowers, and plants with violet flowers in approximately equal numbers. The lilac-flowered plants also produced a number of distinct variegations, which, DE VRIES says, can be split by selection in a plus and in a minus direction, into a pale lilac, or finely striped race on the one hand, and on the other into the dark lilac and frequently striped dame's violet.

CORRENS (1910) reported a study of the inheritance of the self-green condition which appeared as a bud sport on variegated-leaved plants of *Mirabilis Jalapa*, and of the self-red color of the flower which appeared in striped-flowered plants of the same species.

HARTLEY (1902) gave an account of an experiment with variegated maize. In a colorless or light-variegated strain he found an ear with a relatively large patch of red self-colored kernels. These red kernels were found to produce both red and white ears and were doubtless due to a somatic change from variegation, as suggested by EMERSON (1913).

EAST and HAYES (1911) found in a field of dent maize of unknown parentage a partly variegated and partly red ear, similar to the one described by HARTLEY. The red kernels were found to be heterozygous for self-color and no doubt represented a somatic color change from a light variegation.

EMERSON (1913, 1917) was the first to make a careful study of variegation in maize. He attributed the changes in pericarp color or variegation pattern to mutations in the pericarp gene in the course of development, and found that the changes from variegation to self-color are reversible but with different frequencies. The amount of tissue affected by any change in a gene varies from a fractional part of a single kernel to a patch covering a number of kernels and sometimes an entire ear, depending upon the stage in development at which the change occurred. He also found that in homozygous variegated and self-colored strains only one of the homologous genes mutates at a given time; and in plants heterozygous for colorless pericarp it is the variegation or self-color gene, never the colorless one, that changes. EMERSON has clearly shown that his interpretation of the observed changes in maize pericarp fits equally well the results found by DE VRIES in Antirrhinum, and the changes in leaf color and flower color of Mirabilis reported by CORRENS.

HAYES (1917) found mosaic pericarp, a very coarsely variegated type, to be equally or even more variable than the variegated patterns studied by EMERSON. He states that his results could be brought into line with EMERSON'S by assuming a separate factor for medium mosaic, M_m, which is allelomorphic to a factor for light mosaic, M_l and by further assumption of frequent germinal variations of M_l to M_m and *vice versa*. HAYES regards the hypothesis of slight germinal variations for the mosaic factors to be a simpler explanation of the results obtained. These germinal variations are thought to be due to certain heterozygous combinations which produce germinal instability.

GREGORY (1911) described some experiments with a variegated, or flaked, type of Primula, but made no mention of the occurrence of self-colored flowers on the variegated plants. His data indicate that the flaked type is inherited as a simple Mendelian recessive character.

PUNNETT (1922) described an interesting type of variegation in Lathyrus. The flowers of the strain in which the variegated individuals occur normally have a deep red standard and purple wings. In the variegated flowers the purple is replaced in part by a purplish pink, and thus forms a typical variegation. PUNNETT assumes that the variegated plants produce three kinds of gametes: (1) a purple gamete which is pure, (2) a red

gamete which also is pure, and (3) a flaked gamete which is a mosaic and thus impure. In inheritance the variegated plants are inconstant.

TERMINOLOGY

In maize there is a large series of multiple allelomorphs concerned in the production of pigments in the tissues of the cob and pericarp. An extended study of many of these allelomorphic genes was made by Doctor E. G. ANDERSON (unpublished). It was earlier believed by EMERSON (1911) that color in the pericarp and color in the cob are due to separate but closely or completely linked genes. More recent investigations, especially EMERSON'S (1913, 1917) studies of variegated pericarp and ANDERSON'S study of allelomorphism, indicate that a single gene controls the development of color in both pericarp and cob. The genes for cob and pericarp color mentioned in this paper are listed below:

RR, pericarp red, cob red.
WR, pericarp white (colorless), cob red.
WW, pericarp white (colorless), cob white.
OW, pericarp orange, cob white.
V_1V_1, V_2V_2, . . . V_nV_n, variegated pericarp, variegated cob.
RW, pericarp red, cob white.

The genes for colorless pericarp and white cob, colorless pericarp and red cob, and some of the genes for red pericarp and red cob are highly stable, while those for orange pericarp and white cob, and variegated pericarp and variegated cob are quite unstable. It has not yet been definitely determined whether the gene for orange pericarp and white cob and the genes for variegated pericarp and cob to which it gives rise belong to the allelomorphs of *P* described by ANDERSON. Use was made of the stable genes in the study of the unstable orange-pericarp and variegated-pericarp genes, as will be indicated later.

SOURCE OF MATERIAL

All of the material used in the present study originated in pedigreed cultures from a single ear, an illustration of which is shown in figure *A*, plate 1. It has a dilute red or orange pericarp and a white cob. Orange pericarp was found to be inconstant, giving rise to colors ranging from whitish to deep cherry red, and also a number of distinct variegations originate from it. The color variations and variegations will be described in a later part of the paper.

METHODS OF STUDY

The plants whose pericarp colors were to be studied were first crossed with plants having colorless pericarp and red cob. The crosses were made

by using pollen from the plants having the gene for colorless pericarp and red cob. The F_1 plants from such crosses have colored pericarp and red cob, because the colored pericarp of the female parent is dominant over the colorless pericarp of the male parent and the red cob of the male parent is dominant over the white cob of the female parent.

These F_1 plants were then back-crossed with strains having colorless pericarp and white cob. The progenies from such back-crosses consist of ears with colorless pericarp and red cob and ears with colored pericarp and white cob in approximately equal numbers. The ears with colorless pericarp and red cob represent the pericarp gene which was introduced in the original cross and are discarded. The ears with the colored pericarp and white cob, together with an occasional self-red or variegated ear, represent the gene that is being studied. Such ears have the gene for pericarp and cob color associated with the gene for colorless pericarp and white cob. By thus associating the inconstant genes that are being studied with stable genes which produce no color in the pericarp it is possible to eliminate the genes that are introduced in the various crosses, and to detect changes undergone by the gene under observation. For example, a strain with orange pericarp and white cob crossed with a strain with colorless pericarp and red cob will give F_1 plants with orange pericarp and red cob, of the constitution $\frac{OW}{WR}$. Such plants back-crossed with plants having colorless pericarp and white cob give the following two kinds of ears in approximately equal numbers: (1) Ears with colorless pericarp and red cob, of the constitution $\frac{WR}{WW}$. By discarding all ears with colorless pericarp and red cob the *WR* gene, which was associated with the *OW* gene in the first cross, was eliminated. (2) Ears with orange pericarp and white cob of the constitution $\frac{OW}{WW}$. Ears with variegated pericarp, and ears with red pericarp are regarded as being due to modifications of the *OW* gene.

The ears of each progeny were first studied for color intensity, variegation pattern, color changes, and the like, and grouped accordingly. Each ear was examined for color or pattern changes extending over more than a single kernel. The kernels were then shelled off the cob and each kernel was examined separately and classified as shown in the tables.

ACKNOWLEDGEMENTS

The writer is indebted to Doctors R. A. EMERSON and E. G. ANDERSON for the strain of orange-pericarp and white-cob maize used in this study, and for valuable suggestions as to the possible relationships of the various variegated patterns. Valuable assistance has also been rendered by Mr. GEORGE KLINE in making the drawings for figure *C*, plate 1, and in coloring the photographs for figures *A* and *B*, plate 1, and by Mr. J. F. BARHAM in making all of the photographs in the accompanying figures.

INCONSTANCY OF ORANGE PERICARP

The pericarp color which has been given the descriptive term "orange" is in fact a dilute red which is highly inconstant. It not only varies in intensity of color, but changes to colorless, to red, and to a number of distinct types of variegation.

Variation in color intensity of orange pericarp

Since the ears with orange pericarp and white cob in each back-cross progeny came originally from the same gene, a certain uniformity in color intensity was expected. This expectation was not fulfilled. When orange kernels of a certain color intensity are planted progenies are produced which vary in color from almost colorless to deep cherry red. In order to make a classification of these ears, arbitrary classes of color intensity were established, ranging from colorless, class A, to cherry red, class J. In figure *B*, plate 1, is illustrated a series of ears representing color-intensity classes, from class B, with a slight tinge of color, to class I, which is red.

Plantings were made from pedigreed ears of the various color-intensity classes with the results recorded in table 1. The progenies consisted of ears with colorless pericarp and red cob and ears with orange pericarp and white cob in approximately equal numbers. Occasional ears are found with variegated pericarp and variegated cob. In all cases the orange ears varied in color intensity around the color intensity of the parent ear as the modal class. When these ears were grouped in the arbitrary color-intensity classes there resulted distributions which approach that of a normal or skewed curve. Even the lightest ears are capable of producing progenies which range in color from almost colorless to deep cherry red. That these color variations have a genetic basis is well shown by the ear illustrated in figure 1 (page 381). This ear has two shades of red which are sharply delimited. The orange kernels from this ear produced plants with various shades of orange pericarp, typical of this strain, while the red kernels produced plants with dark-red ears.

COLOR CHANGES IN ORANGE PERICARP

The orange color of maize pericarp is due apparently to a reduced amount of pigment which is uniformly distributed throughout the pericarp tissue. Variations in the amount of pigment produce colors of different intensities. A striking feature of orange pericarp is the separation into its component colors, red and white (colorless), as may be seen on the ear illustrated in figure 2 and the kernels illustrated in figure *C*, plate 1. The orange may also change to darker orange and red, as well as to lighter orange and colorless, with no apparent production of the other component color. The ears of the different color-intensity classes were studied separately with the results given in tables 2, 3 and 4. In recording these data a special effort was made to get an accurate classification of the changes from orange to variegation. A kernel with a streak of colorless adjacent to a streak of red pericarp was classes as having a "line" of variegation. Since changes from orange to colorless occur very rarely, most of the apparently colorless areas represent changes to variegation. The data on changes from orange to red are accurate for areas which covered one-eighth of a kernel and larger areas. It will be noted that color changes of small size occur very frequently, while those large enough to cover more than a single kernel are exceedingly rare.

The orange ears were first studied for color changes extending over more than a single kernel and only 17 such changes were found in the two lots of ears studied. Most of these large changes were neither red, colorless, nor variegated, but dark-crown (a non-inherited pattern described by EMERSON (1917). Twelve of the large patches were changes to dark-crown, and 5 were changes to red. No change to variegation covered more than a single kernel. The kernels were then shelled off the ear and studied individually and 42,622 color changes of various kinds were recorded. Of these only 54 covered an entire kernel, 57 extended over approximately three-fourths of a kernel, 117 were as large as a half kernel, 254 covered one-fourth of a kernel, 1,222 were as large as one-eighth of a kernel, and 40,481 were smaller in size. If the size of color change is taken as an index of the stage in development at which the change occurred, these data indicate that the gene for orange pericarp persists until a later stage in development, when it may lose its stability, due possibly to changing conditions in the protoplasm as the plant approaches maturity, or due to a mechanical segregation of pigment-producing and non-pigment-producing *gene elements* as will be described later. Such gene changes are to be expected to occur more frequently in later stages of development because

LEGEND FOR PLATE 1

FIGURE *A*.—The ear with orange pericarp from which all the material used in this study originated.

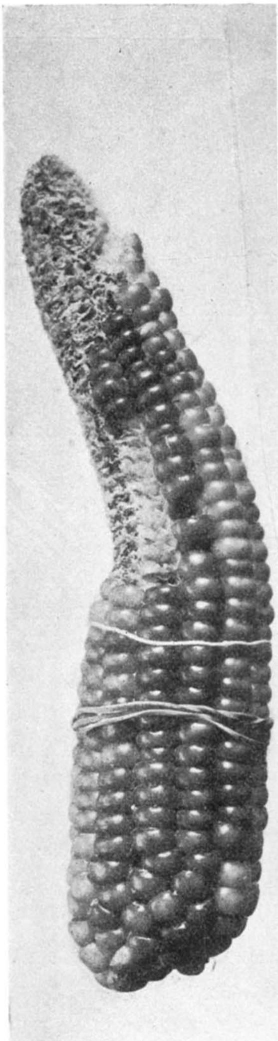
FIGURE *B*.—A series of ears showing the variation in color intensity of orange pericarp.

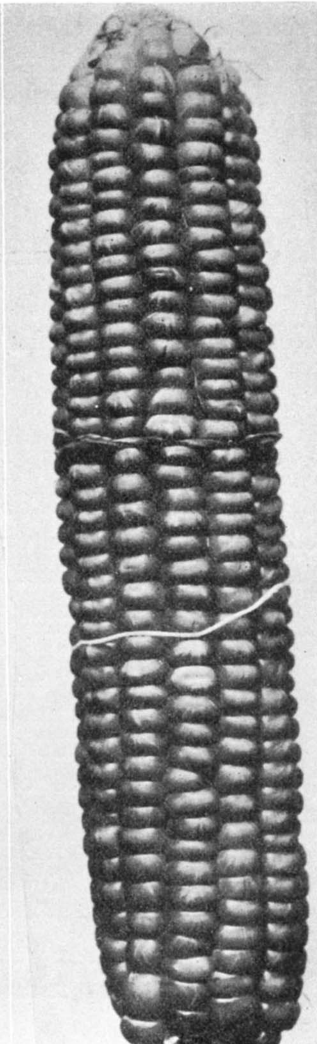
FIGURE *C*.—Orange kernels with equal and adjacent segments of red and white (colorless). A variegation results when this process extends over the entire surface of the kernel. The intensity of the red segments varies with the intensity of the orange of the kernel.

FIGURE *A*

FIGURE *B*

FIGURE *C*





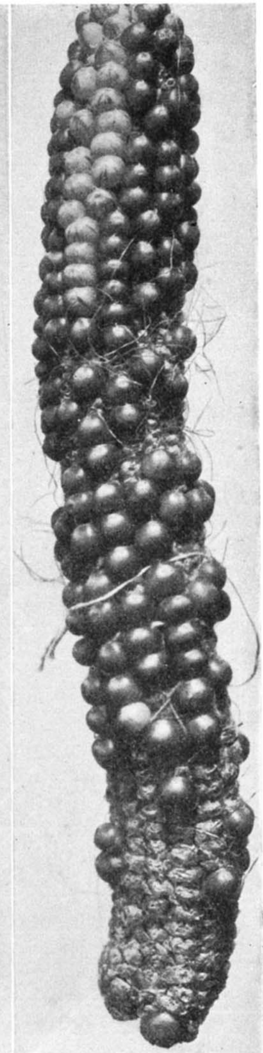


FIG. 1 FIG. 2 FIG. 3

FIGURE 1.—A light-orange ear with a large patch of its surface changed to deep orange or red. This is evidence that such changes have a genetic basis and are due to a change in the gene concerned.

FIGURE 2.—An ear with medium-orange pericarp showing the breaking up of the orange color into adjacent segments of red and white (colorless).

FIGURE 3.—An orange ear with a large patch of its surface changed to a typical variegation. This shows that orange and variegated pericarp are expressions of changed conditions in the same gene.

of the increased number of cells, but the rate of change is accelerated in late stages of development far beyond the expectancy for the increased number of cells. A significant characteristic of orange pericarp is that it persists until a late stage in development, when it breaks up into its component colors, red and white (colorless), but growth stops before the segregation in the somatic cells is completed so that a large part of the pericarp remains orange self-colored.

RELATION OF COLOR INTENSITY TO RATE AND DIRECTION OF COLOR CHANGES

Orange pericarp of different color intensities changes to red, colorless and variegations, but with different frequencies.

Frequency of changes from orange to red

To get a measure of the rate of the color changes from orange to red only those that were accurately classified can be used. As has already been mentioned only the changes to red which extended over approximately one-eighth or more of a kernel were accurately recorded.

In table 2 are recorded the color changes from orange to deeper orange and red. In family 1504 the number of changes in orange pericarp of different intensities varied from 6 to 12 per thousand kernels studied. In the 41,564 kernels observed, 337 changes covering one-eighth of the surface of a single kernel, or larger areas, were recorded. This would be a frequency of 8.2 changes to red per thousand kernels. In family 1525 the changes to darker orange and red were more frequent, varying in orange pericarp of different intensities from no changes to 36 changes per thousand kernels observed. A total of 260 changes to red covering one-eighth of the surface of a kernel, or larger areas, were found in the 15,603 kernels studied. This is a frequency of 17 changes to red per thousand kernels.

Considering the two families together there was a total of 597 changes to red covering one-eighth of a kernel, or larger areas, in the 57,167 kernels observed. This is an average frequency of change from orange to red of about 10 per thousand kernels. Only 5 of the observed changes to red extended over more than a single kernel, 17 were as large as a single kernel, and the remainder were of smaller size. These observations indicate that pericarp color-changes from orange to red are infrequent until late in development, when they occur with a relatively high frequency. In general it may be said the frequency of change from orange to red increases with the color intensity of the orange pericarp.

In table 2 also are given the frequencies of changes to dark crown. In family 1504 the number of such changes in the orange pericarp of different

intensities varied from 12 to 42 per thousand kernels observed. In the 41,564 kernels studied there were 887 changes to dark crown recorded. This is a frequency of 20 dark crowns per thousand kernels. In family 1525 the number of dark crowns varied from 7 to 20 per thousand kernels, with an average frequency of 13 per thousand kernels. In the two families studied there was a total of 1088 dark crowns observed in the 57,167 kernels studied. This would be an average frequency of about 19 changes to dark crown per thousand kernels.

Frequency of changes from orange to lighter orange, light variegations or colorless

It was not possible to classify accurately the changes from orange to lighter colors. When small areas are concerned it is not possible to distinguish between colorless and variegations. In table 3 are listed all changes from orange to lighter colors. There was a total of 407 such changes in the 57,167 kernels observed, or about 7 in every thousand kernels. In general the frequencies of the changes to lighter colors vary inversely as the color intensity of the orange pericarp.

A record was also made of the changes to light crown. A total of 1234 kernels were partly or fully light-crowned. This is a frequency of 22 light crowns per thousand kernels as compared with 19 dark crowns per thousand kernels.

Frequency of changes from orange to variegation

The classification of the changes from orange to variegation was made with sufficient accuracy that all of the classes can be used in obtaining a measure of the frequency of the changes.

In table 4 are listed the changes from orange to variegation for the different color-intensity classes of families 1504 and 1525. There was a total of 14,371 changes from orange to variegation in the 57,167 kernels studied. The frequency of changes varies from 42 to 781 per thousand kernels. It is an interesting fact that variegations occur with a higher frequency in the classes of medium intensity of orange. No variegated areas covering more than a single kernel were found on the ears of families 1504 and 1525. Only 8 variegations covering as much as a kernel were found. Of the 14,317 variegations recorded 761 covered one-eighth or more of the surface of a kernel, while 13,556 were smaller in size.

The 761 variegations covering one-eighth or more of a kernel give a frequency of about 13 changes from orange to variegation per thousand

kernels. Equivalent changes from orange to red occurred with a frequency of about 10 per thousand kernels.

If the size of a color change may be taken as an index of the stage in development when the change occurred, the data in table 4 show definitely that the orange pericarp persists until late in development, when it changes to variegation with a high frequency.

The illustration in figure 3 shows a change from orange to variegation that extended over a number of kernels. Changes that affect so large an area are exceedingly rare.

TYPES OF VARIEGATION ORIGINATING FROM ORANGE PERICARP

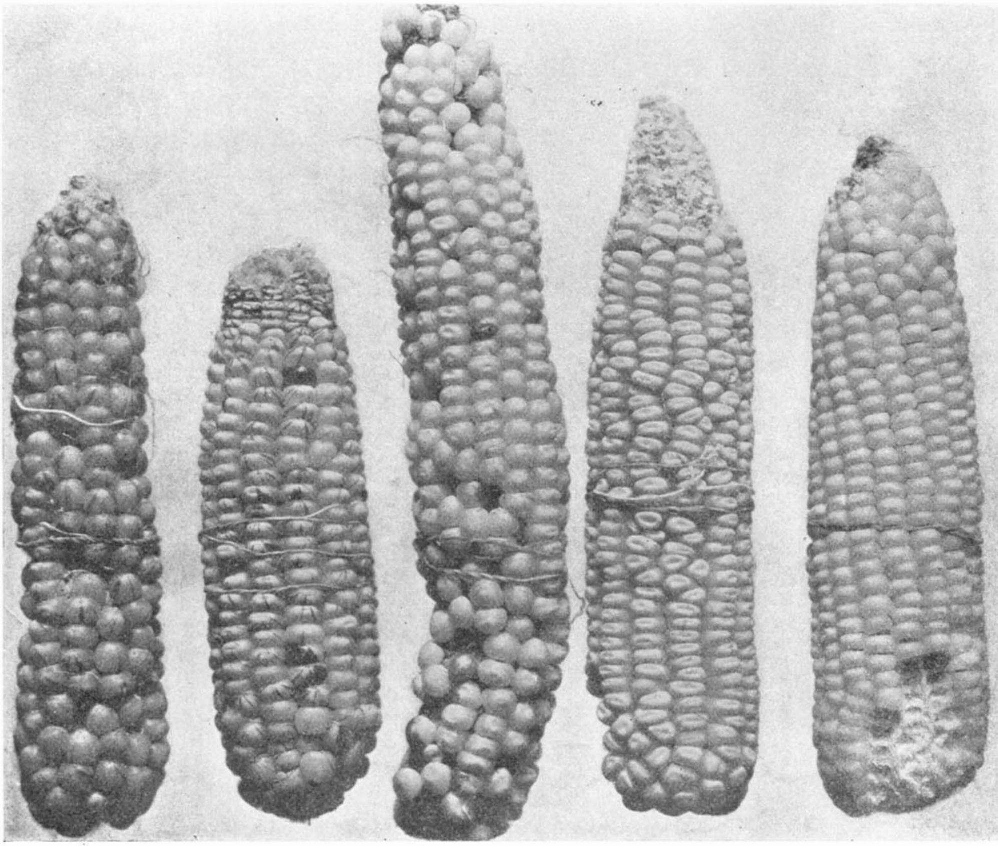
Orange pericarp gives rise to a number of distinct variegated patterns. These range from a type that is exceedingly light, often having a single splash of color on an entire ear, to a very heavily variegated type with much color in the form of heavy lines and bands, and with occasional patches of self-red and dark-crown extending over a number of kernels. There seem to be two fairly well defined series of patterns which, for descriptive purposes, may be called (1) *light* variegations, with markings in the form of splashes, lines, and segments that are well dispersed, and (2) *heavy* variegations, in which the surface of the kernels is thickly covered with color markings.

In figure 4 are shown ears representative of the light-variegation patterns. Ears A and B represent a light variegation with a very coarse pattern. This pattern is distinctive in that the markings are in the form of broad lines or bands, with the remainder of the surface quite free from color markings. Ear C has an intermediate type of light variegation. A number of kernels have large segments or the entire surface colored while many kernels have smaller color markings. The variegated type represented by ear C is different from all other variegations in that the color markings are pink instead of red. The ear E represents an extremely light type of variegation, sometimes with only a single splash of color on an entire ear.

Representative types of heavily variegated patterns are illustrated in figure 5. Ear A has a very coarse pattern, made up of heavy lines and bands of color. Ears B and C represent an intermediate type of heavy variegation, with many lines and splashes of color, but without the coarse bands. The last ears, D and E, are typical of a very finely variegated type. The kernels are heavily marked but all the markings are in the form of fine splashes and lines uniformly distributed over the surface of the kernel.

INHERITANCE OF THE DIFFERENT VARIEGATION PATTERNS

Progenies were grown from each of the ears illustrated in figures 4 and 5 in order to determine the inheritance of the various patterns. The results of these tests are given in table 5.



A B C D E

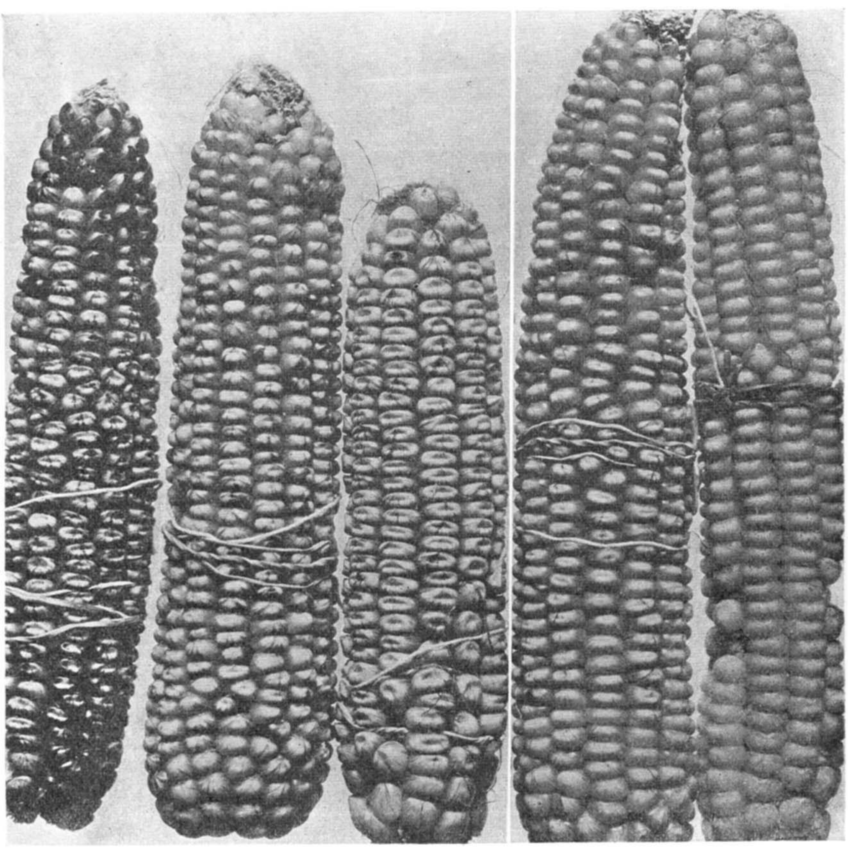
FIGURE 4.—A series of ears having a light pattern of variegation ranging from ears with many bands and lines of red (ear A) to ears that have often only a single splash of red color (ear E).

Inheritance of the light-variegation patterns

The parent plant of ear B, figure 4, had the gene for variegation associated with a gene for red cob and colorless pericarp and was back-crossed with a plant homozygous for white cob and colorless pericarp. The progeny consisted of 25 ears with red cob and colorless pericarp and 22 ears that

were variegated. Three of the variegated ears were coarser in pattern than the parent ear, 16 ears had a pattern quite similar to the parent ear, 2 ears had a distinctly finer pattern and one ear had only a few splashes of color on the entire ear.

The ear C, figure 4, was produced on a plant grown from one of the variegated kernels of the ear illustrated in figure 3. It had a gene for variegated pericarp associated with a gene for red cob and colorless pericarp and was back-crossed with a plant homozygous for white cob and colorless pericarp. The progeny consisted of 70 ears with red cob and colorless pericarp and 66 variegated ears. Three of the variegated ears



A B C D E

FIGURE 5.—A series of ears having a heavy pattern of variegation, ranging from ears with heavy bands and lines of red (ears A and B) to ears with many fine lines and splashes of red uniformly distributed over the kernels (ears D and E).

had a coarse pattern, like ear B, figure 4, 62 ears had the pattern of the parent ear, and one ear had a light pattern like that of ear D, figure 4.

Ear D, figure 4, was open-pollinated and produced a progeny with red cob and colorless pericarp, red cob and red pericarp, and variegated pericarp. All of the variegated ears were of the pattern of the parent ear.

Inheritance of the heavy-variegation patterns

Ears A and B in figure 5 were open-pollinated. A large percentage of the variegated ears of their progenies had the variegation patterns of the parent ears, but ears with medium and fine patterns were also found.

The plant that produced ear C, figure 5, was heterozygous for red cob and colorless pericarp and variegated cob and variegated pericarp and was back-crossed with a plant homozygous for white cob and colorless pericarp. The progeny consisted of 55 ears with red cob and colorless pericarp, 52 ears with variegated cob and variegated pericarp, and one ear with red cob and red pericarp. Thirty-five of the variegated ears had the pattern of the parent ear, 15 ears had a coarser pattern, 11 being like ear B, figure 5, and 4 like ear A, figure 5, and 2 ears had the very fine pattern of ear E, figure 5.

The parent plant of ear D, figure 5, was also heterozygous for variegated cob and pericarp and for red cob and colorless pericarp and was back-crossed with a plant homozygous for white cob and colorless pericarp. The resulting progeny consisted of 36 ears with red cob and colorless pericarp and 37 ears with variegated cob and variegated pericarp. Seventeen of the variegated ears had the fine pattern of the parent ear, 15 ears had a medium pattern much like C, figure 5, and 5 ears had a pattern as coarse as that of ear B, figure 5.

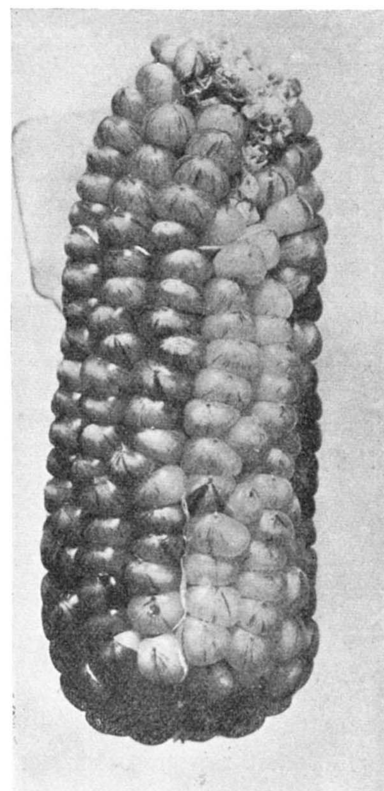


FIGURE 6.—An ear with two patterns of variegation, showing that pattern differences are due to changes in the gene.

The heavy variegations form a continuous series ranging from very coarse to very fine patterns and cannot be grouped into distinct types. That these variegation patterns have a genetic

basis is shown by the occurrence of more than one pattern on the same ear, as may be seen from the illustration in figure 6. Whenever two variegation patterns occur on the same ear they are sharply delimited and evidently represent a change in the variegation gene.

The progenies from both the light and heavy variegations include a number of distinct patterns in the form of a frequency curve, with the pattern of the parent ear as the modal class. In this respect the variegations are like the orange pericarps from which they originated.

In the progeny of every variegated ear tested, ears with red cob and colorless pericarp and ears with variegated cob and variegated pericarp occurred in approximately equal numbers, thus indicating that a single pericarp gene was concerned in the production of each variegation. The variation in the pattern of variegation in each progeny is thought to be due to changes in the variegation gene.

RELATION BETWEEN COLOR INTENSITY OF ORANGE PERICARP AND TYPE OF VARIEGATION

In order to determine the relation between color intensity of orange pericarp and type of variegation several bushels of orange ears were grouped in five color-intensity classes ranging from very light orange to red. All kernels that had enough of the surface variegated to be classified were taken from each group of ears and classed as light variegations or heavy variegations, with the results given in table 6. The very light orange ears produced only light variegations, while the red ears produced nothing but heavy variegations. The number of heavy variegations increases with the intensity of orange pericarp. These results show that there is a definite correlation between the intensity of orange color and the types of variegation that are produced.

Color changes in the variegated patterns

The variegated patterns undergo somatic color changes to dark crown, red orange, colorless, and to other patterns of variegation.

Frequency of changes in light variegation

The ears of the progenies grown from the ears B, C and D, in figure 4, were studied for color changes with the results recorded in table 7. A total of 3181 kernels were observed in the strain having a fine pattern. There were 7 kernels with one-eighth or more of their surface changed to self-red, or approximately 2 such changed kernels for every thousand kernels observed. Also 30 kernels were partly or fully dark-crowned, giving a

frequency of 9.43 such changes per thousand kernels observed. No color change was observed that covered more than a single kernel.

The strain with a medium pattern of light variegation, the progeny of ear C, figure 7, is different from other variegations in that the color is deep pink instead of red. The number of kernels observed was 9286. Of these, 198 kernels had one-eighth or more of the surface pink self-colored. This would be a frequency of change to pink color of 21.28 per thousand kernels observed. The frequency of change to self-color was about ten times as great in the medium as in the fine pattern, the latter having seven kernels with one-eighth or more of their surface changed to red, giving a frequency of change of 0.75 kernels per thousand studied. There were 74 changes to dark crown covering one-fourth of a kernel or larger areas, which is a frequency of 8 changes per thousand kernels observed in the medium pattern, as compared with 9.43 for the fine pattern.

Changes to self-color and dark crown occur much more frequently in the coarse pattern than in the medium and fine patterns. Among the 2966 kernels from coarsely variegated ears, were found 258 changes to red affecting one-eighth or more of a kernel, and 117 changes to dark crown. This would be one change to red for every 11.5 kernels, or 87 changes for every thousand kernels studied, and one change to dark crown for every 25.4 kernels, or 40 per thousand. Changes to self-color occur 40 times as frequently in the coarse pattern as in the fine and 4 times as often in the medium pattern. The changes to dark crown occur about 5 times as often in the coarse pattern as in the medium and fine patterns.

Frequency of changes in heavy variegation

The ears with heavy variegation patterns were separated into groups having coarse, medium and fine patterns, respectively. The ears of each of these groups were studied for color changes to self-color with the results given in table 8. Only areas covering one-fourth or more of a single kernel were recorded.

The ears with a coarse variegation pattern yielded a total of 86,550 kernels. There were 48 changes to red that extended over more than a single kernel; 225 changes were as large as a single kernel, or 2.6 self-red kernels per thousand kernels studied. Color changes affecting smaller areas are more and more frequent as is shown in table 8. There were 1978 color changes affecting one-fourth of a kernel, which is a frequency of 23 changes per thousand kernels. Considering all changes to self-color covering one-fourth of a kernel or larger areas, there was a total of 3840 in the

86,550 kernels observed. This is a frequency of 44 changes per thousand kernels from the coarsely variegated ears.

There was a total of 18,427 kernels taken from the ears with a medium-coarse variegation pattern. Only two changes to self-red covering more than a single kernel were found. There were 7 color changes covering a single kernel which is a frequency of less than 0.4 kernel per thousand kernels observed. Forty-six kernels had one-half of the surface self-colored and 69 kernels had approximately one-fourth of the surface self-colored, with frequencies equal to 2.5 and 3.7 changes per thousand kernels, respectively.

Among the 18,427 medium variegated kernels there was a total of 131 changes to self-color covering one-fourth of a kernel or larger areas. This would be an average frequency of about 7 changes to self-color per thousand kernels, as compared with 44 such changes in the coarsely variegated patterns.

There was a total of 7560 kernels from the finely variegated ears. No color changes extending over more than a single kernel were found. There were 2 self-red kernels, 6 kernels with half the surface red, and 11 kernels with approximately one-fourth of the surface red. Among the 7560 kernels were found a total of 20 changes to red covering one-fourth of a kernel or larger areas. This is equal to an average frequency of 2.6 changes per thousand kernels.

From these results it is evident that changes to self-color increase with the coarseness of the heavily variegated pattern.

Frequency of changes to dark crown in the variegated types

A record was kept of the changes to dark crown in the variegated kernels studied, with the results given in table 9. Of the 86,550 kernels taken from heavy coarsely variegated ears 2739 kernels were recorded as partly dark-crowned, 870 kernels were fully dark-crowned. There were 822 dark-crown patches that extended over more than a single kernel. This would be a total of 4431 dark-crown changes, which is a frequency of about 51 changes per thousand kernels. In the heavy medium variegations 891 changes to dark crown covered a part of a kernel, 142 kernels were fully dark-crowned, and 66 dark-crown changes extended over more than a single kernel. In all there were 1073 changes to dark crown in the 18,427 kernels observed. This a frequency of approximately 58 changes per thousand kernels. In the heavy fine variegation, of the 7566 kernels studied, 300 kernels were partly dark-crowned, 81 were fully dark-crowned and 33 changes to dark crown extended over more than a single kernel.

The total of 414 dark-crown changes in the 7560 finely variegated kernels is a frequency of 55 per thousand kernels. A summary of the changes to dark crown in the variegated patterns follows:

Types of variegation	*Number of dark-crown per 1000 kernels studied*
Heavy coarse,	51.0
Heavy medium,	58.0
Heavy fine,	55.0
Light coarse,	40.0
Light medium,	8.0
Light fine,	9.5

In the heavy variegations dark crowns occurred with about the same frequency in all the types. In the light variegations dark crowns occurred about as frequently in the fine type as in the medium type, but in the coarse type the frequency was five times as high.

Frequency of changes from heavy to light variegations

All the heavy types of variegation studied change to colorless or light-variegated types. Since colorless types originate from the heavy variegations only rarely, it may be assumed that the apparently colorless areas are in reality light variegations. The frequency of change from heavy variegation to light variegation as observed in three lots of ears is given in table 10. In the coarse pattern there was an average of about 8 changes to light variegation per thousand kernels, while in the medium pattern there were approximately two light variegations per thousand kernels. Only changes affecting one-fourth of a kernel or larger areas were recorded.

Reverse changes from variegation to orange pericarp

The variegated types revert occasionally to orange pericarp. While the patches that cover one-fourth of a kernel or larger areas can be distinguished from red easily, the smaller areas are more difficult to classify accurately. Only a few such reverse changes have been observed. In family 1501 were found 2 kernels with one-half of the surface changed to orange, and one kernel with one-fourth of the surface orange-red in a total of 40,975 kernels. Among the medium-variegated kernels of family 5492 one kernel was found with about one-sixteenth of its surface changed to orange in the total of 11,732 kernels observed. Among the 866 finely variegated kernels of family 5492 were found 17 kernels with about one-sixteenth of the surface changed to orange.

Changes from pink variegation to red variegation

In typical variegations in maize pericarp the contrasting colors are white (colorless) and red. In family 5497, as already mentioned, the

colored areas of the variegated kernels are light pink instead of red. This pink type of variegation gives rise to the typical variegation with red-pigmented areas. Of the 9286 pink-variegated kernels studied 7 had red variegations which evidently represent independent changes from the pink type. This would be a frequency of nearly 0.8 changes per thousand kernels.

COLOR CHANGES IN THE CHERRY-RED PERICARP THAT ORIGINATED FROM ORANGE PERICARP

The deep-red pericarps that originate from orange pericarp are fairly constant, but reverse changes do occur as indicated below.

Reverse changes from cherry-red to orange

A large number of ears with cherry-red pericarp that originated from strains having orange pericarp, having a total of 32,568 kernels, were studied for color changes. The kernels were shelled off the ears and examined individually for color changes. The most frequent color change was the reverse change to orange. One kernel was one-half orange, 2 kernels were one-fourth orange, 48 kernels had a band of orange color, and 247 kernels had a fine line of orange color. Excluding the kernels that had only a fine line of orange pericarp, the frequency of change from red to orange was about 1.6 per thousand kernels. Also 71 kernels had a part of the crown changed to orange and 8 kernels were fully orange-crowned.

Reverse changes from cherry-red to variegations

The changes from cherry-red to colorless or variegation were less frequent than the changes to orange. In the 32,568 kernels studied the largest color change to variegation covered approximately one-fourth of a kernel, and only one change as large as this was found. There were 8 kernels with a narrow band of colorless pericarp and 16 kernels with a fine line of colorless pericarp. Excluding the kernels with only a fine line of colorless pericarp, the frequency of change from red to variegation was about one change in three thousand kernels.

There were also a few changes to light crown. One kernel was entirely light-crowned, and 20 kernels were partly light-crowned.

Stability of colorless pericarp originating from orange

A large number of ears with colorless pericarp, derived from the orange through the variegated patterns, were examined for color changes, but no such changes have yet been observed. The kernels were shelled off the ears and examined individually. From these studies it may be concluded

that the gene for colorless pericarp which originates from the orange-pericarp gene has the stability of the ordinary white-cob colorless-pericarp gene.

Summary of color changes in the orange-pericarp series

A summary of the various changes, including the direction and frequency of changes, is given in figure 7. The most frequent changes are from orange to variegation (13 per thousand kernels) and from orange to red (ten per thousand kernels). The heavy variegations also appear to be quite unstable, as they change to lighter variegations with a fairly high frequency (eight per thousand kernels). Changes from red to orange, from red to variegation, and from variegation to orange occur with a low frequency, ranging from 0.3 and 1.6 changes per thousand kernels observed.

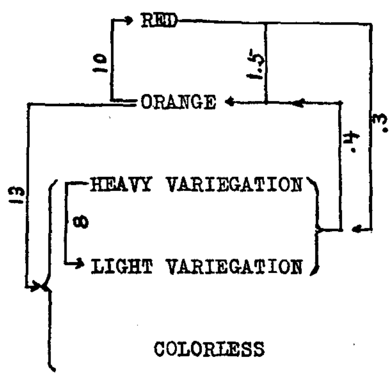


FIGURE 7.—A diagram to show the relative frequencies of pericarp-color and pattern changes expressed in numbers per thousand kernels.

INTERPRETATION AND DISCUSSION

Any interpretation of the pericarp-color and pattern changes described on the foregoing pages must account for the following facts: (1) Orange pericarp is inconstant; it produces progenies that vary in color intensity from a slight tinge of color to deep cherry-red, in the form of a frequency curve. (2) The orange color separates into its component colors, red and white (colorless), to form a variegation. Variegations seem to occur more frequently in the orange pericarp of medium intensity than in the extremely light or extremely dark classes. (3) The variegations are inconstant, varying in pattern from fine to coarse in the form of a frequency distribution. Some patterns are *light*, with few well-dispersed markings, while other patterns are *heavy*, made up of many closely-set color markings. (4) There is a correlation between intensity of orange color and the type of variegation which originates from it. The percentage of heavy variega-

tions increases with the color intensity. (5) All color and pattern changes are reversible, but with different frequencies.

The nature of the gene

The gene is doubtless highly complex in its organization so that changes in its chemical composition or rearrangements of its structural parts occur more or less frequently in all genes. Whatever the nature of the genes may be, the work on Drosophila has shown that they occupy definite loci in the chromosomes. The most distinctive feature of the gene, as pointed out by MULLER (1922), is its property of self-propagation. In preparation for each mitosis each gene must reproduce itself by attracting to itself from the protoplasm materials of a similar kind which are then separated into the daughter genes. Gene constancy demands that the daughter genes be identical in chemical composition and in structural arrangement. That genes do change, and that they are capable of changing so as to produce a number of different effects is shown by the common occurrence of multiple allelomorphs. In most cases the changes are quantitative so as to produce a linear series of effects.

The changes or variations in the gene for orange pericarp form an orthogenetic series of colors ranging from whitish to deep cherry-red. Such a quantitative variation can be most easily explained by assuming that the gene for orange pericarp is a compound structure, made up of pigment-producing *gene elements* and non-pigment-producing *gene elements*. According to this view the intensity of color depends upon the relative numbers of the contrasting gene elements incorporated in the structure of the gene. An excess of non-pigment-producing gene elements would produce a light orange color, while an excess of the pigment-producing gene elements would produce a deep orange or red color.

It has been found that orange pericarp of medium intensity produces a progeny ranging from nearly colorless to dark orange or red in a distribution which approaches that of a normal curve, the modal class being medium orange like the ear from which the planting was made. This distribution can be skewed to the light or dark end of the color range by planting from a light-orange ear or a dark-orange ear, respectively. These results would obtain if the gene elements are self-propagating and are divided by random assortment, at each mitosis, into the daughter genes. DE VRIES's observations indicate that color intensity in Hesperis behaves in inheritance like the corresponding color variations in maize. The seeds of whitish plants produced progenies that were predominately whitish-flowered, but some lilac-flowered plants and a few violet-flowered

plants also appeared. The lilac-flowered plants, which correspond to the medium orange colors in maize, produced offspring with the whole range of color from whitish to violet. Only 5 violet-flowered plants were tested and they produced violet-flowered offspring.

Evidently the various colors in the pericarp of maize and in the petals of Hesperis are the expressions of genes that are made up of definite numbers of pigment-producing and non-pigment-producing gene elements. Each gene must reproduce itself between every two mitoses, and many mitoses occur between the fertilized egg and the formation of the tissues in which the color is expressed. Because of the random assortment of gene elements the existing relation between the contrasting gene elements would be maintained in a relatively large number of plants. In a somewhat smaller number of plants there would be expected a slight excess of the pigment-producing or non-pigment-producing elements in the tissue in which the color is expressed, due to slight inequalities in the separation of the elements at the mitoses, or to a slight difference in the rate of reproduction of the individual gene elements. In the same manner a larger excess of one or the other kind of gene element would be expected in a smaller number of plants, and so on. The progeny of an individual with a gene behaving in development as indicated above would consist of a series of individuals ranging from very light colors, due to a gene with an excess of gene elements for no color, to deep colors, due to a gene with an excess of color-producing gene elements.

A similar quantitative expression of color would result in the presence of multiple modifying factors similar to the modifiers of eosin eye color in Drosophila, reported by BRIDGES (1919). Suitable studies to determine whether or not modifying factors influence color intensity in orange pericarp have not been made, but changes from medium orange to full red, as illustrated in figure 1, would hardly be expected if a large number of modifying factors are concerned.

The most striking as well as the most significant feature of orange pericarp is that it separates into its component colors, red and white (colorless). It will be recalled that in Hesperis a similar separation of colors occurs. In maize pericarp the replacement of orange by adjacent and equal segments of red and white, as illustrated in figure *C*, plate 1, may be considered good evidence that the gene which had been producing the orange color divided into daughter genes in such a way that one of them included all of the pigment-producing gene elements while the other lacked them entirely. The illustrations in figure *C*, plate 1, represent kernels from orange ears of different intensities. The adjacent red and white seg-

ments represent the cell progenies of the daughter genes with and without pigment-producing gene elements, respectively. In orange pericarp the medium colors separate into red and white with a higher frequency than the lighter and darker colors. Apparently, the same thing is true of Hesperis, as DE VRIES (1910) described the lilac-colored flowers as being often striped or spotted. The fact that color segregation in the somatic tissues of both maize and Hesperis occurs most frequently in the colors of average intensity indicates a relationship between the relative numbers of the two kinds of gene elements in the structure of the gene and its stability. Like gene elements are mutually attractive while the unlike ones are mutually repulsive. A gene with only one kind of element in its structure, as the one for colorless pericarp, should be compact, due to the mutual attraction of the like elements, and therefore highly stable. Similarly a gene with unlike elements in its structure, as the gene for orange or variegated pericarp, would tend to be dispersed and its structure would be the resultant of the unlike genes in a state of equilibrium with varying stability.

EMERSON (1922) made the important observation that changes to self-red occur somewhat more frequently in heterozygous than in homozygous variegated ears, and concluded that a gene for variegation is more mutable when associated with a gene for colorless pericarp than when it is present in the duplex condition. It will do no harm, it is hoped, to offer an interpretation of this observation based on the gene structure discussed above. The higher frequency of change to self-red in pericarp tissue which has a gene for variegation associated with a gene for colorless may be due simply to an accumulation of pigment-producing gene elements. Any accumulation of a particular kind of element would be retained if there is no interchange of parts between the highly stable colorless-pericarp gene and the variegated gene with which it is associated. In homozygous variegated pericarp the associated genes are made up of similar structural units. If these genes which are unstable because they are made up of contrasting gene elements, interchange parts between mitoses any accumulation of one kind of gene element in one of the genes might be negatived by an accumulation of the contrasting gene element in the homologous gene, so that the actual number of changes to red would be less than in pericarp tissue where the unstable variegation gene is associated with a highly stable gene like the one for colorless pericarp between which there is no interchanging of parts.

An inconstant gene, like the one responsible for orange pericarp in maize or the one that causes lilac color to develop in the petals of Hesperis may be due to a single chemical change of such a character as to change the

nature of one of the structural elements of the gene. This change followed by a random assortment of the gene elements would provide the mechanism for the quantitative expression of color and for the occurrence of variegations in the tissues of the pericarp of maize and of the petals of Hesperis.

The nature of variegation

The equal and adjacent segments of red and colorless tissue on otherwise orange-colored kernels represent early stages in the production of a variegation. In such kernels the separation of the orange into red and white began too late in development of the pericarp to affect more than a small segment of the tissue. When this separation begins earlier in the development of the pericarp tissue the variegation extends over larger segments, a whole kernel, or a number of kernels.

The fundamental difference between orange pericarp and variegated pericarp is that in the former the pigment is diffused throughout the tissue, while in the latter the pigment is limited to segments and patches of various sizes. In the gene for orange pericarp the complete segregation of unlike gene elements usually occurs not at all, or only very late in development, so that only small segments of red and colorless tissues are produced. In the gene for variegation the segregation of unlike gene elements begins early enough so that they are completely segregated by the end of pericarp-tissue development.

There is a decided correlation between the intensity of orange color and the type of variegation that originates from orange pericarp. Practically all of the variegations that spring from the light orange colors are very light in pattern. The percent of heavy variegations increases with the color intensity of the orange from which they originate. These variegations are not constant in inheritance, but produce progenies that vary in pattern from light to heavy and from fine to coarse. The results are quantitative, quite like the variation in intensity of the orange color from which these variegations sprang. Evidently, the light variegations are produced by genes with a relatively small number of pigment-producing elements, while the heavy variegations are produced when the genes have an excess of pigment-producing gene elements.

It seems evident that a color variegation is produced when a gene includes both pigment-producing and non-pigment-producing *gene elements* which become segregated in the somatic tissue, in the course of development, by the mechanism of mitosis.

SUMMARY

The important features of the present paper may be summarized as follows:

1. Orange pericarp in maize varies in color from whitish to deep cherry-red.

2. The progeny of an ear of medium-orange pericarp includes ears ranging in color from whitish to red in the form of a frequency curve. The curve may be skewed towards the light or dark end of the range by planting from ears that are light- or dark-orange, respectively.

3. The orange pericarp gives rise to variegations of a number of distinct types.

4. Light-orange ears produce variegations that are prevailingly light in pattern, while dark-orange ears tend to give rise to heavy variegations. Evidently, there is a correlation between color intensity of orange pericarp and variegation pattern. According to the interpretation the color intensity of the orange pericarp, and the number and size of the color-markings of the variegations increase with the number of pigment-producing gene elements in the pericarp gene.

5. All color and pattern changes are reversible, but with different frequencies.

6. The gene for orange pericarp is thought to be made up of pigment-producing and non-pigment-producing gene elements. Variations in the orange color are due to different proportions of the contrasting gene elements in the pericarp gene.

7. The occurrence of adjacent segments of red and white (colorless) of equal size, on an otherwise orange-colored kernel, indicates that the gene for orange pericarp divided in such a way that its pigment-producing elements were separated from its non-pigment-producing elements by the mechanism of mitosis.

8. Variegations are produced when the contrasting gene elements become completely segregated in the somatic tissues in the course of development. Since variegations in general, in animals as well as in plants, are fundamentally alike in their inconstancy and in the nature of their color changes, it may be concluded that all typical variegations are produced in a manner similar to that described above for maize pericarp.

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Appendix—Tables 1 to 10

Table 1

Variation in color intensity of orange pericarp.

PEDIGREE	COLOR INTENSITY OF THE ORANGE KERNELS PLANTED	PERICARP COLOR OF THE PROGENY EARS									
		Variegated	Colorless	Orange ears with intensities indicated below:							
				B	C	D	E	F	G	H	I
5485	B			16	13	4	2				
5532	B			11	10	3	1				
Total	B			27	23	7	3				
5533	C				10	2					
5534	C			5	38	6	3				
Total	C			5	48	8	3				
1504	D	1		7	31	50	35	9			
1506	D	1	2	5	16	35	7	1			
1512	D			4	28	77	37	5	3	1	
1521	D	1		4	11	36	18	4			
5535	D					11	4				
5536	D				2	25	2				
Total	D	3	2	20	88	234	103	19	3	1	
1519	E	2		1	3	11	41	8	1		
1520	E	1			1	13	30	11	4	2	
1524	E				9	25	17	7	3		
1525	E			3	14	32	17	10	4		
5537	E				1	6	96	4	1		
5539	E			2	2	3	50	3			
5486	E		1			2	26	4	1		
5487	E		1			8	43	1			
Total	E	3	2	6	30	100	320	48	14	2	
1522	F					6	16	38	18	1	1
5522	F						6	42	4	1	
5527	F				1	1	5	40	3	2	
Total	F				1	7	27	120	25	4	1
1510	G				1	5	11	23	49	15	3
3848	G						7	26	52	19	3
5529	G						1	6	54	2	
Total	G				1	5	19	55	155	36	6
5542	H								4	66	5
5543	H								10	63	12
Total	H								14	129	17
5544	I								1	2	50

TABLE 2

Frequencies of color changes in maize pericarp from orange to red.

PEDIGREE	INTENSITY OF ORANGE PERICARP	NUMBER OF KERNELS OBSERVED	CHANGES FROM ORANGE TO RED EXPRESSED IN KERNELS AS INDICATED IN COLUMN HEADS								DARK CROWN				
			$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	> 1	Total	Number per thousand	Part	Full	> 1	Total	Number per thousand
1504	B	2135	9	5	4	2	1	–	21	9.8	58	3	1	62	42
	C	9206	64	15	22	4	5	–	110	12.0	250	26	4	280	33
	D	13399	39	16	15	4	3	1	78	6.0	139	23	1	163	12
	E	14086	62	22	12	5	1	–	102	7.2	283	40	–	323	23
	F	2738	14	7	3	–	1	1	26	9.1	46	13	–	59	22
1525	C	1645	6	3	4	1	1	–	15	9.1	16	3	1	20	12
	D	3012	36	17	16	–	2	1	72	24.0	42	15	3	60	20
	E	3313	84	16	10	4	3	1	118	36.0	47	13	–	60	18
	F	5493	16	5	4	1	–	1	27	5.0	30	6	1	37	7
	G	1120	18	7	2	1	–	–	28	25.0	6	1	1	8	7
	H	1020	—	—	—	–	–	–	00	——	15	1	–	16	15
Total		57167	348	113	92	22	17	5	597	10.0	932	144	12	1088	19

TABLE 3

Frequencies of color changes in pericarp of maize from orange to lighter orange, light-variegated, or colorless.

PEDIGREE	INTENSITY OF ORANGE PERICARP	NUMBER OF OF KERNELS OBSERVED	CHANGES TO LIGHTER ORANGE, LIGHT VARIEGATED OR COLORLESS IN KERNELS AS EXPRESSED IN COLUMN HEADS BELOW							LIGHT CROWN			
			$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	Total	Number per thousand	Part	Full	Total	Number per thousand
1504	B	2135	11	5	2	1	5	24	11	15	1	16	7
	C	9206	43	11	6	2	2	64	7	167	20	187	20
	D	13399	21	13	16	5	9	64	5	107	55	162	12
	E	14086	76	7	11	1	2	97	7	431	58	489	33
	F	2738	26	3	3	1	1	34	13	89	28	117	44
1525	C	1645	12	4	2	1	–	19	11	19	7	26	16
	D	3012	21	7	6	3	4	41	14	49	9	58	19
	E	3313	20	9	7	2	2	40	12	64	15	79	24
	F	5493	9	1	2	1	1	14	3	30	7	37	7
	G	1120	8	2	—	–	–	10	9	12	3	15	13
	H	1020	—	—	—	–	–	—	0	48	—	48	50
Total		57167	247	62	55	17	26	407	7	1031	203	1234	22

TABLE 4

Frequencies of color changes from orange to variegation in maize pericarp.

PEDIGREE	INTENSITY OF ORANGE PERICARP	NUMBER OF KERNELS OBSERVED	CHANGES EXPRESSED IN KERNELS AS INDICATED IN THE COLUMN HEADS							
			$\frac{1}{16}$	$\frac{1}{8}$	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{1}{2}$	1	Total	Number per thousand
1504	B	2135	149						149	71.4
	C	9206	1600	2	2	1	—	—	1605	174.5
	D	13399	2304	7	7	8	4	2	2332	174.0
	E	14086	3398	95	11	6	9	1	3520	252.1
	F	2738	462	1	2	3	2	—	470	171.5
1525	C	1645	607	17	2	—	—	—	626	380.2
	D	3012	1655	99	17	3	—	2	1776	588.2
	E	3313	2261	287	28	6	1	—	2583	781.2
	F	5493	899	104	6	1	2	3	915	465.5
	G	1120	280	14	3	1	—	—	298	266.0
	H	1020	41	1	1	—	—	—	43	41.7
Total		57167	13656	627	79	29	18	8	14317	250.0

TABLE 5

Variation in type of variegation.

DESCRIPTION OF SEED PLANTED	PROGENY EARS							
	Light variegation				Heavy variegation			
	A	B	C	D	A	B	C	D
Light variegation (figure 4)								
1. Coarse pattern, ear B.......	3	16	2	1				
2. Medium pattern, ear C.......		3	62	1				
3. Fine pattern, ear D.......				All				
Heavy variegation (figure 5)								
1. Coarse pattern, ear B.......					12	41	1	
2. Medium pattern, ear C.......					4	11	35	2
3. Fine pattern, ear D.......					1	4	15	17

TABLE 6

Types of variegations originating from orange pericarp of different intensities of color.

DESCRIPTION OF ORANGE PERICARP	TYPES OF VARIEGATION	
	Percent light	Percent heavy
Very light orange.........	100.0	0.0
Light orange.............	80.6	19.4
Medium orange..........	67.0	33.0
Dark orange.............	57.5	42.5
Red.....................	0.0	100.0

TABLE 7

Frequencies of changes from light variegation to red.

PEDIGREE	PATTERN	NUMBER OF KERNELS OBSERVED	CHANGES TO SELF-RED COVERING PARTS OF KERNELS AS INDICATED IN COLUMN HEADS							
			$\frac{1}{8}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	>1.	Total	NUMBER per thousand
5495	Fine	3181	5	1	—	—	1	-	7	2
5497	Medium	9286	83	63	39	16	2	7	210	23
5498	Coarse	2966	156	49	33	12	5	3	258	87
Total		15433	244	113	72	28	8	10	475	31

TABLE 8

Frequencies of changes from variegation to self-color.

PEDIGREE	PATTERN OF VARIEGATION	NUMBER OF KERNELS OBSERVED	CHANGES FROM VARIEGATION TO SELF-COLOR EXPRESSED IN KERNELS AS INDICATED BELOW						
			$\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	> 1	Total	Number per thousand
1501	Coarse	40975	1129	590	238	139	31	2127	53
1502	Coarse	17777	264	200	76	21	4	565	32
1503	Coarse	21497	471	219	94	44	4	832	40
5489	Coarse	1587	21	30	9	8	2	70	44
5492	Coarse	1826	14	27	4	3	-	48	30
5493	Coarse	2888	79	82	20	10	7	198	66
Total	Coarse	86550	1978	1148	441	225	48	3840	44
1503	Medium	4074	19	6	0	1	—	26	6.4
5489	Medium	2621	22	17	5	2	—	46	17.5
5492	Medium	11732	28	23	2	4	2	59	5.0
Total	Medium	18427	69	46	7	7	2	131	7.0
5489	Fine	6700	11	6	1	2	—	20	3.0
5492	Fine	866	—	—	—	—	—	—	0.0
Total	Fine	7566	11	6	1	2	—	20	2.6
Total, all patterns		112543	2058	1200	449	234	50	3991	35.5

TABLE 9

Frequencies of changes to dark crown in the variegated types.

PEDIGREE	PATTERN	NUMBER OF KERNELS OBSERVED	DARK CROWN COVERING AREAS INDICATED BELOW				
			Part of kernel	Entire crown	Patch of more than one kernel	Total	Number per thousand
1501	Coarse	40975	1101	315	384	1800	44
1502	Coarse	17777	497	170	162	807	45
1503	Coarse	21497	730	277	216	1223	57
5489	Coarse	1587	133	29	20	182	114
5492	Coarse	1826	109	18	13	140	77
5493	Coarse	2888	191	61	27	279	97
Total	Coarse	86550	2739	870	822	4431	51
1503	Medium	4074	156	17	7	180	45
5489	Medium	2621	161	45	25	206	78
5492	Medium	11732	574	80	33	687	59
Total	Medium	18427	891	142	66	1073	58
5489	Fine	6700	255	75	33	363	54
5492	Fine	866	45	6	—	51	59
Total	Fine	7566	300	81	33	414	55

TABLE 10

Frequencies of changes from heavy variegation to light variegation.

PEDIGREE	PATTERN OF HEAVY VARIEGATION	NUMBER OF KERNELS OBSERVED	CHANGES TO LIGHT VARIEGATIONS EXPRESSED IN KERNELS AS INDICATED BELOW					
			$\frac{1}{4}$	$\frac{1}{2}$	1	>1	Total	Number per thousand
1501	Coarse	40975	190	108	66	2	366	9
1502	Coarse	7800	72	14	6	--	92	12
1503	Coarse	21497	92	25	25	-	142	7
Total	Coarse	71272	354	147	97	2	600	8
1503	Medium	4074	3	2	2	—	7	2