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Genetic Relations of Plant-
Colors in Maize.

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

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R. A. Emerson

Under the designation "plant colors" are included the colors other than those related to chlorophyll, commonly seen in, but not limited to, such external plant parts of maize as the culm, the staminate inflorescence, the husks, the leaf sheaths, and to some extent the leaf blades. In contrast to this group are colors and color patterns related to chlorophyll or associated with the pericarp and the cob, the silks, the endosperm, the aleurone. The colors included in the group considered here are due to water-soluble pigments, but the same is true of some of the other color groups named above. Moreover, colors of the chlorophyll group (Lindstrom, 1918) are found in the same plant parts as are the "plant" colors considered in this account. The plant colors as a whole are closely interrelated, but they are closely related also to aleurone colors and to certain of the silk and pericarp colors. It is obvious, therefore, that, while this classification is a more or less natural one, it is based primarily on convenience.

The term "genetic relations" in the title to this memoir is to include not merely an account of the genetic analysis of the material at hand by means of hybridization experiments — tho that constitutes the greater part of the paper — but also some consideration of the variations of the several color types induced by or associated with environmental diversities. Some little attention to matters of this kind was made necessary by the fact that presumably homozygous material exhibited marked variations in extent and intensity of pigmentation when grown under diverse conditions. Since, as will be apparent later, the principal differences between certain of the color types under investigation are apparently quantitative ones, and since the materials at best exhibit no little complexity with respect to factorial interrelations of a genetic nature, little progress could have been made without some notion of the response of particular color types to certain factors of the environment. But this study has

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been wholly subsidiary to the main purpose, namely, a genotypic analysis of the color types under observation. The writer's realization of the superficial nature of the environmental studies reported in this account in no way weakens his belief in the importance of acquiring an accurate knowledge of the chemistry of the pigments concerned and of instituting fundamental investigations into the physiology of their development — problems that must await the interest and effort of other workers.

The studies reported here were begun in a small way in 1909 and have been continued, along with other problems in the genetics of maize, to the present time. The work was conducted at the University of Nebraska and supported by funds of that institution from 1909 to 1914. During 1911 facilities for growing and studying a considerable part of the cultures then in hand were generously afforded the writer by the Bussey Institution at Harvard University. Since 1914 the work has been conducted at Cornell University.

During these years, the writer has been assisted by a number of persons, among whom he desires to mention particularly Dr. E. W. Lindstrom and Dr. E. G. Anderson. Some data from the records of students associated with the writer are included in this account. The cultures giving these borrowed data are indicated in the tables by initial letters preceding the pedigree numbers, as follows: A = E. G. Anderson, L = E. W. Lindstrom, and S = Sterling H. Emerson.

The illustrations are from water-color drawings by C. W. Redwood, Miss Carrie M. Preston, and Miss Bernice M. Branson.

PREVIOUS INVESTIGATIONS

So far as the writer is aware, little work with the plant colors of maize has been reported previous to this time. Webber (1906) reported the results of studies of the interrelations of aleurone, silk, anther, and glume colors, with the conclusion that color in all these parts is closely correlated but that there are definite breaks in the correlation. This conclusion, in terms of present-day usage, is apparently equivalent to the idea of close linkage with some crossing-over. East and Hayes (1911) identified certain aleurone-color genes, which are shown in the present account to be related to plant colors as well as to aleurone colors, and reported data concerning the inheritance of silk and anther colors. The writer (Emerson, 1918) added another aleurone-color pair also known to

be concerned in plant-color development. He had earlier (1911) announced some of the plant colors discussed in the present paper and placed on record some evidence as to their genetic behavior. Gernert (1912) described types of maize that differ widely in color of anthers, glumes, silks, sheaths, and husks, and reported simple mendelian behavior in F_1 and F_2 of certain crosses. With this exception, Gernert's extensive investigation of plant-color types has not been reported, but the writer has been able, thru an exchange of material, to compare some of Gernert's types with those in his own cultures.

SOURCE AND DESCRIPTION OF MATERIALS USED

The plant-color types discussed in this paper came in the main from the crossing of two little-known varieties, one of which was obtained at a national corn exposition and the other from an exhibit at a local agricultural fair. One of the color types produced by this cross is the same as that of the dent varieties generally grown thruout the Corn Belt; a second is not infrequently seen in certain pop, flint, and sweet corn varieties; and a third occurs in the fields of flour corn of certain Indian tribes of the Southwest. One of the color types produced by the cross had no existence, so far as the writer knows, until it appeared in his cultures. Modifications of several of the six color types noted above have been produced by crossing with a color type common in a few varieties of sweet corn and closely related to the type most common in field maize. The principal color types concerned in this account are discussed in some detail in the descriptive notes below. They are:

I — Purple
II — Sun red
III — Dilute purple
IV — Dilute sun red
V — Brown
VI — Green

PURPLE, TYPE I

Material of the purple type was first obtained as a single ear from a local agricultural fair at Nehawka, Nebraska, in 1906. The varietal name is unknown. The uncrossed stock was a smooth-seeded pop corn

of medium size. No other stock of purple has been used in the crosses described later in this account, and the writer has never seen this color type in cultivation outside his own cultures. A sample of dent corn of apparently the same color type was seen at a national corn exposition in 1909. A stock of purple was obtained from Dr. Gernert in 1914 but was not used in genetic studies. Another stock of purple was received more recently (1919) from Messrs. Collins and Kempton, the seed having come originally from Bolivia.

Seedlings of the purple type are usually indistinguishable from those of types II, III, and IV (described more fully under type IVa, page 12), altho, unlike the other types, they develop some color when grown in darkness. Half-grown plants of type I usually have the lower sheaths prominently colored, in which respect they exceed type II plants in intensity of pigmentation and are sharply differentiated from types III and IV. At the flowering stage, plants of type Ia have much purple color in nearly all parts, such as the culm, the brace roots, the leaf sheaths, the husks — even the inner ones — the cob, and the staminate inflorescence including the rachis, the spikelets, and the anthers (Plates I, 1, and V, 1). In some cases the color extends over the whole leaf, and it is always seen in the midrib. The purple pigment of type Ia develops in local darkness, as has been shown by covering various parts of growing plants with several thicknesses of heavy black paper (Plate VIII, 1). The color persists in mature plants with slight fading in the outer parts due to weathering (Plate VII, 1). The pericarp of type Ia is either colorless, red, or cherry, and the aleurone is either purple, red, or colorless. With red aleurone the anthers are reddish purple, and with cherry pericarp they are usually very dark purple, almost black (Plate I, 2 and 3).

A subtype of purple known as weak purple, or type Ib, is similar to Ia but the pigmentation is less intense, particularly in the culm and the inner husks (Plate V, 2). In early stages of growth it is often difficult to distinguish Ib from IIa. The anthers of Ib are usually deep purple, as are those of Ia, and the pericarp is the same as for Ia. Another subclass of purple, Ig, is like Ia except that the anthers are green (Plate I, 4) and the pericarp is red or colorless, never cherry. The aleurone color is the same as in Ia.

SUN RED, TYPE II

Sun red, tho not a common color type, is encountered in a few varieties of sweet corn and pop corn. It is always produced in F_2 of certain crosses, notably in purple x green.

While this type is less highly colored than Ia, it has such strong color that it is not easily distinguished from the latter in early stages of growth. At the flowering stage, type IIa is sharply differentiated from type Ia in several respects. The staminate inflorescence of IIa is lighter than that of Ia, and the anthers are deep pink instead of purple (Plate III, 1). In type IIa, pigmentation of the culm, the leaf sheaths, and the husks is limited almost wholly to parts exposed to sunlight, hence the name *sun red.* The inner husks are therefore without red color, and rarely does much color develop in any but the outer layer of husks (Plate V, 3) notwithstanding the fact that sufficient light penetrates to the inner husks to induce the development of some chlorophyll in them. A tassel inclosed in a black paper bag produces no red color in either glumes or anthers (Plate VIII, 4). Since the color of sun red plants is so largely superficial, it disappears almost wholly from mature plants thru weathering (Plate VII, 2). Sun red plants have either red or colorless, but never cherry, pericarp, and either purple, red, or colorless aleurone.

Sun red of type IIg differs from IIa merely in having green instead of pink anthers. Type IIb, known as weak sun red, differs from IIa in the lesser intensity and extent of its pigmentation. Particularly the leaf sheaths and the husks are less highly colored than in type IIa. Often the color of the husks develops in alternate dark and light bars parallel to the upper margins of the overlapping husks (Plate V, 4). Types IIb and IIg have the same pericarp and aleurone colors as IIa.

DILUTE PURPLE, TYPE III

The dilute purple type, as well as the sun red, occurs regularly in F_2 of purple x green, and most of the dilute purple material in the writer's cultures came originally from this and other crosses. It was first observed in the progeny of such crosses in 1909. Recently two stocks of this color type have been received from G. N. Collins, one obtained from the Hopi Indians of southwestern United States and the other from Bolivia.

Seedlings and young plants of type IIIa show no more color than do those of type IVa, and apparently do not develop color in darkness. As the plants approach the flowering stage, they usually show somewhat more color than do plants of type IVa, particularly at the base of the culm and in the brace roots, and sometimes in the leaf sheaths. The staminate inflorescence is usually, tho not always, somewhat more highly colored than that of type IVa. The anthers are deep purple, like those of type Ia (Plate II, 1). With red aleurone the anthers are usually reddish purple, and with cherry pericarp they are dark purple, sometimes appearing nearly black (Plate II, 2 and 3). The anther color develops fully in darkness, but the glumes are slightly if at all colored when protected from light by black paper bags (Plate VIII, 3). As the plants mature, considerable color develops in the inner husks (Plate VII, 3), on the leaf sheaths, and particularly in the culm even where it is protected from strong light by the sheaths. In some cases the culm and the sheaths ultimately become nearly as strongly pigmented as type Ia, but ordinarily the mature plant is considerably less highly colored than the purple type (Plate VII, 4). The color seen in mature plants develops well in local darkness, in which respect also type IIIa is like Ia. Dilute purple differs from purple, therefore, mainly in a less intense pigmentation and in a delayed development of pigment. The pericarp of type IIIa is either red, cherry, or colorless, and the aleurone is either purple, red, or colorless, just as in type Ia.

There exists a type of plant color which is closely related genetically to type IIIa, but which lacks red or purple color in culm, sheaths, silks, glumes, and anthers and is consequently known as *Green, type IIIg* (Plate II, 4). The aleurone of this type is either purple, red, or colorless, and the pericarp is either red or colorless, never cherry. With respect to aleurone and pericarp, therefore, type IIIg is like type Ig.

DILUTE SUN RED, TYPE IV

Dilute sun red is the commonest color type of maize in cultivation. It is practically the only color type seen in the dent varieties grown in the Corn Belt of the United States, and is common in flint, flour, sweet, and pop corns. Like the sun red and the dilute purple types, it always appears in crosses of purple Ia with green VIc.

The seedlings of type IVa usually show more or less sun red pigment in the coleoptile, the leaf sheath, and the leaf margins. The young

plants ordinarily have considerable color at the base of the lower sheaths, but little or no color except green in other parts except in the margins of the leaves (Plate IX, 1). When the plants are grown on infertile soil, much bright red color develops in all parts exposed to light except the youngest leaves (Plate IX, 2). The seedlings and the very young plants are not ordinarily distinguishable from those of types Ia, IIa, and IIIa. Some time before the flowering stage, the plants of this type are sharply differentiated from those of types Ia and IIa, and are usually somewhat less highly colored than those of type IIIa. In normally grown plants, the color is confined mostly to the brace roots, and to the sheaths and the exposed parts of the culm at the base of the plants. Even at the flowering stage almost no color is seen in the upper sheaths or the upper part of the culm, and very little in the husks (Plate VI, 1). The staminate inflorescense is colored much as is that of the sun red type, tho the glumes are lighter than those of type IIa and the rachis is usually nearly devoid of color. The anthers show more or less pink, as do those of type IIa. There is much variation in the extent and intensity of pigmentation of glumes and anthers (Plate III, 2, 3, and 4), due in part to genetic differences and in part probably to environmental influences. Late in the life of the plant, type IVa usually shows some color in the outer husks and also in exposed parts of the culm. Different strains show considerable variation in this respect (Plate VI, 1 and 2). Due to the slight development of pigment and because of weathering, the dry parts of mature plants show little red color (Plate VII, 6). Light is essential to the development of color in dilute sun red, IVa, just as in sun red, IIa. The aleurone and pericarp colors of dilute sun red, IVa, are the same as those of sun red, IIa.

A wholly green type, that is, one devoid of pigment other than green in the plant parts here under consideration, is closely related genetically to type IVa and is therefore known as type IVg (Plate II, 4). Phenotypically it is the same as type IIIg. Just as in case of types Ig, II, IIIg, and IVa, the pericarp of IVg is either red or colorless, never cherry, and the aleurone is either purple, red, or colorless. Genotypic diversities in the amount of color are noted for type IVa above. The lightest types of dilute sun red show no color except mere traces of red in the staminate spikelets. This condition is found in most plants of at least two varieties of sweet corn, Black Mexican and Crosby. From these varieties there

have been isolated strains that lack even this minimum of color. These strains furnished the original stock of type IVg. In no environment as yet encountered has any red or purple plant color developed in type IVg.

BROWN, TYPE V

The brown type was first seen in 1912, when it occurred in F_2 of the cross purple Ia x green VIc. So far as the writer has been able to learn, brown plant color had not been reported previously, and he is unaware of its existence outside of his own cultures or of stocks grown from them.

Seedlings and young plants of type V are wholly green. Before the flowering period is reached, a brown pigment begins to appear in the lower sheaths. At the time of flowering, the culm, the sheaths, the husks (Plate VI, 3), and the staminate inflorescence (Plate IV, 1 and 2) are brown. The anthers are usually green. The brown color extends to the inner husks, to the culm beneath the leaf sheaths, and to the cob (Plate VII, 5). That light is not essential to the development of brown is shown further by the fact that the color appears under several thicknesses of black paper (Plate VIII, 2). It is not uncommon to find traces of purple associated with the brown in the brace roots and at the base of the inner husks (Plate VI, 3). Abnormally developed tassels, not infrequently seen on plants grown in small pots in the greenhouse, in some cases show a little purple (Plate XI). The aleurone of brown plants is always colorless, except for xenia grains, and the pericarp is either brown, brownish, or colorless, never red nor cherry. Brown pericarp color of type V corresponds to red of types I, II, III, and IV, and brownish to cherry of types I and III.

GREEN, TYPE VI

The writer's stock of the green type originated from a single ear obtained at a national corn exposition held at Omaha in 1909. The corn was exhibited from southern Missouri, where it is grown locally. It is a large dent variety, rather late in season.

Cultures of type VIc, derived from this stock, show no plant color other than green at any stage of development or under any environmental conditions to which they have as yet been subjected (Plates IV, 3, and VI, 4).

Three subclasses of type VI are recognized. One of these, VIa, is like VIc in every respect except that a slight amount of brown is sometimes seen in the outer husks and sheaths (Plate VI, 5). The second, VIb, is green except for a slight tinge of brown in the spikelets of the staminate inflorescence (Plate IV, 4). As a rule, the development of brown pigment in VIa and VIb is not sufficient to differentiate with certainty the one from the other, or either from VIc. The three subclasses, a, b, and c, are therefore usually classed together as type VI. Both VIa and VIb have been isolated from crosses involving VIc. The aleurone of all type VI plants, just as in those of type V, is colorless, except for such color as may be due to xenia. The pericarp of VIa and VIc is either brown or colorless, never brownish, while that of VIb is brown, brownish, or colorless, as in the case of type V. With brownish pericarp, type VIb usually shows unmistakable brown color in the staminate spikelets.

RELATION OF PLANT COLORS TO ENVIRONMENT

From the preceding descriptive notes and accompanying illustrations, it is clear that many of the differences separating the six major color types and their several subclasses are quantitative. Purple plants are more strongly colored than are sun red or dilute purple plants. Dilute sun red plants have less color than sun red or purple plants. Weak purple plants have less color than purple ones, but more than dilute purple ones, and weak sun reds are intermediate between sun reds and dilute sun reds. Dilute sun red plants vary, from those showing considerable color to those which, except for green, are nearly colorless. Wholly green plants are classed as subgroups of both dilute purple and dilute sun red. The subclasses of type VI differ so little with respect to color that they are ordinarily thrown together as one green type. Heterozygous brown plants are lighter than homozygous ones, and, since more than one factor pair is concerned, there is a fairly smooth gradation from the darkest to the lightest browns. Plants of types VIa and VIb, when they show any brown, differ in the parts colored. The color of the staminate inflorescence, and even of other parts, of purples, dilute purples, browns, and greens of type VIb is darker when the pericarp is cherry or brownish than when it is red, brown, or colorless.

The natural intergrading of genetic types in this somewhat complex series is often made still more confusing by the variations accompanying

environmental diversities. A prominent geneticist, on observing some of the writer's cultures, was led to say that there were no sharply differentiating characteristics by which other than an arbitrary classification could be made, and asserted that he could select from a single progeny a series grading from the darkest to the lightest colors. The writer has some doubt that this could have been done, but the instance illustrates well the difficulties that confront one unacquainted with the materials. It is fortunate that some environmental influences which increase the difficulty of assorting certain color types make other types stand out more sharply than they otherwise would. Without some notion of these environmental effects, a genetic analysis of the material would indeed be difficult.

SUNLIGHT A FACTOR IN COLOR DEVELOPMENT

The relation of sunlight to the development of color has been noted briefly in the descriptions of some of the color types. The effects of sunlight or of local darkness, instead of adding to the confusion of color types, afford a means of sharp differentiation between certain types. So far as is known at present, no color develops in sun red or dilute sun red plants, or in the early stages of growth of dilute purple plants, except under the influence of fairly strong light. In the case of purple and of the later stages of growth of dilute purple, there is no doubt that the color develops more rapidly at first in light than in darkness, but ultimately color develops fully, or apparently so, even in local darkness (Plate VIII). The seedlings of purple plants develop some color when germinated and grown in a dark chamber where no part of the plant receives light. There is some, tho very little, evidence that the development of brown pigment of type V is hastened by the influence of light, and what little brown color ever develops in type VIa is confined to parts exposed to sunlight (Plate VI, 5).

It would not be surprising to find that the pigments seen in the purple, dilute purple, sun red, and dilute sun red types are the same chemically. In fact they look alike in water solution and apparently react in the same way to simple chemical tests. If they prove to be identical, it would seem to follow that purple and dilute purple plants have some inherent mechanism, perhaps an organic catalyzer, capable of initiating or hastening chemical reactions, and that this mechanism is lacking in sun red

and dilute sun red plants, in which the same reactions may possibly be brought about thru the action of sunlight.

Usually a single thickness of black paper, such as is employed to protect photographic plates from light, is sufficient to prevent the development of color in sun red plants (Plate VIII, 4). That more intense light is necessary for the production of sun red pigment than for the production of chlorophyll is shown by the almost entire absence of red color in all but the outer husks, while even the innermost husks are somewhat green (Plate V, 3). The pigments of purple and brown plants, on the contrary, develop well even when there is too little light for the formation of chlorophyll (Plate VIII, 1 and 2).

That the effect of light on color development is a definitely local one is shown by the sharp line of demarcation between colored and colorless areas in culms, husks, and sheaths partly exposed and partly protected by overlapping sheaths or husks (Plate V, 3). Even a single piece of wrapping cord tied closely about a young ear, sheath, or culm of a sun red plant is sufficient to prevent the development of color beneath it. Evidently sun red pigment does not diffuse appreciably from the cells in which it forms. It is not meant to suggest by these observations that sunlight has no effect other than a local one on color development. On the contrary, there is evidence that the development of sun red color is influenced by the presence of an abundance of carbohydrates which in turn are dependent on sunlight for their formation.

A striking example of the relation of sunlight to color development is afforded by the barred pattern seen in the husks of some weak sun red plants (Plate V, 4). The pattern consists of alternate bars of red and green parallel to the upper margin of the overlapping husk next below them. By tracing in pencil on each exposed husk of a rapidly growing ear the margin of the husk overlapping it, it has been ascertained with certainty that the red bars correspond to the areas that are pushed out from under the overlapping husk between early morning and late afternoon, while the green bars correspond to the areas pushed out during the late afternoon and night. Why color develops in only those parts of the husk that receive the sunlight when first exposed to the air, and not in the parts exposed some hours previously, is not known. Another illustration of the effect of sunlight on freshly exposed husks was seen in a very light type of weak sun red (Plate V, 5). Of two ears on the same culm, both very lightly

and about equally colored, the lower had its husks torn apart in the early forenoon so that the fresh inner husks were exposed at once to direct sunlight. In a few hours some red color began to show, and in a few days all the newly exposed husks were brilliantly colored, while the undisturbed upper ear remained only slightly colored. Similar results followed in repeated trials, and, in fact, failed only when the atmospheric conditions were such as to cause the newly exposed husks to wither during the first day. It is of interest to note also that similarly treated ears of dilute sun red plants, which rarely show any red color in the outer husks of young ears, failed to develop color when the husks were torn apart, even tho they remained fresh for some days.

It is evident from all this, that, with respect to their relation to sunlight, there exists a series of color types varying more or less abruptly from dilute sun red, in which little or no sun red develops in even freshly exposed husks, thru weak sun red, in which color forms in only freshly exposed husks, and strong sun red, in which much color develops in all exposed parts of the husks but not in parts protected from light, to strong purple, in which, tho sunlight may hasten color development, it is not essential to its formation.

Tests of the influence on color development of light of different wave lengths have not been uniformly successful. Cramer photographic color screens were placed in partial contact with the uncolored inner husks of sun red plants, and the entrance of light otherwise than thru the screens was prevented by means of strips of black paper. These screens, by cutting out light of certain wave lengths, not only change the quality of light passing thru them but lessen the intensity of the light. While the results, therefore, can have little value, it may be of interest to physiologists to note that considerable sun red formed under the orange and the bright red screens, and little or none under the green and the blue screens.

MOISTURE IN RELATION TO COLOR

It is well known that under field conditions maize does not grow well in wet soil. In such situations, not only are the plants small, with their leaves pale green, but they often develop much red pigment. The writer has repeatedly observed that young plants, in flooded parts of fields where the soil had been covered with water for some days, were brilliantly red in all parts except the youngest leaves, while near-by plants on slightly

higher land showed only the slight red at the base of the culms characteristic of young dilute sun red plants.

For a study of the effect of soil moisture on color development under controlled conditions, plants of well-known stocks of purple Ia, sun red IIa, dilute purple IIIa, dilute sun red IVa, brown V, and green VIc and IVg, were grown in rich soil in earthen jars in the greenhouse during the summer of 1914. When the plants had reached a height of from 10 to 15 centimeters, the jars were separated into three lots — one with dry soil, another with moist soil, and a third with wet soil. The dry-soil lot received only sufficient water to keep the plants growing slowly and not enough to prevent wilting during the hotter part of the day. The moist-soil lot received just sufficient water to insure normal growth. The wet-soil lot was kept constantly in saturated soil with some free water above the soil surface. The test was continued until the plants of all lots reached the flowering stage.

The plants in moist soil made the most rapid growth and flowered somewhat earlier than the plants of the other lots. Their leaves were of normal green color and they showed the colors characteristic of the several color types. The plants in dry soil were smaller and very dark green. The development of purple, red, and brown color was practically the same as with the plants in moist soil. The plants in wet soil grew less rapidly than those in moist soil, but more rapidly than those in dry soil. Their leaves were somewhat lighter green than those of the moist-soil lot, but they showed practically the same amount of purple, red, and brown color. In fact the only differences between the three lots with respect to color at any time during the test were such as might well be related to the stage of development of the plants. All color types show more color in the later stages of growth. The moist-soil lot developed somewhat more rapidly than did the others and for a time showed slightly more color, but ultimately all lots had practically the same amount of color. Evidently the reddening of plants in flooded fields is not due directly to the excess of soil moisture.

TEMPERATURE IN RELATION TO COLOR

Since moisture is not the direct cause of the reddening of maize plants in flooded fields, tho certainly connected with the phenomenon in some way, it follows that the effect must be produced by some indirect action

of the excess of water. Wet soils in spring are cold soils, and if the wet areas are of considerable extent the air above them is doubtless somewhat cooler than that above drier soil. It has been frequently observed that young plants which show much color during a cold spring show considerably less in the leaves developed after the weather has become warmer. Young plants of early-planted maize sometimes have more color than plants that are started later. Moreover, full-grown plants from late plantings often develop more color in the cool weather of autumn than similar plants that mature in the warm weather of late summer. It seemed important, therefore, to study the effects of various temperatures on color development.

The same color types and the same stocks— in one test the identical plants— used in the soil-moisture test were grown in the greenhouse under diverse temperatures. Altho both rich and poor soils of diverse water content were used, the comparisons noted here were made between plants in the same kind of soil and with practically the same soil-moisture conditions. Two lots were grown during the winter of 1913–14 and two during the following summer. During the winter, one lot was kept in a warm house at temperatures varying from about 18° to 26° C., and one was kept in a cool house at temperatures varying normally from about 7° to 15° C. but during a part of the test dropping at night to 1° or 2° C. Both lots were exposed to the full winter sunlight of the houses. During the summer test, one lot was kept as cool as possible by partial shading and free ventilation, the temperatures ranging from about 15° to 40° C. but occasionally exceeding these limits, and the other lot was kept in an unshaded house the ventilators of which were never opened. The night temperatures of the closed house averaged not more than one degree higher than those of the open house, but the maximum day temperatures in the closed house varied usually from about 44° to 50° C. and on three consecutive days reached 55° C. This extreme heat killed most of the plants grown in rich soil but did not seriously injure those in poor soil. Of course the relative humidity, as well as the intensity of the light, was materially different for the closed and the open house.

As a result of these tests, no final differences in the development of color in any of the color types were observed between the lots grown at the very diverse temperatures. Of course differences were observed at certain times, but they are readily accounted for by the facts that the

plants developed less rapidly at both excessively high and excessively low temperatures than at more moderate temperatures, and that color shows less during the early stages of development than during later stages. It may be safely concluded, therefore, that color development in maize is not notably influenced, except perhaps indirectly, by diverse temperatures.

SOIL FERTILITY AND COLOR DEVELOPMENT

There is still another way in which it was thought the excess of water might indirectly affect the development of color in maize plants in flooded fields. Not only may nutrient salts be removed in part by an excess of water, but certain of these salts — nitrates — are not formed normally in very wet soils. Tests were made, therefore, of the relation of soil fertility to color development.

Rich compared with poor soil

The same plant-color types as were employed in the soil-moisture and temperature tests were included in these soil-fertility tests. In fact, for one of the tests the same plants were used as in the moisture and temperature studies. One lot of plants was grown in rich soil and a duplicate lot in poor soil. Field soil furnished the basis of both soils. To one lot was added about 50 per cent by measure of thoroly decayed stable manure, and to the other about 50 per cent of clean sand.

The effect of soil fertility on color development of certain color types was strikingly apparent from the time the seedlings were two or three weeks old. At this age and for some time later, there was no appreciable difference in color between purples, sun reds, dilute purples, and dilute sun reds. In the rich soil all these color types had very little red color. There was some color in the coleoptile and the lower leaf sheath, but none in the leaf blades except for a slight amount in their margins. The same color types in poor soil had considerable color in the leaf blades and much color in the leaf sheaths. The plants in rich soil grew rapidly and were dark green, even the lower leaves remaining healthy. The plants in poor soil, on the contrary, grew less rapidly and were lighter green, and their lower leaves soon became yellow and died. In all cases the leaf blades became brilliantly red before they died. This is in strong contrast with the condition of the lower leaves of plants in dry, rich soil. When the

death of the lower leaves is caused by drouth, there is no corresponding development of red color.

At the age of six weeks, the plants in rich soil were beginning to show slightly the color differences that in later stages are characteristic of purples, sun reds, dilute purples, and dilute sun reds. In poor soil, on the contrary, no color differences were seen. All the four types were highly colored thruout except for the youngest leaves (Plate IX, 1 and 2).

At the flowering period, the plants in rich soil exhibited all the peculiarities of color by which purples, sun reds, dilute purples, and dilute sun reds are normally differentiated. Even in the poor soil something of the same color differences were discernible between the purples and sun reds on the one hand and the dilute purples and dilute sun reds on the other, but it is doubtful whether these two groups could have been separated accurately from a mixed culture. It would have been very difficult also to separate with certainty the purples from the sun reds or the dilute purples from the dilute sun reds, except by differences in anther color and by an examination of the inner husks and other parts protected from sunlight. Differences between the plants in rich and in poor soil were still pronounced in the case of dilute purples and dilute sun reds, but were scarcely discernible in the case of purples and sun reds except that the leaf blades were somewhat more highly colored with poor than with rich soil and that thruout the plants the colors appeared brighter in the former case owing to the less intense green of the poor-soil lots.

The seedlings of both brown and green color types showed no brown nor red color in either the rich or the poor soil. At the age of two months, some brown pigment began to show in the lower sheaths of the brown type, and at the flowering stage the plants had the typical coloration of brown plants. The difference in the development of brown between rich and poor soil was at no time very noticeable. The color showed perhaps slightly earlier, and was perhaps slightly more intense, with the poor soil. Even this apparent difference, however, may have been due merely to the fact that the plants in poor soil were lighter and more yellowish green than those in rich soil. Dark green might readily mask the brown color somewhat. Green plants of both type VIc and type IVg exhibited no red nor brown color at any stage of development in either rich soil or poor soil.

From these observations it is apparent that variations in soil fertility may effectively obscure genetic differences. A knowledge of the influence of soil fertility on color development is therefore essential to careful genetic work with the plant colors of maize. Moreover, since soil fertility is subject to control thru cultural methods, different degrees of fertility can be used as an aid to the sharp differentiation of certain genetic types. If, for instance, it is desired to separate, in the seedling stage, greens and browns on the one hand from the red-purple series on the other, this can be accomplished most readily in poor soil. In fact, the writer's practice, in studies requiring this separation, is to grow the seedlings in pure sand. In this medium seedlings of the purple-red series of color types become highly colored at a very early age, while seedlings of the green and brown types show absolutely no red color. If, however, it is desired to distinguish sharply between purple and dilute purple or between sun red and dilute sun red, fairly fertile soil is essential, and, usually, the more fertile it is, the more easily can the separation be made. The stronger colors develop almost as well in rich as in poor soil, while the weaker colors develop much less intensely in rich soils than in poor ones. On very poor soils, it is difficult to separate sun reds from dilute sun reds, and almost if not quite impossible to distinguish with certainty between sun reds and weak sun reds or between weak sun reds and dilute sun reds.

Lack of particular nutrient elements

It having been established that differences in soil fertility result in marked differences in the development of red color in maize plants, it seemed important to determine whether particular nutrient salts are more concerned than others. Accordingly, plants of all the color types included in the tests previously reported were grown in glazed earthen jars in clean quartz sand and watered with nutrient solutions. The quartz sand was obtained from the Department of Agronomy of the University of Nebraska, and was known to be practically free from nutrient elements except iron. The nutrient salts and distilled water were obtained from the Department of Agricultural Chemistry of the same institution. The nutrient solution employed was one that had given good results with maize in certain experiments conducted previously by the Department of Agronomy. The complete nutrient solution, 0.2 per cent strength, contained per liter of water the following salts: 1 gram $Ca(NO_3)_2$, 0.25

gram KNO_3, 0.25 gram K_2HPO_4, 0.25 gram $MgSO_4$, and 0.25 gram NaCl. Other solutions of approximately equivalent molecular strength, but each lacking one of the nutrient elements of the complete solution, were used. In the nitrogen-free solution, 0.7 gram $CaCl_2$ and 0.22 gram K_2SO_4 were substituted for $Ca(NO_3)_2$ and KNO_3, respectively; in the phosphorus-free solution, 0.25 gram K_2SO_4 for K_2HPO_4; in the potassium-free solution, 0.2 gram $NaNO_3$ and 0.2 gram Na_2HPO_4 for KNO_3 and K_2HPO_4, respectively; in the calcium-free solution, 1 gram $NaNO_3$ for $Ca(NO_3)_2$; in the magnesium-free solution, 0.3 gram Na_2SO_4 for $MgSO_4$; and in the sulfur-free solution, 0.2 gram $MgCl_2$ for $MgSO_4$. A complete nutrient solution of four times the strength indicated above, 0.8 per cent, was also used, and one lot was given water without the addition of nutrients. After the first three weeks, the nutrient solutions were all used at double strength, 0.4 and 1.6 per cent, and clear water was occasionally given. This treatment, owing to considerable evaporation of water, doubtless resulted in a gradual increase in the strength of the solutions. The tests were carried on at the same time with one of the tests of rich and poor soil, so that the latter might serve as a check on the nutrient-solution tests.

At first the seedlings given 0.2-per-cent complete nutrient solution reacted about as did those in poor soil, while those given 0.8-per-cent nutrient solution were no more highly colored than those in rich soil. At one month of age, the plants watered for three weeks with 0.2-per-cent and one week with 0.4-per-cent complete solution were growing rapidly and were no more highly colored than those in rich soil, while the plants in the very strong solutions (0.8 and 1.6 per cent) were beginning to wilt, perhaps from the toxic effect of the solutions. Thruout the remainder of the test, the plants given 0.4-per cent solution, alternated occasionally with clear water, were practically like those growing in rich soil both as respects vigor of growth and color development.

In striking contrast to the plants given complete nutrient solution were the ones given clear water and those in nitrogen-free nutrient solution. Both these lots showed much color even at two weeks after germination, and soon thereafter the seedlings were red to the tips of their leaves. At the age of six weeks the plants of these two lots were much shorter and slenderer than those given complete nutrient solution. Their upper leaves were pale yellowish green, with much red, and the lower leaves were dead but still showing the red color that had developed earlier.

Next in point of coloration to the seedlings given nitrogen-free nutrient solution and those given water alone, were the ones grown in phosphorus-free nutrient solution. The latter did not show red color so quickly as did the nitrogen-free lot, and at no time did they develop quite so much color. They showed, however, considerably more color at the age of one month than did seedlings in the complete nutrient solution. When six weeks old the plants of the phosphorus-free lot were relatively small, and had pale green upper leaves with little red color and dead lower leaves which still retained much red pigment. While somewhat larger than the plants in nitrogen-free solution and those in clear water, the phosphorus-free lot began wilting when about six weeks old and died considerably in advance of the nitrogen-free lot. Their roots showed early indications of injury, perhaps from toxic effects of the solution.

Plants of all the other lots, in which one or another nutrient element had been omitted from the solution, exhibited little or no color reaction to the lack of a particular element. All of them were more vigorous in growth than the nitrogen-free and phosphorus-free lots, but much less so than the lot given complete nutrient solution. The sulfur-free lot for a time seemed to be developing more red, but later showed perhaps even less red, than the lot with complete nutrient solution. The magnesium-free lot showed prominent dark and light green stripes in the leaves similar to the green-striped chlorophyll pattern (Lindstrom, 1918). In some cases the tissue of the lighter stripes died and there was often some red coloration next to the dead tissue. The potassium-free lot had about the same amount of red color as the lot given complete nutrient solution, while the calcium-free lot showed less red color than any other lot in the test.

It is perhaps noteworthy that in the nitrogen-free lot, and to some extent in the phosphorus-free lot, the new growth seemed to take place at the expense of the older leaves. The lower leaves first became light or yellowish green, then red, and finally died. That the development of red pigment is not necessarily connected, however, with the breaking down of the protoplasm, is seen in the failure of seedlings to develop red color in the older dying leaves of the lot in complete nutrient solution and of the potassium-free, magnesium-free, and calcium-free lots. In the calcium-free lot, growth was stopped by the death of the youngest parts, including the partly unrolled upper leaves, and yet these parts showed

no red. Moreover, the dying of the lower leaves due to excessively dry soil, or of the upper leaves from intense heat, is not accompanied by the development of red pigment.

In similar tests with cuttings of *Tradescantia viridis* and *T. lockensis* grown in distilled water, in complete nutrient solutions, and in solutions each lacking one nutrient element, namely, N, P, K, Ca, Mg, or S, Czartkowski (1914) found that after five weeks red color appeared in the newly developed leaves in the cases of only distilled water and nitrogen-free solutions. He states, however, that Susuki reported a similar effect on plants of Hordeum from a lack of phosphorus. It will be recalled that in the writer's tests with maize, lack of nitrogen gave the most pronounced effect and lack of phosphorus induced considerable color development, while lack of sulfur seemed for a time to have an effect but no effect was apparent later.

From the results of the tests reported above, it is apparent that the reddening of young plants in flooded fields, as well as the intensification of color in older plants grown on poorly drained heavy soils, is not due to any direct effect of the excess of water in the soil or to a direct effect of the somewhat lower temperatures accompanying such conditions, but rather, perhaps, to the lessened fertility of cold, wet soils or to inability of the plant to obtain adequate nutrients under such conditions. An excess of water not only may remove certain nutrient salts from the soil, but also may prevent or greatly check nitrification. Moreover, under these conditions the soil solution is probably less concentrated. The reddening of young plants in cold, wet soils in spring, the greater development of color in plants maturing in the cool weather of late autumn, and the excessive development of red in plants on very light sandy soils, are possibly all due to the plants' inability to get from such soils an adequate supply of nutrient salts, particularly of nitrates.

RELATION OF CARBOHYDRATES TO COLOR

Several authors, notably Wheldale (1911), have discussed the relation of sugars to the production of anthocyanins in plants. Knudson (1916: 24, 62) found that maize and vetch grown in nutrient solutions containing certain sugars developed markedly more red color than did plants grown in sugar-free solutions. The writer has observed repeatedly an apparent relation between an excess of carbohydrates and the development of red

color in maize leaves. Of course the relation has been observed only in types that normally produce some red pigment. Neither brown, type V, nor green of either type IVg or type VI, has ever been observed with red color in the leaves, no matter what treatment has been given the plants. When leaves are folded at right angles to the midrib and the margin of the fold is creased sufficiently to break the softer tissues but not enough to break the water-conducting vessels, the part beyond the crease does not wilt, but within a few days it begins to lose some of its chlorophyll and within a week it becomes highly colored red (Plate X, 1). When leaves are similarly treated late in the afternoon of a bright day and the plants are kept in a dark room until the following day, the starch is, of course, found to have disappeared by translocation from the part of the leaves below the crease, while the cells of the bundle sheaths of the part beyond the crease are found to be packed with starch. There is so much starch in this part of a creased leaf that, on extraction of the chlorophyll with alcohol and treatment with iodin, the whole end of the leaf becomes almost black. While this does not prove a direct relation between an excess of carbohydrates and the development of red pigment, taken in connection with all the other observations it strongly suggests such a relation.

It has been observed repeatedly that sweet-corn plants from which the ears have been removed in the edible stage develop within a week or two much more color than do neighboring plants that still retain their ears. Barren stalks also frequently show more color than do their ear-bearing neighbors. While no direct determination of the matter has been made it seems likely that barren plants, as well as plants from which the immature ears have been removed, may carry, in their leaves, husks, and culms, an excess of carbohydrates which would normally have been deposited in the developing seeds.

The strong development of red pigment in the white, chlorophyll-free stripes of the japonica-striped type, when leaves are creased or when plants are grown in poor soil, may well be due to the passage of sugars from the green to the white parts. In some instances the red color seems to develop more quickly in the white stripes than in the green (Plate X, 2). Whether this difference is a real one, due perhaps to the readier access of light to the white parts, or is only an apparent difference due to the

masking effect of the green color, is not known. Certainly red pigments develop first in the chlorophyll-free epidermal cells.[2]

Czartkowski (1914) suggested, in connection with the account of his study of the relation of nutrient elements to color development, that lack of nitrogen may check protein synthesis, thus leaving unused the carbohydrates that would otherwise be used in growth, and that the excess of carbohydrates may favor anthocyanin formation. He was unable to understand why a lack of phosphorus or of sulfur did not likewise influence color development, since these elements also are necessary to protein synthesis. Lack of phosphorus does apparently bear some relation to color development in maize, but the writer's tests afforded little or no evidence of such a relation between a lack of sulfur and pigment formation. If lack of nitrogen induces anthocyanin formation thru the checking of growth, thus allowing an accumulation of carbohydrates, it is not clear why other means of checking growth, such, for instance, as dry soil, do not also favor pigment formation, unless these other growth-checking factors at the same time limit photosynthetic activity. It is of interest to recall in this connection that plant colors of maize — brown no less than the red-purple series — develop first in the older parts where growth first ceases, such as the lower sheaths and the upper parts of the internodes of the culm.

SUMMARY

Whatever is the final outcome of studies of the relation of environmental factors to plant-color development in maize, enough has been noted to indicate a very complex relation. What is more complex than this chain of events — a chain that lacks many links in the way of particular chemical reactions: cold, wet soil checks or inhibits nitrification; lack of nitrogen in available form limits protein synthesis, which in turn allows an accumulation of carbohydrates; an excess of carbohydrates favors anthocyanin formation. The result is that young maize plants in cold, wet soil become highly colored. But to all this must be added the factor of sunlight, without which no red color develops in the leaves of young plants. And not the least consideration is the important fact that only plants of certain genetic constitutions show this color reaction to wet soils. It is to be hoped that some day, thru the coordinated efforts of

[2] The histology of color development of the several plant-color types has been investigated by Dr. E. G. Anderson, but the observations have not been published.

biochemists, physiologists, and geneticists, it may be possible to reach conclusions in this field of quite as fundamental importance to biology as the recent results of similar efforts of cytologists and geneticists.

GENETIC ANALYSIS OF COLOR TYPES

In the preceding parts of this paper the several plant-color types of maize are described and the variations induced in them by diversities of environment are discussed. The remainder of the paper is devoted to a presentation of data of a more distinctly genetic nature, and to an attempt at a factorial analysis of these data.

The data are presented as if the F_2 generation of the more complex crosses were the first which were obtained and on which hypotheses were formulated and appropriate tests made. As a matter of fact, this was not in all cases the actual procedure. In several instances the results of some of the simpler crosses were at hand and were used as an aid to the interpretation of the more complex ones when the latter were obtained. Moreover, the hypothesis presented here was not the only one, nor indeed the first one, formulated. As is usual in such work, various hypotheses were devised, tested, and discarded, until finally a factorial interpretation was found that fitted fairly well all the facts known. Many results with a bearing on plant color were obtained in other studies extending over a period of some eight or nine years. Since the practice of the writer is to number his pedigrees consecutively from year to year, an inspection of the pedigree numbers, as listed in the tables, suggests at once that some of the data presented as checks on other results could not have been obtained after these other results. Any data applicable as a test have been so used whether obtained for that purpose or in connection with other studies. Whether this mode of presentation is the best one must be left to the judgment of others. This at any rate is certain: the data could not have been presented chronologically and discussed in relation to such hypotheses as happened to be under test at the time any particular results were obtained, without adding unnecessarily to the complexity of the paper.

CROSSES INVOLVING THE FACTOR PAIRS *A a, B b, Pl pl*

Purple Ia x green VIc

Generations F_1 and F_2.— When purple plants with purple anthers (type Ia) are crossed with plants lacking all red, purple, or brown

pigment, commonly known as green (type VIc), the F_1 offspring are full purple. Whether or not a quantitative determination of purple pigment might reveal a difference, no dilution of the purple color is apparent to the eye in the F_1 plants. Four crosses of this sort with a total F_1 progeny of 111 purple plants are listed in table 1 (appendix, page 121).

Seven F_2 progenies of the F_1 plants recorded in table 1 are listed in group 1 of table 2. Fourteen other similar F_2 progenies are shown in group 2 of the same table. The F_1 plants from which these fourteen F_2 progenies came are not recorded in table 1 because their purple parents were not homozygous. Some of the purple plants used as parents in these crosses were F_1's of the original cross of purple with green. Others were from F_1 or some later generation of other crosses having the purple type as one parent. In every case the other parent was a green plant of type VIc. Since the purple F_1 plants of these crosses were presumably the same genotypically as the F_1's shown in table 1, their F_2 progenies may well be included tentatively with those of group 1 of table 2. Each of the twenty-one F_2 lots exhibited six distinct classes of plants with respect to color. The 2117 plants were distributed among the six classes as follows:

Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
952	305	275	91	278	216	2,117

Obviously no simple 3:1 mendelian behavior is in evidence here. Moreover, only four classes are expected in dihybrids where dominance is exhibited. With dominance trihybrids ordinarily give eight classes in F_2 in the well-known numerical relation of 27:9:9:3:9:3:3:1, while only six classes were observed. Inspection of the distribution of the 2117 individuals given above, however, suggests the possibility of a 27:9:9:3:9:7 relation, which should be realized in a trihybrid if the last three classes were indistinguishable. A comparison of observed numbers with those expected on this hypothesis follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed.....	952	305	275	91	278	216	2,117
Calculated[3].....	893	298	298	99	298	232	2,118
Difference.....	+59	+7	—23	—8	—20	—16	—1

[3] In this and most of the following comparisons, the theoretical distributions are calculated to the nearest whole number.

There are rather large differences between observed and expected numbers. The purples are considerably, and the sun reds slightly, in excess of expectation, while each of the other four classes has too few individuals. The probability that these deviations may be due to chance is approximately 0.11. One might expect, therefore, to encounter chance deviations of the magnitude observed here about once in nine such trials. This, of course, does not substantiate the three-factor hypothesis, but merely indicates that it is not necessarily out of keeping with the observed facts.

Backcrosses with green VIc.— A better criterion perhaps is afforded by the backcross of F_1 purples with the green parent type. Records of such crosses are shown in table 3. The backcrosses with F_1's of table 1 are listed in group 1, and backcrosses with similar F_1 purples of other lots in group 2. The same six phenotypes observed in the regular F_2 generation occurred here also. On the basis of the three-factor hypothesis and with the assumption that there are three sorts of greens indistinguishable from one another, the individuals of this backcross should be distributed equally to five classes with the sixth class containing three times as many individuals as any other class. The observed distribution of the 1317 individuals of the fourteen progenies is here compared with the expected distribution:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed.....	170	160	176	160	172	479	1,317
Calculated.....	165	165	165	165	165	495	1,320
Difference.....	+5	—5	+11	—5	+7	—16	—3

While a few of the backcross progenies listed in table 3 exhibit considerable deviations from the expected distribution, the fourteen lots taken together approximate it closely. The probability that the observed deviations may be due to chance in random sampling is about 0.85. Deviations as great as these are to be expected thru chance alone, therefore, in about six out of seven trials.

Working hypothesis.— To the three factor pairs used to interpret the results here reported, the symbols *A a*, *B b*, and *Pl pl* have been assigned. The gene *A* is an anthocyanin factor. In the presence of *a a* ordinarily no anthocyanic pigment develops, tho brownish, or flavonol (Sando and Bartlett, 1921), pigment may be formed. The pair *B b* is named for its

connection with the development of brown pigment, tho when both *A* and *B* are present, sun red pigment is produced. The pair *Pl pl* is so termed because of its relation to purple pigment. The phenotypic formulae assigned to the several classes of plant color under consideration here are as follows:

A B Pl —	Ia,	purple
A B pl —	IIa,	sun red
A b Pl —	IIIa,	dilute purple
A b pl —	IVa,	dilute sun red
a B Pl —	V,	brown
a B pl —	VIa	green
a b Pl —	VIb	green
a b pl —	VIc	green

Obviously the hypothesis in accordance with which the above factorial assignments have been made is subject to several genetic tests. Naturally the first tests to suggest themselves are studies of the behavior of the several F_2 types in F_3 and later generations. Next in order are intercrosses between the several classes. For reasons that will appear shortly, one of these intercrosses is here dealt with before consideration is given to F_3 generations from the several F_2 classes.

Dilute sun red IVa x brown V

From an examination of the factorial assignments listed above, it is evident that crosses of dilute sun red, *A b pl*, with brown, *a B Pl*, should produce purple F_1 plants, *A B Pl*. Moreover, these F_1 purples should be heterozygous for all three factors, *A a B b Pl pl*, just as was assumed for the original cross of purple, *A B Pl*, with green, *a b pl*. The F_2 and later behavior of this cross should also, barring linkage, be like that of the original cross, so that the two can most conveniently be considered together.

Generations F_1 and F_2.— The F_1 generation of twenty-six crosses of dilute sun red with brown plants is given in table 4 (page 123). The dilute sun red parent plants were chosen from any convenient lots known to be homozygous with respect to *A*, *b*, and *pl*. The brown parent plants, on the other hand, were from the F_2 and later generations of the original cross of purple and green or from other crosses. It was to be expected, therefore, that some of the brown plants would be homozygous for both *B* and *Pl*, and some would be heterozygous for *B*, some for *Pl*, and some

for both *B* and *Pl*. This expectation was fully realized. In group 1 of table 4 are recorded the progenies of nine crosses with a total of 263 individuals. All but one plant of the lot were purple. The one dilute sun red plant was presumably due to accidental pollination of the dilute sun red mother plant. Since the dilute sun red parents of all these crosses were *A A b b pl pl*, the brown parents of the crosses listed in group 1 must presumably have been *a a B B Pl Pl*. Similarly, the seven crosses listed in group 2 gave purple and sun red plants only, 143 of the former and 147 of the latter. Evidently the brown parents of these crosses were *a a B B Pl pl*. Again, the six crosses shown in group 3 gave 105 purple, 123 dilute purple, and no other plants. The brown parents of the crosses were therefore, presumably, *a a B b Pl Pl*. Finally, the four crosses listed in group 4 gave 9 purple, 11 sun red, 19 dilute purple, and 17 dilute sun red. The brown parents of these four crosses are assumed, consequently, to have been *a a B b Pl pl*.

The F_2 results from the purple F_1 plants of these crosses of dilute sun red with brown are recorded in table 5. Fourteen progenies of the F_1 plants listed in table 4 are shown in group 1 of table 5, and five progenies from similar F_1 plants not listed in table 4 are entered in group 2. Here, just as with the results of the cross of purple with green (table 2), fairly marked discrepancies between theory and observation appear when the several progenies are taken separately. When, however, the nineteen progenies are considered together, very close agreement is found between observation and expectation, as is shown by the comparison below. The probability that such deviations as are observed may be due to chance is approximately 0.88, which means that only about once in eight trials would as good a fit be expected. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed.....	847	282	281	94	267	233	2,004
Calculated....	845	282	282	94	282	219	2,004
Difference....	+2	0	—1	0	—15	+14	0

Backcrosses with green VIc.— In addition to the F_2 results noted above as derived from self-pollinated F_1 purple plants, a few F_1 purples were back-

crossed with the triple recessive green, type VIc. The records of these crosses, seven in all, are presented in table 6. The results are, as expected, in close agreement with the backcross data from the cross of purple with green. The comparison below indicates a good fit of calculated to observed frequencies for the lot as a whole. The probability that such deviations as are observed may be due to mere chance is about 0.82, indicating that as great departures from expectation as these might be expected about four times in five trials. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed.....	84	72	78	72	79	249	634
Calculated....	79	79	79	79	79	237	632
Difference....	+5	—7	—1	—7	0	+12	+2

Backcrosses of Ia x VIc and IVa x V with IVa

Purple plants of F_1 of the crosses purple x green and dilute sun red x brown were crossed with homozygous dilute sun red stocks. On the basis of the hypothesis used above, the F_1 plants are assumed to be *A a B b Pl pl* and the dilute sun red plants *A A b b pl pl*. Four classes of plants, purple, sun red, dilute purple, and dilute sun red, should be produced in equal numbers by this cross. The data are presented in table 7 (page 125). Progenies of F_1 plants from the cross purple x green are listed in group 1 and those from the cross dilute sun red x brown in group 2. As will be seen from the comparison below, the observed numbers are in fair agreement with the hypothesis. The probability that such deviations as occur may be due to chance is approximately 0.67. In other words, there are two chances in three that deviations of this sort are due to errors of random sampling alone. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed.....	299	270	288	291	1,148
Calculated.....	287	287	287	287	1,148
Difference.....	+12	—17	+1	+4	0

Behavior of F_2 color types in later generations

From all the foregoing it appears that the results obtained are in close accord with the proposed three-factor hypothesis in the case of both the cross purple x green and the cross dilute sun red x brown, and not alone for the F_1 and F_2 generations but also for backcrosses with green and with dilute sun red. It is now in order to inquire into the behavior of these crosses in F_3 and later generations. In the presentation of the additional data, the two crosses purple x green and dilute sun red x brown will be considered together.

Later behavior of F_2 purple Ia.— Purple plants of the F_2 generation of the crosses under consideration are expected to be of eight genotypes. The expected F_2 genetic formulae and the F_3 color classes, together with the relative numbers of each, are as follows:

F_2 genotypes	F_3 color types					
	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VI
1 — *A A B B Pl Pl*	1	.....	.....	.....	.....	.....
2 — *A A B B Pl pl*	3	1	.....	.....	.....	.....
2 — *A A B b Pl Pl*	3	.....	1	.....	.....	.....
2 — *A a B B Pl Pl*	3	.....	.....	.....	1	.....
4 — *A A B b Pl pl*	9	3	3	1	.....	.....
4 — *A a B B Pl pl*	9	3	.....	.....	3	1
4 — *A a B b Pl Pl*	9	.....	3	.....	3	1
8 — *A a B b Pl pl*	27	9	9	3	9	7

If, instead of being selfed, the F_2 purple plants are backcrossed to green of type VIc, the same F_3 color classes are expected but the several classes should, of course, be equally frequent except in case of the F_2 triple heterozygotes, which should throw three times as many greens as of each of the other five types.

The F_3 data from thirty-five F_2 plants are recorded in table 8 (page 125). In group 1 of the table are listed the progenies of eight selfed and one backcrossed F_2 plants. From the backcross six color types appeared in frequencies of 4:4:11:4:4:18. The theoretical number for the first

five classes is 5.6 and for the sixth class is 17. The probability that such deviations as occur are due to chance is approximately 0.35, or more than one in three. The eight self-pollinated plants gave together the six types in frequencies as follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed.....	193	66	60	16	57	34	426
Calculated.....	180	60	60	20	60	46	426
Difference.....	+13	+6	0	—4	—3	—12	0

The probability that such deviations as occur may be due to errors of random sampling is practically 0.27. Similar deviations might therefore be expected somewhat more than once in four trials. It will be noted that two progenies lacking class IV are included in this lot (group 1, table 8). The total number of plants in these progenies were 37 and 17, respectively, and they should therefore have had, respectively, two and one plants in class IV.

Five F_2 purple plants (group 2, table 8) gave four color types (Ia, IIa, IIIa, and IVa) in F_3, with total frequencies as shown below. Here the probability, P, equals 0.75, indicating that deviations of this magnitude might be expected thru chance in three out of four trials. The comparison of observed with theoretical distributions follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed.....	102	36	29	13	180
Calculated.....	101	34	34	11	180
Difference.....	+1	+2	—5	+2	0

Progenies of seven other purple F_2 plants (group 3, table 8) consisted of the four color types Ia, IIa, V, and VIa. Four of these F_2 plants were self-pollinated and gave a total of 164 F_3 plants. Four, including one that was also selfed, were backcrossed to green and yielded a total of 209 F_3 plants. For the progenies from selfed F_2 plants $P = 0.20$, and for those from backcrossed plants $P = 0.57$. There is, therefore, one chance in five

in the one case and considerably more than an even chance in the other case that deviations of the kind noted may have been due to errors of random sampling. The comparisons follow:

	Color types	Purple Ia	Sun red IIa	Brown V	Green VIa	Total
Selfed	Observed	95	31	23	15	164
	Calculated	92	31	31	10	164
	Difference	+3	0	—8	+5	0
Backcrossed	Observed	54	58	44	53	209
	Calculated	52	52	52	52	208
	Difference	+2	+6	—8	+1	+1

Seven self-pollinated F_2 purple plants gave progenies consisting of the four color types Ia, IIIa, V, and VIb (group 4, table 8). Here $P=0.75$, indicating that there are three chances in four that such deviations as are shown are due to chance. The comparison follows:

Color types	Purple Ia	Dilute purple IIIa	Brown V	Green VIb	Total
Observed	318	114	111	42	585
Calculated	329	110	110	37	586
Difference	—11	+4	+1	+5	—1

Five F_2 purple plants from self-pollination gave only two color types (Ia and IIa) in F_3 (group 5, table 8). The total number of F_3 individuals was 183, of which 139 were of color type Ia and 44 were of color type IIa, the expected numbers being, respectively, 137 and 46, and the deviation equaling 2 ± 4. One of these F_2 plants was also backcrossed to two greens, resulting in 12 purple and 9 sun red F_3 plants where equality of the two classes was expected. The deviation here is 1.5 ± 1.5.

Finally, two self-pollinated F_2 purple plants produced 217 F_3 individuals (group 6, table 8) of color types Ia and IIIa. There were 168 purple

and 49 dilute purple where the expected numbers were 163 and 54, respectively — a deviation of 5 ± 4.3.

It is seen, then, that in every case the F_3 progenies of F_2 purple plants were of color types expected on the basis of the three-factor hypothesis, and that the F_3 distributions within any group were in close agreement with expectation. It is particularly noteworthy, however, that not all types of F_3 behavior were observed, and that the distribution of the progenies of the thirty-five F_2 plants tested was in rather imperfect agreement with expectation. Thus, no F_2 purple plant bred true in F_3 where one such plant was expected, and none gave progenies of purple and brown only where at least two with such behavior were expected. It has already been pointed out (page 35) that eight classes of behavior of F_2 purples are looked for, and that any twenty-seven F_2 purple plants should be distributed with respect to their F_3 behavior in the relation 1:2:2:2:4:4:4:8. The actual and theoretical distributions are compared as follows:

Observed.....	0	5	2	0	5	7	7	9	35
Calculated.....	1.3	2.6	2.6	2.6	5.2	5.2	5.2	10.4	35.1
Difference.....	—1.3	+2.4	—0.6	—2.6	—0.2	+1.8	+1.8	—1.4	—0.1

While mere inspection of the above comparison might suggest poor agreement between theory and observation, nevertheless P = 0.36, indicating that such deviations as occur might be expected in more than one out of three trials, which is not a bad fit. So far, therefore, the available data are in fair accord with the three-factor hypothesis.

Before taking up a consideration of the F_3 behavior of other F_2 color types, it will be well to consider briefly the F_4 behavior of F_3 purple plants. Only one F_3 purple of the lot having all six color types (table 8, group 1), comparable to F_2 purples, was tested in F_4. This one plant gave an F_4 with the four color types Ia, IIa, V, and VIa.

Only eight other F_3 purple plants were tested in F_4. All these belonged to the lot consisting of color types Ia, IIIa, V, and VIb (group 4, table 8). The F_2 purple plants giving rise to this group are assumed to have been of the genotype *A a B b Pl Pl*. The F_3 purple plants should therefore have been of four genotypes and should have given F_4 behavior as follows:

F_3 genotypes	F_4 color types			
	Purple Ia	Dilute purple IIIa	Brown V	Green VIb
1 — *A A B B Pl Pl*	1	.....	.....	.....
2 — *A A B b Pl Pl*	3	1	.....	.....
2 — *A a B B Pl Pl*	3	.....	1	.....
4 — *A a B b Pl Pl*	9	3	3	1

The data are presented in table 9. Four F_4 progenies (group 1) were made up of the four color types Ia, IIIa, V, and VIb. The total numbers of plants of each of the four types, as seen below, were in close accord with expectation, P equaling 0.57. There is more than an even chance that such deviations as those observed may have been due to errors of random sampling. The comparison of observed with calculated results follows:

Color types	Purple Ia	Dilute purple IIIa	Brown V	Green VIb	Total
Observed	185	68	74	20	347
Calculated	195	65	65	22	347
Difference	—10	+3	+9	—2	0

Three of the eight purple F_3's (group 2) gave in F_4 only purple and dilute purple plants, 88 of the former and 28 of the latter. The expected numbers were 87 and 29, respectively, showing a deviation of 1 ± 3.1.

One of the eight F_3 purples (group 3) gave 67 purple and 21 brown plants in F_4, while the expected numbers were 66 and 22, respectively. The deviation here is only 1 ± 2.7.

None of the eight F_3 purples bred true, but only one in nine was expected to do so. As already indicated, the theoretical distribution of nine F_3 purples of the sort here under consideration, with respect to the four kinds of behavior in F_4, is 1:2:2:4. The observed distribution was 0:3:1:4. There is more than an even chance that these deviations may have been due to errors of random sampling, P equaling 0.57.

It should not be forgotten that, while a very poor fit of observation to hypothesis, as measured by values of P, throws doubt upon the correctness of the hypothesis, it does not follow that a good fit proves the hypothesis to be true. This is particularly true where small numbers are dealt with. It will be recalled in this connection that, owing probably to the small numbers tested, no F_2 purple has been found to breed true in F_3 and none has been found to give only purple and brown offspring. It has been shown, however, that purple plants of the genotype *A a B B Pl Pl* exist, since one F_3 purple threw only purple and brown plants in F_4. Moreover, one of these F_4 purples repeated this behavior in F_5. Similarly it can be said that purples of the genotype *A A B B Pl Pl* have been recovered from the crosses under consideration, for two F_4 purple plants of the lot composed of purples and dilute purples (group 2, table 9), when backcrossed to green, gave 18 purple plants and no other types in the next generation, and one of these two F_4 purples, when crossed back to dilute sun red, gave 34 purple plants. Two other purples of the same F_4 lot, when similarly crossed, gave both purple and dilute purple, 23 of the former and 18 of the latter. Purple plants of all the expected genotypes have therefore been recovered in one or another generation from F_2 to F_4 from the original crosses of purple x green and dilute sun red x brown. Moreover, these genotypes have been found in numbers not far from what might reasonably be expected considering the relatively small numbers tested. It now remains to inquire into the F_3 and later behavior of F_2 color types other than purple.

Later behavior of F_2 sun red IIa.— Sun red plants of F_2 of the crosses purple x green and dilute sun red x brown are expected, in accordance with the three-factor hypothesis, to be of four sorts with respect to their behavior in F_3, as follows:

F_2 genotypes	F_3 color types		
	Sun red IIa	Dilute sun red IVa	Green VIa, c
1 — *A A B B pl pl*	1	.....	.....
2 — *A A B b pl pl*	3	1	.....
2 — *A a B B pl pl*	3	.....	1
4 — *A a B b pl pl*	9	3	4

Only nine F_2 sun red plants were tested by their F_3 behavior, and no later generations were grown. All the available data are given in table 10 (page 128). Five F_2 plants, when self-pollinated (group 1 of the table), gave the expected three classes of progeny, sun red, dilute sun red, and green, with a distribution of the F_3 plants as given below, and in addition a single brown plant. To include this unexpected plant in the comparison with the calculated distribution would give zero as the value of P, which is equivalent to saying that even in an infinite number of trials there is no chance of finding such a plant thru errors of random sampling. The single off-type plant is readily accounted for by supposing that a grain of foreign pollen was accidentally admitted in the pollination of the parent plant. Tho it is realized that, with such a convenient supposition always at hand, almost any result can be made to fit a theory, the reality of just such accidental pollinations will not be questioned by any one who has had experience in the technique of maize pollination. With the elimination of this one plant, the fit of observation to hypothesis is almost perfect. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	126	42	55	223
Calculated	125	42	56	223
Difference	+1	0	—1	0

Three F_2 sun red plants, including one of the five in the former test, were crossed back to green (group 1, table 10). The same three color types were observed as in the self-pollinated plants, with the addition again of a single off-type plant, this time a purple one. Even if this plant is left out of consideration as due to an accidental pollination, the fit of observed with calculated numbers is not very good. Such deviations from theoretical behavior are to be expected thru chance alone only once in eight trials, P equaling 0.12. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	14	18	50	82
Calculated	20.5	20.5	41	82
Difference	—6.5	—2.5	+9	0

A single F_2 sun red plant (group 2, table 10) gave, from self-pollination, 23 sun red and 9 dilute sun red F_3 plants, a deviation from expectation of 1 ± 1.7.

A single F_2 sun red plant (group 3, table 10), when crossed with green VIc, gave 50 sun reds and 43 greens where equality was expected, a deviation of 3.5 ± 3.3.

By way of summary of the behavior of F_2 sun red plants, it must be noted that, while four sorts of behavior were expected, only three sorts were observed. While any nine such F_2 plants should be distributed with respect to the four kinds of behavior in the relation 1:2:2:4, the observed relation was 0:1:1:7. While mathematically this is not a very bad fit considering the small numbers involved, P equaling 0.24, it is inadequate for a determination of the possible genotypes of F_2 sun red plants. Fortunately, certain crosses considered later (page 51) involving the sun red type, with presumably the same genetic constitutions as the F_2 sun reds of this cross, afford a more nearly adequate test of the matter.

Later behavior of F_2 dilute purple IIIa.— F_2 dilute purple plants should present the same types of behavior in F_3 as F_2 sun reds, but, of course, with somewhat different color types appearing, as follows:

F_2 genotypes	F_3 color types		
	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c
1 — *A A b b Pl Pl*	1	.....	.....
2 — *A A b b Pl pl*	3	1	.....
2 — *A a b b Pl Pl*	3	.....	1
4 — *A a b b Pl pl*	9	3	4

The available data from this test are given in table 11 (page 129). Four F_2 dilute purples (group 1) yielded the three color types expected, dilute purple, dilute sun red, and green, in the numbers shown below. There is considerably more than an even chance that the deviations from expectation may be due to errors of random sampling, P equaling 0.58. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed	95	31	50	176
Calculated	99	33	44	176
Difference	—4	—2	+6	0

One of the dilute purple F_2 plants used in this test was backcrossed with green VIc (group 1, table 11), with the result shown below. There is practically an even chance that the observed deviations may be due to errors of random sampling, P equaling 0.49. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed	21	25	57	103
Calculated	26	26	52	104
Difference	—5	—1	+5	—1

One F_2 dilute purple gave 57 dilute purple and 21 dilute sun red plants in F_3 (group 2, table 11). The expected numbers were 58.5 and 19.5, respectively, the deviation being 1.5 ± 2.6.

Three F_2 dilute purples gave a total of 85 dilute purple and 20 green plants (group 3, table 11), the theoretical numbers being 79 and 26, respectively. The deviation from expectation, 6 plants, is just twice the probable error.

One F_2 dilute purple bred true in F_3, producing 21 dilute purple plants and no other types (group 4, table 11). Thus, all the sorts of behavior expected of F_2 dilute purples were realized in F_3. The distribution of the F_2 plants with respect to the four sorts of behavior was 1:1:3:4, instead of the theoretical distribution 1:2:2:4. Differences of this sort might be expected thru chance in four out of five trials, P equaling 0.80.

Only three plants of these lots were tested in F_4. One was a dilute sun red of the lot made up of dilute purples and dilute sun reds, and this one bred true in F_4 as was expected of it, producing 34 dilute sun red plants. The other two plants tested further were dilute purples of the lot containing the three color types III, IV, and VI. Both again gave these three

types, the total numbers of the respective classes being 29, 5, and 18. The expected numbers, 29, 10, and 13, show a deviation from expectation which might result thru chance about once in nine trials, P equaling 0.11.

Later behavior of F_2 dilute sun red IVa.— Dilute sun red plants of F_2 should be of two sorts, *A A b b pl pl* and *A a b b pl pl*. Five such plants were tested, with results as shown in table 12 (page 129). Of these five, two bred true, producing a total of 92 dilute sun red plants (group 2). One of these two, when backcrossed with green, gave 69 dilute sun red plants. Three of the five F_2's gave in F_3 dilute sun reds and greens, 62 of the former and 17 of the latter (group 1). The theoretical numbers were 59 and 20, respectively. The deviation of 3 plants is only a little greater than the probable error, $\pm$ 2.6. With two of the F_2 dilute sun red plants breeding true and three again throwing segregates, expectation was very nearly realized.

Later behavior of F_2 brown V.— Brown plants of F_2 are expected to be of four genotypes and to show consequent differences in behavior in F_3 as follows:

F_2 genotypes	F_3 color types	
	Brown V	Green VI
1 — *a a B B Pl Pl*	1	.....
2 — *a a B B Pl pl*	3	1
2 — *a a B b Pl Pl*	3	1
4 — *a a B b Pl pl*	9	7

Data for F_3 from fourteen F_2 brown plants are presented in table 13 (page 130). Five self-pollinated F_2 browns (group 1) gave, in addition to one sun red presumably due to accidental pollination, 96 browns and 74 greens in F_3, which is almost exactly a 9:7 relation, the deviation being 0.4 $\pm$ 4.4. Nine other selfed F_2 browns (group 2) gave in F_3 a total of 354 brown and 104 green plants. An exact 3:1 ratio for the total of 458 would be 343.5 and 114.5, respectively, the deviation being 10.5 $\pm$ 6.3. Such a deviation might be expected thru chance alone about once in four

trials. One of the F_2 brown plants that, when selfed, gave a 3:1 ratio in F_3, when crossed with green gave 34 brown and 41 green plants where equal numbers were expected, the deviation being 3.5 ± 2.9. None of the fourteen F_2 brown plants bred true in F_3. The fourteen plants should theoretically have given F_3 ratios of 1:0, 3:1, and 9:7 in approximately the respective numbers of 1.6, 6.2, 6.2, while the observed numbers were 0, 9, 5. Such deviations might occur by chance once in five trials, P equaling 0.22.

It is often difficult and sometimes practically impossible from ordinary F_3 progenies to distinguish between the two genotypes of brown which throw 3:1 progenies, namely, *a a B B Pl pl* and *a a B b Pl Pl*. The green plants thrown by the former often show some brown pigment in the exposed parts of the sheaths and husks (type VIa), a condition not seen in the greens (VIb) thrown by the latter. In some lots the brown pigment is fairly conspicuous but in others it is very weak or is absent. Again, the greens of type VIb thrown by browns of the genotype *a a B b Pl Pl* show considerable brown in the glumes of the staminate flowers. This is particularly pronounced when r^{ch} (a gene for cherry pericarp which is effective only in the presence of *Pl*) is present, but when this factor is lacking the brown color is often so faint that it is impossible to distinguish between a green plant carrying *Pl* and one lacking it. If r^{ch} is present, the green plants carrying *Pl* develop a light brownish pericarp at maturity while those lacking *Pl* never show this pericarp color whether or not *B* is present. Here again, however, the light brownish pericarp due to r^{ch}, *Pl*, and *a a* may be wholly masked if there happens to be present another pericarp color gene, *P*, which with *a a* brings about a strong brown color of the pericarp whether or not *Pl* or *B* is present.[4] On the whole, therefore, it is difficult, and often impossible, to determine the genotype to which a brown plant belongs, by an inspection of the green plants occurring in its progeny. Because of this, the 3:1 lots of F_3 progenies of F_2 brown plants are lumped together in group 2 of table 13 without any attempt to separate them into the two classes expected. Fortunately, it is readily possible to distinguish between brown plants of the two genotypes under consideration here by means of appropriate crosses.

[4] An account of these pericarp-color factors is to be published later by Dr. E. G. Anderson, who is making a study of the pericarp colors of maize.

When brown plants of all the genotypes expected in F_2 of the crosses of purple x green or dilute sun red x brown are crossed with homozygous dilute sun red plants, the following behavior is expected in the next generation:

F_2 genotypes	F_2 x *A A b b pl pl*			
	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1 — *a a B B Pl Pl*	1	.....	.....	.....
2 — *a a B B Pl pl*	1	1	.....	.....
2 — *a a B b Pl Pl*	1	.....	1	.....
4 — *a a B b Pl pl*	1	1	1	1

A few such tests of F_2 brown plants are recorded in table 14. Two plants (group 1), on being crossed with dilute sun reds, gave purples and sun reds only, 38 of the former to 45 of the latter, where equality was expected, the deviation being 3.5 ± 3.1. One of these plants has progeny from self-pollination listed in table 13, in group 2, the 3:1 lot. This plant was expected, of course, to throw only two color types from the cross with dilute sun reds, for otherwise it should not have given a 3:1 progeny on being selfed. The two brown plants in group 1 of table 14 must have been *a a B B Pl pl*. Two other F_2 brown plants (group 2) gave 32 purple and 38 dilute purple instead of the equal numbers expected, the deviation being 3.0 ± 2.8. These plants are assumed to have been *a a B b Pl Pl*. A single F_2 brown plant (group 3) when crossed with dilute sun red gave 15 purple plants, and is therefore assumed to have been *a a B B Pl Pl*.

The behavior of several F_3 brown plants when crossed with dilute sun reds is also shown in table 14. Three of these plants were from 9:7 F_3 lots and therefore are presumably comparable with F_2 browns. One of these three (group 4) gave the four color types I to IV in the numbers 1:2:6:3. It was probably *a a B b Pl pl* and should have given a 9:7 progeny if it had been selfed. The other two F_3 browns of the 9:7 lot gave 49 purple plants (group 7) and are consequently regarded as *a a B B Pl Pl*. All the other F_3 brown plants tested were from the

3:1 lot listed in table 13, group 2. None of these should give more than two types when crossed with dilute sun red. One gave 46 purple and 1 dilute sun red (group 7), the latter doubtless from an accidental pollination of the dilute sun red mother plant. Two F_3 browns gave 22 purple and 24 sun red plants (group 5), and four produced 73 purple and 85 dilute purple plants (group 6).

To summarize, all the theoretically possible genotypes of brown plants have been found either in F_2 or in such F_3 lots as showed a 9:7 ratio of brown to green. Since these F_3's are comparable with F_2 browns, they may be added to the F_2's in this summary. Of the twenty-one brown plants thus grouped, the numbers found to belong to each genotype are compared below with the calculated numbers. The deviations are such as might be expected to occur once in three trials, P equaling 0.34. The comparison follows:

	a a B B Pl Pl	*a a B B Pl pl* or *a a B b Pl Pl*	*a a B b Pl pl*	Total
Observed.....	3	12	6	21
Calculated.....	2.3(+)	9.3(+)	9.3(+)	21
Difference.....	+0.7(—)	+2.7(—)	—3.3(+)	0

Later behavior of F_2 green VI.— All F_2 green plants should breed true phenotypically in F_3. Data from eight such F_3 progenies are given in table 15, group 1 (page 132). There were observed a total of 179 green plants, and no other types. Progenies of sixteen green plants of the F_2 lots listed in tables 3 and 6 (pages 122 and 124), produced by backcrossing F_1 purples to greens, are given in table 15, groups 2 to 5. The total number of green plants in these progenies is 311. A single brown plant found in one of these progenies is assumed to have been due to accidental pollination. Green plants are therefore found to breed true green as expected, but there is nothing in this fact to indicate that green plants of the crosses under consideration are genotypically alike. That the five genotypes expected on the basis of the three-factor hypothesis were present among the progenies listed in table 15 is demonstrated in the next section of this paper.

Intercrosses of F_2 color types

It has been shown in the preceding pages that all the six color types occurring in F_2 of a cross between purple and green behave in F_3 and later generations as is expected on the basis of the three-factor hypothesis suggested to account for the F_2 results. It remains to determine whether the several color types behave in accordance with the hypothesis when intercrossed one with another. Of the fifteen possible intercrosses between phenotypically different types, two have already been discussed. The cross of purple with green has formed the basis of the whole discussion. The cross of dilute sun red with brown, since it was expected to give the same results as the original cross of purple with green, was most conveniently considered with that cross in generations later than F_2. The results of this second cross have been in accord with expectation. The other thirteen intercrosses are now to be considered, together with intercrosses of some types that are phenotypically alike.

Dilute sun red IVa x green VIa, VIb, VIc.—The progenies of self-pollinated green plants were listed in table 15 in several groups in accordance with what was learned of their genotypic constitution by the crosses to be considered here. The regular F_3 lots, from self-pollinated F_2 greens of self-pollinated F_1 purples, were put in group 1 of table 15. Only one of the same F_2 greens (table 16, group 2) was crossed with homozygous dilute sun red, *A A b b pl pl.* The result was 67 dilute purple plants. Another green plant, an F_3 from a self-pollinated F_2 green, gave, when similarly crossed, 9 dilute purple plants (group 2). Evidently both these green plants were *a a b b Pl Pl.* Four other F_3 green plants, when crossed with dilute sun red, gave a total of 148 sun red plants (group 1, table 16). One of these four belonged to an F_3 lot containing browns and greens in a 3:1 relation, and could not, theoretically, have done other than give all sun red or all dilute purple when crossed with dilute sun red. Two of the four were from greens of an F_3 lot made up of purples, sun reds, browns, and greens, and were therefore assumed to be *a a B B pl pl,* as the crosses with dilute sun red showed them to be. One of the four green plants, however, belonged to an F_3 lot of browns and greens in a 9:7 relation and was consequently comparable to an F_2 green. A sixth F_3 green also belonged to a 9:7 lot, comparable to an F_2 lot. When crossed with dilute sun red (group 3, table 16), it gave 24 dilute sun red plants,

and is therefore assumed to have been *a a b b pl pl*. All three of the theoretically possible homozygous genotypes have therefore been demonstrated among the F_2 greens or among F_3's comparable to F_2's.

In addition to the green plants of the direct F_2 and F_3 generations, noted above, fifteen other greens were crossed with dilute sun red. All these greens belonged to a single progeny, 2019, which was the result of a backcross of an F_1 purple with a green, *a a b b pl pl* (table 3, group 1). All of them should therefore have been heterozygous for *B* or *Pl*, or have lacked these dominant genes. Seven of the fifteen, when crossed with dilute sun red, gave 110 sun red and 85 dilute sun red plants (group 4, table 16), a deviation from equality of 12.5 ± 4.7. The green parent plants are consequently regarded as *a a B b pl pl*. Five others of the fifteen green plants (group 5) gave a total of 56 dilute purple and 65 dilute sun red, a deviation from equality of 4.5 ± 3.7, and hence are assumed to have been *a a b b Pl pl*. Three of the fifteen (group 6) gave a total of 106 dilute sun red plants. These three must, it is supposed, have been *a a b b pl pl*.

Naturally, in the course of the writer's maize studies, many other crosses between green and dilute sun red have been observed. But no purpose can be served by presenting here all this mass of data. Much of it has accumulated in connection with a study of the interrelations of plant and aleurone color, and will find its appropriate place in a later publication on that topic. A few F_2 and backcross progenies of dilute sun red F_1's of such crosses are, however, listed in table 17 (page 134), to serve as an indication of the behavior of all. Three F_2 progenies (group 1, table 17) contained 269 dilute sun reds and 99 greens, a deviation from the expected 3:1 ratio of 7 ± 5.6. Five progenies of F_1 dilute sun reds backcrossed to green VIc (group 2) included 357 dilute sun reds and 358 greens, a deviation from the expected 1:1 ratio of only 0.5 ± 9.0.

The behavior of a number of the sun red and dilute purple plants listed in table 16 has been studied in F_2 and later generations. Consideration of this later behavior is conveniently deferred to a later section of this paper (pages 51 and 53), where it is taken up with other crosses which should theoretically give similar results.

Green x green, VIa, VIb, VIc.— A number of green plants of progeny 2019, discussed above, were intercrossed. That these green plants bred true green when selfed was shown by the records of table 15 (groups 3

to 5). That they were of three distinct genotypes was shown by the data recorded in table 16 (groups 4 to 6). The behavior of random intercrosses of the same green plants is now to be considered. The data are given in table 18.

The green plants that served as parents of the crosses listed in group 6 of table 16, it was decided, must have been *a a b b pl pl*. When such plants are crossed with green plants of any of the other genotypes, nothing but green plants should result. A single cross of one of these greens with a green of the constitution *a a B b pl pl* (table 16, group 4) gave 23 green plants (table 18, group 1) as expected. Another cross of one of these greens with a green of the genotype *a a b b Pl pl* (table 16, group 5) gave 22 green plants (table 18, group 2). Crosses of green plants belonging to like genotypes should, of course, give only green plants. Three crosses of plants shown to be *a a B b pl pl* (table 16, group 4) gave 72 green plants (table 18, group 3). A single cross between plants shown to be *a a b b Pl pl* (table 16, group 5) gave 24 green plants (table 18, group 4). Five crosses of plants of genotype *a a B b pl pl* with plants of genotype *a a b b Pl pl* gave a total of 40 brown and 105 green plants (table 18, group 5). Here a 1:3 ratio of brown to green is to be expected. The theoretical numbers are therefore 36 and 109, respectively, and the deviation is 4.0 ± 3.5. The important fact here is that all these intercrosses of greens gave the color types expected on the basis of the results of crosses of the same individual green plants with dilute sun reds. The writer deems himself fortunate in having been able to obtain results approximating so closely a complete demonstration of the several genotypes of green, since the selfing, the crossing with dilute sun reds, and the intercrossing of greens, were made at the same time, with the green plants chosen wholly at random.

Brown V x green VIc.— When brown plants are crossed with green plants of type VIc, the F_1 plants are brown, and browns and greens alone appear in F_2. Since brown is supposed to be *a B Pl* and type VIc green *a b pl*, the F_2 progenies should exhibit 9:7 ratios. Eleven F_2 progenies are listed in table 19 (page 135), with a total of 317 brown and 223 green plants. The theoretical numbers are 304 and 236, respectively, showing a deviation of 13 ± 7.8. There is more than one chance in four that such a deviation is due to errors of random sampling, P equaling 0.27.

Of any nine F_2 brown plants of this cross, theoretically one should breed true in F_3, four should give a 3:1 ratio, and four should give a 9:7 ratio. Six F_2's were tested, with the results shown in table 20. Two bred true, with a total of 29 brown plants (group 1). Two gave ratios classed as 3:1, the totals (group 2) being 100 brown to 40 green, a deviation of 5.0 ± 3.5. Two gave progenies interpreted as 9:7 (group 3), totaling 39 brown and 39 green, the deviation being 5.0 ± 3.0. Of the 3:1 F_3 lot, two browns bred true in F_4, producing 59 brown plants, and one green bred true, producing 56 green plants.

The distribution of the F_2 brown plants with respect to their F_3 behavior — two breeding true, two throwing a 3:1 ratio, and two a 9:7 ratio — was as near expectation, 1:4:4 in nine, as could perhaps be expected from such small numbers. If these six F_2 browns are combined with the fourteen F_2 browns of the original cross of purple x green noted earlier in this paper (page 44), a very good fit of the hypothesis and observation is found ($\chi^2 = 0.88$). Theoretically these two lots of F_2 browns should be of the same genotypes, so that they may well be so combined. The comparison follows:

F_3 ratios	1:0	3:1	9:7	Total
Observed	2	11	7	20
Calculated	2	9	9	20
Difference	0	+2	—2	0

Sun red IIa x green VIc.— When both parents are homozygous, the cross of green of type VIc with sun red results in sun red plants only. Three such crosses gave 112 sun red plants. Crosses with heterozygous sun red plants gave F_1 progenies of sun red together with dilute sun red or green or both, depending presumably upon whether one or the other or both of the factors *A* and *B* were heterozygous. F_1 sun red plants of such crosses are presumed to have the formula *A a B b pl pl*, and should therefore produce in F_2 the three color types sun red, dilute sun red, and green, in the relation 9:3:4. Sixteen F_2 progenies of such crosses are listed in table 21, group 1 (page 136). It has already been shown (page 48) that crosses of some green plants, *a B pl*, with dilute sun reds, *A b pl*, give sun red F_1 offspring, which are also assumed to be *A a B b pl pl*. Five F_2 progenies of such crosses are, for convenience, considered here

(group 2, table 21) with the crosses of sun red and green. While certain of the individual progenies, due perhaps to the small numbers concerned, deviate considerably from the expected results, the twenty-one progenies (groups 1 and 2, table 21) taken together approach so closely to expectation that there is more than one chance in four that the observed deviations may be due to errors of random sampling, P equaling 0.28. The comparison of observed with expected numbers follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed:				
IIa x VIc	827	268	383	1,478
IVa x VIa	343	120	179	642
Total	1,170	388	562	2,120
Calculated	1,193	398	530	2,121
Difference	—23	—10	+32	—1

F_1 sun red plants, *A a B b pl pl*, were also backcrossed with green plants of type VIc, *a b pl*. Fifteen progenies of these backcrosses are listed in table 21, the progenies from the cross IIa x VIc in group 3 and those from the cross IVa x VIa in group 4. The expected relation of 1:1:2 was realized fairly well in the results, the odds against the observed deviations' being due to chance being about three to two, P equaling 0.39. The observed and expected results are compared as follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed:				
(IIa x VIc) x VIc	134	123	267	524
(IVa x VIa) x VIc	442	465	962	1,869
Total	576	588	1,229	2,393
Calculated	598	598	1,196	2,392
Difference	—22	—10	+33	+1

Dilute purple IIIa x green VIc.— Since dilute purple differs from sun red merely in having the dominant *Pl* factor instead of *B*, crosses of dilute purple with green of type VIc should behave just as did the crosses considered in the preceding section, except that dilute purples take the place of sun reds in the progeny. Eight crosses of dilute purple with green of type VIc resulted in 91 dilute purple plants. The F_2 results of these crosses are given in table 22, group 1. Since the F_1 plants of these crosses are assumed to have been *A a b b Pl pl*, the F_2 results should be the same as those expected from crosses of greens of type VIb with dilute sun reds. The F_1's of the latter crosses have already been discussed (page 48). The F_2 results, six progenies, are for convenience considered here (group 2, table 22). While the expectation of a 9:3:4 relation was not very closely realized in the observed results, such deviations as those found might be expected thru chance about once in eight trials, P equaling 0.13. The comparison of observed and expected distributions follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed:				
IIIa x VIc	416	149	173	738
IVa x VIb	274	102	107	483
Total	690	251	280	1,221
Calculated	687	229	305	1,221
Difference	+3	+22	—25	0

A single F_1 plant backcrossed with green gave the same three color types in the relation 26:20:56. The theoretical distribution is 25.5:25.5:51.0. Deviations of the observed order might be expected somewhat more than twice in five trials, P equaling 0.44.

Seven F_2 greens bred true in F_3 with a total of 359 individuals. One dilute sun red F_2 plant bred true with a progeny of 156 dilute sun red plants. Of the F_2 dilute purples, some bred true, some threw the three types seen in F_2, some gave only dilute purple and dilute sun red, and some gave only dilute purple and green. Notwithstanding the rather poor fit in F_2, therefore, the fact that practically all the expected classes

of behavior were exhibited in F_3 makes it seem likely that the deviations in F_2 were due mainly to chance.

Sun red IIa x brown V.— A single cross of brown with sun red gave purple plants only, as was expected. Since both parents were homozygous, all the F_1 plants should have been of the genotype *A a B B Pl pl* and should have produced in F_2 the four types purple, sun red, brown, and green, in the relation 9:3:3:1. The three F_2 progenies of this cross are recorded in table 23 (page 137). The expected color types were produced in approximately the expected numbers. The odds against the observed deviations' being due to chance are three to two, P equaling 0.40. A comparison of observed with expected distributions follows:

Color types	Purple Ia	Sun red IIa	Brown V	Green VIa	Total
Observed	120	29	37	10	196
Calculated	110	37	37	12	196
Difference	+10	—8	0	—2	0

Purple Ia x brown V.— Crosses of brown with purple gave purple F_1's, and four F_2 progenies gave a total of 116 purple and 38 brown plants, which is very near the 3:1 ratio expected from F_1 plants of the genotype *A a B B Pl Pl*, the deviation being 0.5 ± 3.6. Nine F_1 purples backcrossed to browns gave progenies totaling 484 purple and 477 brown plants, a deviation from the expected equality of 3.5 ± 10.5.

Purple Ia x sun red IIa.— Purples and sun reds should differ by a single factor pair, *Pl pl*. The F_1 purples backcrossed to sun red should give a 1:1 ratio of the parental types. Five such backcrosses gave 47 purple and 57 sun red plants, a deviation from expectation of 5 ± 3.4. No progenies of selfed F_1's were observed.

Purple Ia x dilute purple IIIa.— Purples are assumed to differ from dilute purples by the factor pair *B b*. Six F_1 purples backcrossed with dilute purple gave 40 purple and 52 dilute purple plants. This is a deviation from the expected equality of 6 ± 3.2. No other tests of the cross of purple x dilute purple were made.

Sun red IIa x dilute sun red IVa.— Sun reds and dilute sun reds should differ in one factor pair, *B b*, and should therefore give a simple 3:1 result in F_2. The F_1 generation of six crosses of these color types consisted of 135 sun red plants. Sixteen F_2 progenies listed in group 1 of table 24

(page 138) totaled 998 sun red and 314 dilute sun red, a deviation from the 3:1 ratio of 14 ± 10.6.

Fourteen backcrosses of F_1 sun red plants with dilute sun reds (group 2, table 24) resulted in 811 sun reds and 742 dilute sun reds, a deviation from the expected equality of 34.5 13±.3.

Two F_2 dilute sun reds bred true in F_3 as expected (table 25, group 1), with a total of 50 dilute sun red offspring. Two F_2 sun red plants (group 2) gave a total of 19 sun reds in F_3, and a third F_2 plant, on backcrossing with dilute sun red, gave 101 sun reds. Four other F_2 sun red plants gave both sun reds and dilute sun reds in their F_3 progenies (group 3), the respective numbers being 373 and 127; the calculated numbers are 375 and 125, respectively, showing a deviation of 2 ± 6.5. Of the seven F_2 sun reds tested, four were heterozygous and three apparently homozygous for the *B* factor. On the whole, therefore, the crosses of sun red with dilute sun red behaved approximately as expected.

Dilute purple IIIa x dilute sun red IVa.— Five crosses of dilute sun red with dilute purple gave a total of 344 F_1 plants, all dilute purple. Since these F_1's are supposed to be heterozygous for the *Pl* factor only, a 3:1 F_2 distribution of color types should result. Seven F_2 progenies listed in group 1 of table 26 (page 139) had a total of 261 dilute purple and 87 dilute sun red plants, exactly a 3:1 relation. Five F_1 plants were backcrossed with dilute sun red (group 2) and resulted in 275 dilute purples and 263 dilute sun reds. The deviation from the theoretical 1:1 relation is 6 ± 7.8.

Only two F_2 dilute purples were tested by their F_3 behavior. Neither bred true, the total produced being 38 dilute purples to 17 dilute sun reds, a deviation from the 3:1 ratio of 3.3 ± 2.2. As far as they go, then, the results are in close agreement with what is expected of the crosses here under consideration.

Sun red IIa x dilute purple IIIa.— Theoretically, crosses of sun red, *A B pl*, with dilute purple, *A b Pl*, should give purple, *A B Pl*, in F_1. Two crosses, as shown in group 1 of table 27 (page 140), gave a total of 24 purple and no other types. Here the parents were doubtless homozygous. If one or the other of the parents is heterozygous two color types are to be expected in F_1. A single cross (group 2, table 27) gave 74 purple and 75 sun red plants. Such a result is to be expected when the sun red parent is homozygous, *A A B B pl pl*, and the dilute purple parent is heterozygous, *A A b b Pl pl*. Two other crosses (group 3) gave

a total of 28 purple and 29 dilute purple plants. The parents are therefore assumed to have been *A A B b pl pl* and *A A b b Pl Pl*, tho the same results should have been obtained if one or the other, but not both, of the parents had been *A a*. The important point here is that purple plants were produced in all crosses, showing that sun red and dilute purple carry complementary factors for purple. The factors are assumed, in keeping with the hypothesis under test, to be *B* and *Pl*.

In accordance with this hypothesis, the F_1 purple plants should be *A A B b Pl pl* and should throw four color types in F_2. No direct F_2 progenies have been observed, but seven progenies from backcrosses of F_1 purples with dilute sun reds are recorded in table 28. While the deviations from the expected equality among the four classes are rather large, they are not greater than might occur by chance about once in four trials, P equaling 0.26. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed	99	110	104	83	396
Calculated	99	99	99	99	396
Difference	0	+11	+5	—16	0

Purple Ia x dilute sun red IVa.— Crosses of purple with dilute sun red should give purple F_1 plants, *A A B b Pl pl*, and 9:3:3:1 F_2 progenies. Four such crosses resulted in 65 purple plants in F_1. The F_2 results are reported in table 29, group 1. The distribution of the individuals of the twenty-six progenies taken together is shown below in comparison with the calculated distribution. The four color types expected were observed in approximately the expected numbers. Deviations such as shown might be expected thru chance about twice in eleven times, P equaling 0.18.

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed	1,013	316	296	100	1,725
Calculated	970	323	323	108	1,724
Difference	+43	—7	—27	—8	+1

Some of the F_1 purple plants were crossed back to dilute sun red, with results as given in group 2 of table 29 and summarized below. The seventeen progenies together approached the expected equality of the four color types so closely that the observed deviations might be expected thru chance more than twice in five trials, P equaling 0.44.

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	323	306	325	289	1,243
Calculated	311	311	311	311	1,244
Difference	+12	—5	+14	—22	—1

Sixteen F_2 purple plants were tested by their F_3 progenies (table 30). Seven F_2 purples (group 1) gave again the four color types purple, sun red, dilute purple, and dilute sun red, the several classes being represented by 268, 105, 78, and 28 individuals, respectively, while the calculated numbers were 269, 90, 90, and 30. The odds against such deviations being due to chance are about three to one, P equaling 0.24. One of the seven F_2 purple plants was crossed with green *a a b b pl pl* and gave the same four classes of progeny, represented by 26, 25, 24, and 21 plants, respectively. Evidently these F_2 purples were like the F_1's, *A A B b Pl pl.*

Four other F_2 purples (group 2, table 30) gave only purple and sun red progenies. Three of these when selfed gave 60 purple and 22 sun red. Two of these three and one other, when backcrossed with dilute sun red or green, gave 32 purples and 31 sun reds. The four F_2's are therefore regarded as *A A B B Pl pl.*

Five F_2 purples (group 3) gave purples and dilute purples only. Four of these, which were selfed, gave 162 purples and 48 dilute purples, while the fifth, which was backcrossed to dilute sun red, gave 17 purples and 15 dilute purples. These five F_2's are consequently regarded as *A A B b Pl Pl.*

None of the sixteen F_2 purples tested bred true in F_3, *A A B B Pl Pl.* A single F_3 purple (group 6), however, which occurred in the F_3 lot showing the four color types (group 1) and which was therefore comparable to the F_2 purples, bred true in F_4, producing 69 purples on being selfed and 18 on being backcrossed to green. Of three other F_3 purples of the same

F_3 lot, two (group 4) gave only purples and sun reds, and one (group 5) gave only purples and dilute purples.

The twenty F_2 and F_3 purples tested, therefore, were distributed with respect to the four kinds of behavior in the relation 7:6:6:1, in contrast to the calculated distribution of approximately 8.9:4.4:4.4:2.2. There is more than an even chance that such a difference may be due to errors of random sampling, P equaling 0.53. On the whole, therefore, the F_2 purples of this cross behaved in later generations as was expected of them.

F_2 sun red plants of the cross purple x dilute sun red showed two types of behavior in F_3 (table 31, group 1). Three F_2's bred true, with 53 sun red plants in F_3. Four gave a total of 70 sun red and 24 dilute sun red plants. Where an expected ratio of one true breeding to two segregating progenies was expected, the observed relation of three to four is not a bad fit.

F_2 dilute purples also showed the two types of behavior expected in F_3 (group 2, table 31). Three bred true, with a total of 97 dilute purple plants, and six gave a total of 217 dilute purple and 86 dilute sun red plants. The 1:2 ratio was therefore exactly realized.

Three F_2 dilute sun reds bred true in F_3 (group 3) as was expected of them, producing a total of 72 dilute sun red plants.

Numerous F_3 plants of the several color types of the cross under consideration here were tested by F_4 and F_5 progenies, with results wholly consistent with expectation. It is deemed unnecessary to give the records of these later generations in detail.

Evidence from aleurone-color and linkage relations

The evidence presented up to this point in support of the three-factor hypothesis, involving *A a*, *B b*, *Pl pl*, has had to do with the behavior of the several F_2 color types in later generations and in intercrosses. There remain to be discussed some bits of evidence which, while less direct, are perhaps no less trustworthy. This evidence deals with (1) the relation of aleurone color to plant-color types, (2) the linkage of certain plant-color types with endosperm color, and (3) the linkage of other color types with the liguleless leaf.

Relation of aleurone color to plant color.— Of the plant-color factors considered in this section of the paper, the pair *A a* is concerned also in the development of aleurone color. It has been shown by the writer

in a previous paper (Emerson, 1918) that the presence of three dominant factors, *A*, *C*, and *R*, is necessary for the development of aleurone color. It is assumed that the factor pair *A a* for aleurone color is identical with the pair *A a* for plant color. Some of the evidence on which this assumption is based may well be considered at this point in order to justify the use of the same symbols for both plant and aleurone color. After the identity of *A a* has been established, certain relations of aleurone color to plant color can be used to check up some of the conclusions previously drawn with respect to the genetic interrelations of the several plant-color types.

It will be recalled that dilute sun red crossed with green gave dilute sun red in F_1 and a 3:1 ratio of the two types in F_2 (table 17, group 1, page 134), and that backcrosses of F_1 with green gave a 1:1 ratio (group 2). The F_2 seeds of these F_1 plants also exhibited a 3:1 relation — 424 colored and 127 colorless, deviation 10.8 ± 6.9 — thus showing that only one factor pair, *A a*, *C c*, or *R r*, was heterozygous. The colorless seeds produced 98 green plants, and the colored ones produced 269 dilute sun reds and 1 weak plant, recorded as green, which died in the seedling stage. Obviously the factor that differentiates dilute sun red from green is the same as the one that in these cases differentiated the colored from the colorless seeds, or some factor very closely linked with it. Fortunately, F_1 plants closely related to the ones which when selfed showed the behavior noted above, were backcrossed with green, colorless-seeded *A* testers (Emerson, 1918). Of the resulting seeds 632 were colored and 590 were colorless, evidently a 1:1 relation — the deviation being 21 ± 11.8 — showing that the F_1 plants were, with respect to aleurone color, *A a C C R R*. The colored seeds gave rise to 357 dilute sun red plants and the colorless seeds to 358 green plants. Evidently, therefore, it is the *A a* pair that differentiates dilute sun red from green. This is in support of the assumed genotypes *A b pl* and *a b pl* for dilute sun red and green, respectively.

The single progeny recorded in group 3 of table 9 (page 127) came from a plant known to be *A a* with respect to aleurone color and producing 130 colored and 41 colorless seeds. The 3:1 aleurone-color relation shows it to have been heterozygous in only one aleurone-color factor, and therefore *A a C C R R*. The colored seeds, *A C R*, produced 67 purple plants, and the colorless ones, *a C R*, produced 21 brown plants.

Evidently, purples are differentiated from browns by the *A a* pair alone, just as dilute sun reds are differentiated from greens. This is quite in keeping with the assumed genotypes, *A B Pl* and *a B Pl*, for purple and brown, respectively.

Two of the progenies recorded in group 3 of table 8 (page 126) involved both aleurone and plant color. The heterozygous parents were back-crossed with green *A* testers and produced 125 colored and 127 colorless seeds. The factor pair differentiating these two seed classes was therefore *A a*. The colored seeds, *A C R*, produced 15 purple and 14 sun red plants, while the colorless seeds, *a C R*, gave 9 brown and 14 green plants. Since it is shown in the preceding paragraph that purples and browns differ with respect to the pair *A a* alone, it may be inferred that the sun reds and the greens of these lots also differed with respect to *A a* alone. The assumption heretofore made with respect to the genotypes of these color classes, *A B Pl*, *A B pl*, *a B Pl*, and *a B pl*, for purple, sun red, brown, and green, respectively, is given support by this relation of aleurone color to plant color.

Two of the progenies recorded in group 1 of table 9 (page 127), and one in group 4 of table 8 (page 126), were grown from self-pollinated plants known to be *A a* with respect to aleurone color and found to have 644 colored and 228 colorless seeds. The 3:1 seed-color relation shows them to have been *A a C C R R*. The colored seeds, *A C R*, gave 294 purples and 113 dilute purples, while the colorless seeds, *a C R*, gave 119 browns and 40 greens. If purples and browns differ with respect to *A a* alone, as they have been shown to do, presumably the dilute purples and the greens of these lots also differ in the same way. This is in keeping with the assumption that the genotypes of the color classes are *A B Pl*, *A b Pl*, *a B Pl*, and *a b Pl*, for purple, dilute purple, brown, and green, respectively.

These comparisons of the relations of aleurone color to plant color have confirmed definitely the supposition that purples, sun reds, dilute purples, and dilute sun reds have the dominant factor *A*, and browns and greens the recessive factor *a*. The comparisons have also afforded some support for the assumed genetic constitution of the several color types with regard to *B b* and *Pl pl*. More definite evidence for the latter, however, is afforded by the linkage relations now to be discussed.

Linkage of plant color with endosperm color.— It has been known since 1912 that a linkage exists between the factor pair *Pl pl* and endosperm

color. The data suggest irregularities or complexities which cannot be straightened out until more definite information is at hand with regard to the two or more factor pairs concerned in the development of yellow endosperm.[5] Only such data are presented here as are necessary to show the relations of the several plant-color types to endosperm color.

A single progeny recorded in table 27, group 2 (page 140), was made up of 74 purple and 75 sun red plants. The lot resulted from a cross of a white-seeded sun red plant with a dilute purple plant which was heterozygous with respect to both yellow endosperm and plant color. The yellow seeds produced 58 purple and 20 sun red plants, and the white seeds produced 16 purple and 55 sun red plants. The yellow-seeded sun reds and the white-seeded dilute purples are known to be the crossover classes. The ratio of non-crossovers to crossovers is 113:36, and the percentage of crossing-over, therefore, is 24.2. Evidently a factor pair for yellow endosperm, *Y y*, is linked with the factor pair that differentiates purple from sun red. In accordance with the hypothesis under test, this plant-color factor pair is *Pl pl* — purple = *A B Pl*, and sun red = *A B pl*.

Two other progenies (table 26, group 1, page 139) had a total of 116 dilute purple and 42 dilute sun red plants. The selfed parent plants were heterozygous for yellow endosperm as well as for plant color. The yellow seeds gave 99 dilute purple and 17 dilute sun red plants, and the white seeds gave 17 dilute purple and 25 dilute sun red plants. This F_2 distribution, as shown below, is very close to expectation ($\chi^2 = 0.26$) on the basis of 25 per cent of crossing-over between the factor pair *Yy* and the pair that differentiates dilute purple from dilute sun red. It seems likely, therefore, that the same plant-color factors, *Pl pl*, are concerned here as in the progeny consisting of purples and sun reds. This is in keeping with the theoretical genotypes, *A b Pl* and *A b pl*, assumed for dilute purple and dilute sun red, respectively. The comparison between the observed F_2 distribution and that calculated on the basis of 25 per cent of crossing-over follows:

Observed	99	17	17	25	=	158
Calculated	102	17	17	23	=	159
Difference	—3	0	0	+2		—1

[5] This problem is being investigated by Dr. E. G. Anderson.

A single progeny (table 8, group 3, page 126) from a selfed parent heterozygous for yellow endosperm, contained purple, sun red, brown, and green plants, totaling 63, in the relation 35:15:6:7. These four color types are expected to occur in a total of 64 in the relation 36:12:12:4 from a selfed plant of the genotype *A a B B Pl pl*. The observed deviation from expectation might occur by chance once in nine trials, P equaling 0.11. Theoretically, the green plants of this lot, *a B pl*, are differentiated from the browns, *a B Pl*, by the same factor pair, *Pl pl*, that differentiates the sun reds, *A B pl*, from the purples, *A B Pl*. If this is true, the same linkage relations should exist for yellow endosperm with the brown-green lot as with the purple-sun-red lot. From yellow seeds there came 29 purples and 8 sun reds, and from white seeds 6 purples and 7 sun reds. Such a distribution should be very closely realized ($\chi^2 = 0.97$) from 30 per cent crossing-over between *Y y* and *Pl pl*. The yellow seeds produced also 5 brown and 3 green plants, and the white seeds 1 brown and 4 green plants. While the number of individuals is too small to give a reliable indication, it is of interest to note that the coefficient of association (Collins, 1912) calculated from the series 5:3:1:4, or 0.739, is practically that calculated from 26 per cent of crossing-over. In so far as these records go, therefore, they support the assumption that brown and green in this lot are differentiated by the same factor pair as are purple and sun red, and thereby support the hypothesis under test.

A plant heterozygous for the three plant-color pairs *A a*, *B b*, *Pl pl*, and for *Yy*, backcrossed with a white-seeded green plant of type VIc, *a b pl y*, gave the six color types, purple, sun red, dilute purple, dilute sun red, brown, and green, in the numerical relation 10:13:17:11:9:33 (table 6, page 124), which is a close fit (P = 0.61) to the expected relation, 1:1:1:1:1:3. From yellow seeds the resulting series was 8:6:13:2:7:17, and from white seeds it was 2:7:4:9:2:16. When the classes having *A Pl*, purple and dilute purple, were lumped together, and similarly those having *A pl*, sun red and dilute sun red, the yellow seeds gave 21 plants with *Pl* and 8 with *pl*, while the white seeds gave 6 with *Pl* and 16 with *pl*. Of these 51 plants, there were 14 in the crossover classes, or a percentage of crossing-over of about 27.5 ± 4.1, approximately the same as in the cases cited above. In this lot there are theoretically three kinds of greens, *a B pl*, *a b Pl*, and *a b pl*, one of which has *Pl* and two of which have *pl*, while all the browns, *a B Pl*, have *Pl*. If there be

assumed 25 per cent of crossing-over between *Y y* and *Pl pl*, equivalent to a 3:1:1:3 gametic series, yellow seeds should give 3 brown to 5 green, and white seeds 1 brown to 7 green, as shown below:

	Yellow	White
Brown, *a B Pl*	3	1
Green, *a B pl*	1	3
Green, *a b Pl*	3	1
Green, *a b pl*	1	3
	5	7

The yellow seeds actually gave 7 brown to 17 green and the white seeds 2 brown to 16 green, which is a close fit to the calculated relation, 3:5:1:7 (P = 0.59). In this case as in the others, then, the linkage relations between *Y y* and *Pl pl* afford additional support for the belief that the several color types actually bear to one another the relation assumed in the assignment of hypothetical genetic formulae (page 32).

Linkage of plant color with leaf type.— It has been known for some years that a leaf type termed *liguleless* (Emerson, 1912) is linked with the factor pair that differentiates sun red from dilute sun red. As an illustration of this, two backcross progenies, 8250 and 8253, with a total of 145 sun red and 147 dilute sun red plants, may be cited. These progenies came from a cross of normal-leaved sun red, *A B pl Lg*, with liguleless-leaved dilute sun red, *A b pl lg*, backcrossed with liguleless dilute sun red. Of the normal-leaved plants 104 were sun red and 41 were dilute sun red, while of the liguleless-leaved plants 48 were sun red and 99 were dilute sun red. The non-crossovers were to the crossovers as 203:89, or a percentage of crossing-over of 30.5. Since the factor pair that differentiates sun red from dilute sun red has been assigned the symbol *B b*, the linkage noted here is evidently between *B b* and *Lg lg*.

Six progenies from backcrosses of heterozygous normal-leaved purples with liguleless dilute sun reds gave purples, sun reds, dilute purples, and dilute sun reds in the relation 197:177:178:167, which is not far from the equality expected, P equaling 0.46. Among the normal-leaved plants, the four color types occurred in the relation 123:117:47:55, and among the liguleless-leaved plants in the relation 74:60:131:112. Evidently the purples bear the same relation to the dilute purples as the sun reds do to

the dilute sun reds. For sun reds and dilute sun reds, the non-crossovers are to the crossovers as 229:115, or a crossover percentage of 33.4 ± 1.7. For purples and dilute purples, the relation is 254:121, or a crossover percentage of 32.3 ± 1.5. It follows from this that the factor pair, *B b*, which differentiates sun red, *A B pl*, from dilute sun red, *A b pl*, is the same as that which differentiates purple from dilute purple. And this is in keeping with the hypothesis under test, in accordance with which purple and dilute purple have been assigned the genotypes *A B Pl* and *A b Pl*, respectively.

In a single progeny resulting from a backcross of a heterozygous normal-leaved purple plant with a liguleless-leaved green plant, greens occurred, as expected, with about three times the frequency of the average of the other five color classes. The progeny included 14 browns and 49 greens. Of the normal-leaved plants there were 10 browns and 19 greens, and of the liguleless-leaved plants 4 browns and 30 greens. On the basis of the hypothetical genotypes assigned to browns and greens, and with the assumption of 33 per cent of crossing-over between *B b* and *Lg lg*, the four classes, normal brown, normal green, liguleless brown, and liguleless green, should bear the relation 2:4:1:5. For a total of 63 plants, the relation would be approximately 11:21:5:26, whereas the observed relation was 10:19:4:30. The deviations from expectation are such as might occur by chance in more than three out of four trials, P equaling 0.78. In this case, as in the others reported, the linkage relations between *B b* and *Lg lg* afford support for the view that the several color types bear the relation to one another inferred from the hypothetical genotypes assigned them.

Summary of results involving A a, B b, Pl pl

The results of the cross of purple with green — which gave in F_2 six color types, namely, purple, sun red, dilute purple, dilute sun red, brown, and green, with a numerical relation of approximately 27:9:9:3:9:7 from selfed F_1's and about 1:1:1:1:1:3 from F_1's backcrossed to green — have been interpreted on the basis of the interaction of three factor pairs, *A a*, *B b*, and *Pl pl*. This hypothesis has been subjected to practically every genetic test available, as summarized below.

Each of the six F_2 color types has in turn been tested by its behavior in F_3, and in several cases behavior in F_4 and even in later generations

has been noted. All the possible combinations of intercrosses between the several types have been studied, except dilute purple x brown. In most cases these intercrosses have been carried to the F_2 generation, and in several instances to F_3 and F_4. Thruout the tests, the results have been in close agreement with those expected from the hypothesis. In almost every instance all the color types expected in each generation of the several crosses, and no others, have appeared. Moreover, the numerical relations found to exist between the several color types and also between the several classes of behavior have been reasonably close to expectation. It is true that in some instances the fit of observation to hypothesis has not been particularly good, but even here the observed deviations have been of such an order as might be expected to occur occasionally thru the chance errors of random sampling.

In addition to the tests afforded by the behavior of the several F_2 color types in later generations and in intercrosses, the relations of aleurone color involving the factor pair *A a* to the several plant colors, and the linkage relations of the plant-color factors *Pl pl* with the endosperm-color factors *Y y* and of the plant-color factors *B b* with the leaf-type factors *Lg lg*, have been included in the investigation. These tests have shown that the several color types bear to one another the relations to be deduced from the hypothetical genotypes assigned them.

The conclusion seems justified, therefore, that the three-factor hypothesis proposed as an interpretation of the F_2 results obtained in crosses of purple with green has been substantiated, in so far as it is possible to substantiate any hypothesis.

CROSSES INVOLVING THE MULTIPLE ALLELOMORPHS B, B^w, b^s, b

In the preceding section of this account, six color phenotypes of maize have been discussed, namely, purple, sun red, dilute purple, dilute sun red, brown, and green. In addition to these six phenotypes, green plants have been shown to consist of three genotypes, which in some instances are slightly different phenotypically. Besides these six sharply separable phenotypes, there exist certain intermediate forms. The constancy of these types from year to year, under fairly uniform environmental conditions, leaves no doubt that they are genotypically as well as phenotypically distinct from the types considered heretofore.

One of these forms, known as weak purple, type Ib, is intermediate in certain respects between purple and sun red, and in other respects between purple and dilute purple. Plants of this type, prior to the flowering stage, frequently resemble sun reds more than purples. The pigmentation of the sheaths is less intense than with purples, and in some instances less than with strong sun reds. There is, however, sooner or later a tendency for pigment to develop on the stalk beneath the sheaths (Plate V, 2). In this respect weak purples resemble dilute purples as the latter often appear in a late stage of their development. The anthers of weak purples are usually full purple, like those of purples and dilute purples, in which respect they show no resemblance to sun reds.

A second intermediate form, known as weak sun red, type IIb, stands between sun red and dilute sun red. The sheaths and husks are less extensively and less intensely pigmented than is true of full sun red, and yet exhibit much more color than in dilute sun red (Plate V, 4). The anther color of weak sun red is like that of both sun red and dilute sun red.

While the difference between the extreme sun-color types, sun red and dilute sun red, is probably only a quantitative one — as is also presumably true of the difference between purple and dilute purple — little difficulty is experienced in separating sun red from dilute sun red plants on the one hand, or purple from dilute purple plants on the other. Frequently, however, it is difficult, or even impossible, at early stages of plant growth, to separate sun reds from purples. The existence of such intermediate forms as weak purple and weak sun red adds materially to the difficulties of classification. In fact, correct classification of all these types by inspection alone is possible only at the flowering stage. For certainty in classification, even at the flowering stage, environmental conditions, particularly soil fertility, must have been favorable thruout the growing period of the plants. While infertile soil exaggerates the difference between dilute sun red and green, by bringing about an excessive development of red pigment in the one type while no color develops in the other, on fertile soil only are revealed the finer distinctions between sun red, weak sun red, and dilute sun red. It is perhaps fortunate that the genetic relations of these several types are such that ordinarily not all of them occur in a single progeny.

Interrelations of sun red IIa, weak sun red IIb, and dilute sun red IVa

Numerous crosses of weak sun reds, IIb, with dilute sun reds, IVa, have given weak sun reds in F_1 and approximately three weak sun reds to one dilute sun red in F_2, just as crosses of strong sun red with dilute sun red give three strong to one dilute sun red (table 24, group 1, page 138). Records of such crosses are given in table 32 (page 144). Twelve F_2 progenies, totaling 1729 individuals, showed the two types in the relation 1300:429, almost exactly a 3:1 ratio, the deviation being 3.3 ± 12.1. The data for F_3 of these crosses are like those for crosses of strong sun red with dilute sun red (table 25). One weak sun red F_2 bred true in F_3 with a total of 77 weak sun red offspring (table 33, group 1). Four others gave both weak and dilute sun reds (group 2), in the relation 128:54, a deviation of 8.5 ± 3.9 from a 3:1 ratio. One dilute sun red bred true (group 3), with 95 dilute sun red plants in F_3.

A cross of weak sun red, IIb, with strong sun red, IIa, gave strong sun red in F_1 and the two parent types in F_2 in the relation 71:16, a deviation from the 3:1 ratio of 5.75 ± 2.72. There is, therefore, nearly one chance in six that the observed deviation may be due to errors of random sampling, P equaling 0.16.

In none of these crosses, strong with weak, weak with dilute, and strong with dilute sun red, have other than the parent types appeared in F_2. If weak sun red is due to the action of some additional modifying factor, not heretofore considered, types other than those of the parents should have occurred in some of the crosses. The natural conclusion, therefore, is that weak sun red, IIb, is due to an allelomorph of *B* and *b*, the pair concerned with the difference between sun red, IIa, and dilute sun red, IVa. This third allelomorph, responsible for weak sun red, may well be designated B^w.

Further evidence in support of the assumption that an allelomorph of *B* and *b* is concerned with weak sun red is afforded by linkage studies involving strong, weak, and dilute sun red with leaf type. Evidence has been offered (page 63) to show that *B b* and *Lg lg* are linked with about 30 to 33 per cent of crossing-over.

A single progeny, 8252, from a sun red plant heterozygous for leaf type and plant color backcrossed to liguleless weak sun red, contained 108 sun red and 109 weak sun red plants. Of the normal-leaved plants 80

were sun red and 38 were weak sun red, while of the liguleless-leaved plants 28 were sun red and 71 were weak sun red. The ratio of non-crossovers to crossovers is 151:66, or 30.4 ± 2.1 per cent of crossing-over. The percentage of crossing-over between *Lg lg* and the factor pair differentiating sun red and weak sun red, $B\ B^w$, is, therefore, practically the same as the linkage between *Lg lg* and *B b*.

Four backcross progenies, 8246–8249, involving sun red, contained 469 weak sun red and 396 dilute sun red plants. Of the normal-leaved plants 153 were weak sun red and 261 were dilute sun red, while of the liguleless-leaved plants 316 were weak sun red and 135 were dilute sun red. The non-crossovers are to the crossovers as 577:288, or 33.3 ± 1.1 per cent of crossing-over. Here again, therefore, the linkage between *Lg lg* and the factor pair differentiating weak sun red from dilute sun red, $B^w\ b$, is practically the same as that between *Lg lg* and *B b* or between *Lg lg* and $B\ B^w$.

From the facts (1) that in crosses between any two of the three types sun red, weak sun red, and dilute sun red, the third type is not produced, and (2) that the linkage value between *Lg lg* and the factor pairs differentiating weak sun red from sun red and from dilute sun red is approximately the same as that between *Lg lg* and *B b*, it seems evident that weak sun red is due to a factor B^w belonging to the triple allelomorphic series B, B^w, b.

It seems probable that this series of allelomorphs contains other members in addition to the three listed above, but there is at present little conclusive evidence in support of the idea. There are certainly several forms, commonly classed as dilute sun red, that differ considerably in the amount of red pigment developed, and certainly some of these differences are genetic. As is shown in the next section of this account, some of these differences, particularly with respect to silk, anther, and leaf-blade color, are due to the effect of the aleurone-color factors *R r*. Environmental conditions, particularly soil fertility, influence the development of this pigment so greatly that the problem becomes a difficult one. There is, however, some evidence that at least two forms of dilute sun red are differentiated by a factor pair belonging to the series B, B^w, b. These forms differ principally in the amount of color in the fresh husks (Plate VI, 1 and 2), and to some extent in the sheaths, which are the plant parts most strikingly different in sun red, weak sun red, and dilute sun red.

A type of dilute sun red with stronger husk pigmentation than ordinary dilute sun red shows was crossed with an ordinary dilute purple. Leaf type also was involved in the cross. The F_1 plants were dilute purples with somewhat more pigment in the husks of young ears than is usual with that type. A single progeny, grown from an F_1 backcrossed with liguleless dilute sun red of a light type, consisted of 25 dilute purples and 18 dilute sun reds. Each of these classes was sorted with some difficulty into light and more strongly colored subclasses, in accordance with the amount of color on the husks of the young ears. Of the more strongly pigmented dilute sun reds 4 had normal and 6 had liguleless leaves, while of the lighter dilute sun reds 6 had normal and 2 had liguleless leaves. Of the more strongly colored dilute purples 4 had normal and 13 had liguleless leaves, while of the lighter ones 4 had normal and 4 had liguleless leaves. While these numbers are small and the behavior was somewhat irregular, it is perhaps noteworthy that the factor pair differentiating the lighter from the more strongly colored plants, of both the dilute sun red and the dilute purple classes, exhibited an apparent linkage with *Lg lg* of a value not far from that observed between *Lg lg* and *B b*, *B* B^w, and B^w *b*. The observed percentages of crossing-over were 32.0 for the dilute purples, 33.3 for the dilute sun reds, and 32.6 for the entire lot. This evidence, slight as it is, plainly suggests a fourth member, b^s, of the *B* series of allelomorphs, which may be stated tentatively as *B*, B^w, b^s, *b*.

Relation of weak purple Ib to purple Ia, dilute purple IIIa, and weak sun red IIb

By methods similar in the main to those outlined above, Dr. E. G. Anderson has been able to show that weak purple is differentiated from purple on the one hand and from dilute purple on the other by the same factor, B^w, that differentiates weak sun red from sun red and from dilute sun red. At the time when Dr. Anderson undertook to determine the genetic relations of weak purple, nothing was known of the relation of weak sun red to sun red and dilute sun red as presented above. Furthermore, there was no indication as to whether weak purple was differentiated from purple and dilute purple by an allelomorph of *B b* or of *Pl pl*, or by some distinct factor pair that might modify the ordinary result of the interaction of the pairs *A a*, *B b*, and *Pl pl* then known to be concerned in the production of plant colors. The evidence to be presented here

is taken almost wholly from Dr. Anderson's records, and the conclusions derived from it are his. It is with Dr. Anderson's permission and at his suggestion that, for the sake of completeness of this account of the inheritance of plant colors, his results are here presented.

A cross of a weak purple Ib with a homozygous dilute purple IIIa resulted in 25 weak purples only, while a cross of another weak purple with a homozygous dilute purple, a sib of the plant used in the first cross, gave 63 weak purples and 53 dilute purples. Two of the F_1 weak purples were backcrossed to dilute purples, and a third to dilute sun red. The result (table 34, group 1, page 145) was 141 weak purples and 163 dilute purples, a deviation of 11 ± 5.9 from equality. Five crosses of weak purples with dilute sun reds gave a total of 32 weak purples and 25 dilute purples, a deviation from equality of 3.5 ± 2.5, while two other such crosses gave 29 weak purples only. Evidently these weak purple plants differed from dilute purples by a single factor pair. This pair could not have been *Pl pl*, for the crosses of weak purple with dilute purple, *A b Pl*, gave the same results as those with dilute sun red, *A b pl*. This leaves the possibility that *B b* or some unknown factor pair was concerned.

Three crosses of weak purple Ib with purple Ia resulted in 52 purple plants. A single cross of weak purple with sun red IIa gave 18 purples. Evidently both purple and sun red carry some factor that acts to change weak purple to purple. Unfortunately, no later generations of any of these crosses were grown, but it is evident from the F_1 results and from what is known of the interrelations of purple, sun red, and dilute purple that the dominant factor *B*, common to both purple and sun red, is concerned in the change from weak purple to purple. Since the crosses of weak purple with dilute purple, *A b Pl*, and with dilute sun red, *A b pl*, gave no purples, while crosses of weak purple with purple, *A B Pl*, and with sun red, *A B pl*, gave purple, the *Pl pl* pair is not concerned in the difference between weak purple and purple any more than in that between weak purple and dilute purple. These results, however, do not exclude the possibility that weak purple may be *A b Pl*, like dilute purple, with the addition of some unknown dominant modifying factor.

A single weak purple plant, which was, so far as known, unrelated to the weak purples considered above, when crossed with two unrelated dilute sun reds gave progenies consisting of 15 weak purples and 13 weak sun reds. Seven progenies of these F_1 weak purple plants backcrossed

with dilute sun reds are listed in table 34, group 2. These progenies consisted of four color types, weak purple, weak sun red, dilute purple, and dilute sun red, in the numerical relations given below:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	481	526	460	537	2,004
Calculated	501	501	501	501	2,004
Difference	—20	+25	—41	+36	0

The deviations from equality of the four classes expected of a dihybrid are so great that they would not occur by chance alone more than once in twenty trials, P equaling 0.05. Dr. Anderson's notes indicate that there was considerable difficulty, in the case of two of the cultures, in distinguishing dilute purple from dilute sun red. Whether this difficulty may account in part for the poor fit is not known. The outstanding fact, however, is the appearance of the four classes and no others. Since weak sun red is known to differ from dilute sun red by the factor pair B^w b, the inference is clear that weak purple differs from dilute purple by the same pair and by no others. The formulae assumed for the four color types are, therefore, $A\ B^w\ Pl$, $A\ B^w\ pl$, $A\ b\ Pl$, and $A\ b\ pl$, respectively.

If the foregoing conclusion is correct, crosses of weak sun reds with dilute purples should give weak purples in F_1 and the same four color classes in F_2 as are noted above for crosses of weak purple with dilute sun red. A single cross of a dilute purple with a homozygous weak sun red resulted in 18 weak purple plants. Two crosses of dilute purples with weak sun reds heterozygous for B^w b gave 12 weak purples and 11 dilute purples. That the production of weak purples in these crosses was not due to the b or Pl factors of the dilute purple parents is evidenced by the fact that crosses of the same dilute purple individuals with sun reds gave full purples in F_1. One of the F_1 weak purples, $A\ A\ B^w\ b\ Pl\ pl$, of the above crosses was backcrossed with dilute sun red, $A\ b\ pl$, with the result (table 34, group 3) shown below. The expected equality of the

four color types was closely approached in the results, χ^2 equaling 0.80. The comparison of observed with expected results follows:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	21	28	22	27	98
Calculated	24.5	24.5	24.5	24.5	98
Difference	—3.5	+3.5	—2.5	+2.5	0

The progeny of a purple plant heterozygous for $B\,B^w$, $Pl\,pl$, and the endosperm color pair $Y\,y$, backcrossed with a white-seeded weak sun red plant, $A\,B^w\,pl\,y$, affords evidence of another kind with respect to the interrelations of strong and weak purple and of strong and weak sun red. It has been noted previously (page 60) that $Pl\,pl$ and Yy are linked, with a somewhat irregular percentage of crossing-over. The backcross gave the four color types purple, weak purple, sun red, and weak sun red, in the numerical relation 60:48:59:62. The observed deviations from the equality expected of a dihybrid are such as might occur by chance more than once in two trials, P equaling 0.54. The distribution of these 229 plants to the four color types when the progeny of yellow seeds and that of white seeds are considered separately is as follows:

Color types	Purple Ia	Weak purple Ib	Sun red IIa	Weak sun red IIb	Total
Yellow seeds	48	36	8	17	109
White seeds	12	12	51	45	120

Evidently weak purple, assumed to be $A\,B^w\,Pl$, here bears the same relation to weak sun red, $A\,B^w\,pl$, that purple, $A\,B\,Pl$, is known to bear to sun red, $A\,B\,pl$. In case of the purples and the sun reds alone, the linkage of $Pl\,pl$ with $Y\,y$ is shown by 99 non-crossovers to 20 crossovers, or 16.8 ± 2.7 per cent of crossing-over. When the weak purples and the weak sun reds are alone considered, the non-crossovers are to the crossovers as 81:29, a crossover percentage of 26.4 ± 2.8. While the

difference between these two percentages of crossing-over, 9.6 ± 3.9, is considerable, it is probably not statistically significant, P equaling 0.09.

Still further evidence in favor of the assumption that weak purple is differentiated from dilute purple by the factor pair B^w *b*, just as weak sun red is differentiated from dilute sun red, is afforded by data from six of the progenies recorded in group 2 of table 34. These data, it will be recalled, were obtained from F_1's of weak purple x dilute sun red backcrossed to dilute sun red. The F_1 weak purples were heterozygous for liguleless leaf as well as for plant color, *A A* B^w *b Pl pl Lg lg*, and the dilute sun reds with which they were backcrossed were liguleless, *A b pl lg*. The 1724 plants were distributed as follows:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Normal leaves.....	296	315	119	164	894
Liguleless leaves.....	108	125	280	317	830

Evidently the linkage relations of liguleless with weak purple and dilute purple are similar to those already known for liguleless with weak sun red and dilute sun red (page 67). Of the 921 weak sun reds, *A* B^w *pl*, and dilute sun reds, *A b pl*, 632 belong to the non-crossover and 289 to the crossover class, a percentage of crossing-over of 31.4 ± 1.0. Similarly, of the 803 weak purples and dilute purples, the non-crossovers are to the crossovers as 576:227, a percentage of crossing-over of 28.3 ± 1.1. The difference between these two percentages of crossing-over, 3.1 ± 1.5, is such as might occur by chance once in six trials, P equaling 0.16.

By way of summary, it may be noted that, from appropriate intercrosses of the several color types and from determinations of the linkage relations of these types with liguleless leaf and with yellow endosperm, weak purple and weak sun red have been shown to have the genotypes *A* B^w *Pl* and *A* B^w *pl*, respectively. This establishes the existence of the triple allelomorphs, *B*, B^w, *b*. There is some evidence in favor of the occurrence of a fourth member of this series, b^s.

CROSSES INVOLVING THE MULTIPLE ALLELOMORPHS R^r, R^g, R^{rg}, r^r, r^g, r^{ch}

In an earlier section of this account (page 29) dealing with crosses involving only *A a*, *B b*, and *Pl pl*, three types of green plants were reported,

namely, *a B pl* (VIa), *a b Pl* (VIb), *a b pl* (VIc). Still another type of green — a type wholly devoid of purple, red, or brown pigment — has been used in several crosses, with results quite unlike those obtained from corresponding crosses with the other green types. For reasons that become apparent later, this fourth type of green is regarded as genetically similar to dilute sun red and is known as type IVg.

Green IVg x brown V

Generations F_1 and F_2.— When brown, *a B Pl*, is crossed with green of any of the three types previously studied, brown appears in F_1 and brown and green in F_2. If green VIc, *a b pl*, is used in the cross, the F_2 ratio approaches 9:7, while if green VIa, *a B pl*, or VIb, *a b Pl*, is used, 3:1 F_2 ratios are of course expected (tables 19 and 20, page 135). In striking contrast with such results are those obtained from a cross of brown with green IVg. Two such crosses gave 78 purple plants in F_1, and a third cross resulted in 72 purple and 63 sun red plants. It will be recalled that just such results as these were obtained from crosses of dilute sun red with brown (tables 4 and 14, pages 123 and 131). The brown plant, 2031–20, which gave purple and sun red F_1 plants when crossed with green IVg, was the identical plant previously reported (table 4, group 2) to have given 55 purples and 55 sun reds when crossed with a dilute sun red plant. Moreover, this same brown plant was shown (table 20, group 2, page 135) to have produced from self-pollination 82 browns and 34 greens. Evidently it was *a a B B Pl pl*. The important point here is that crosses of brown with green IVg give exactly the same results in F_1 as if green IVg were a dilute sun red, *A A b b pl pl*.

There are other reasons, in addition to the F_1 results of crosses with brown, for supposing that green IVg has the factor *A*. When the pericarp-color gene *P* occurs together with *A*, the resulting pericarp color is always red, but when *P* and *a a* are associated the pericarp color is brown. When green IVg plants have pericarp color it is red rather than brown, while that of greens VIa, VIb, and VIc is always brown. Again, the *A* factor is known to be essential to the production of aleurone color (Emerson, 1918), and the stock of IVg green plants used in these crosses, a strain of the variety Black Mexican sweet corn, was homozygous for purple aleurone. It is noteworthy in this connection that many, perhaps most, plants of this variety show very slight traces of sun red, and these traces are

limited commonly to the glumes of the staminate inflorescence. Apparently the stock of green IVg, which under no environmental conditions to which it has been subjected has ever been observed to produce the slightest trace of sun red, is merely an extreme minus variation of dilute sun red.

Not only were the F_1 results of the cross of brown with green IVg like those of the cross of brown with dilute sun red, but the same major color types appeared in F_2 (table 35, page 145). The distribution of all the individuals of six F_2 progenies to the six major color types heretofore recognized is compared below with the theoretical distribution calculated on the assumption that the green IVg parent was genotypically a dilute sun red, *A A b b pl pl*:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed.....	309	100	67	19	88	98	681
Calculated.....	287	96	96	32	96	74	681
Difference.....	+22	+4	—29	—13	—8	+24	0

The outstanding features of this comparison are the relatively small deviations, in comparison with the number of individuals, for the purple, sun red, and brown types, and the relatively large deviations for the dilute purple, dilute sun red, and green classes. The relative importance of the several deviations is best seen by a comparison of the quotients of calculated frequencies into the squares of corresponding deviations, from which χ^2 and P are derived (Elderton's and Pearson's tables). These quotients for the several classes are:

Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green
1.69	0.17	8.76	5.28	0.67	7.78

If these quotients were no greater in the case of dilute purple, dilute sun red, and green than for purple, sun red, and brown, there would be about two chances in five that the observed deviations might be due merely to errors of random sampling, a fairly good fit being shown — $\chi^2 = 5.06$, $P = 0.41$. But as they stand, these deviations could be expected to occur thru chance alone not more than once in five thousand similar trials, a

very poor fit being shown — $\chi^2 = 24.35$, $P = 0.0002$. Evidently, green IVg does not give the same results in F_2 of this cross as does dilute sun red.

It is to be supposed, of course, that green IVg differs in some essential genetic way from dilute sun red, else it would not remain true green for generation after generation while the typical dilute sun red constantly produces a conspicuous amount of sun red pigment. It was therefore to be expected that the dilute sun red class would be deficient in F_2 while the green class would show a corresponding excess. But if the 24 green plants in excess of the calculated number be added to the dilute sun red class, that class becomes too large by eleven individuals, the excess now becoming almost as great as the observed deficiency. Moreover, the dilute purple class, it must be remembered, remains greatly deficient. If it be supposed that the excess of greens came about at the expense of dilute purples as well as of dilute sun reds, a very good fit of observation to theory is obtained. On redistribution of the 24 greens in excess of expectation to the dilute purples and dilute sun reds in the 3:1 relation usually existing between these classes, the corrected distribution for the six classes is as shown below. There are almost two chances in five that the deviations may be due to random sampling, P equaling 0.38.

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Corrected distribution	309	100	85	25	88	74	681
Calculated	287	96	96	32	96	74	681
Difference	+22	+4	—11	—7	—8	0	0

Mere closeness of fit cannot, of course, be regarded as proof of the supposition on which the corrected distribution was made. But there are other considerations which greatly strengthen the hypothesis. In the case of all the F_2 progenies listed in table 35, it was observed that some of the purple plants, altho quite as strongly colored otherwise as normal purples, had wholly green anthers in place of the usual dark purple ones (Plate I, 4). Likewise some of the sun red plants had green instead of pink anthers. In striking contrast to this, not a single dilute purple or dilute sun red plant with green anthers was seen in the whole lot, the dilute

purples, so far as observed, having dark purple anthers and the dilute sun reds pink anthers, just as in the lots considered in the first section of this paper. Counts of the purple and the sun red plants with different anther colors were made for only three of the six F_2 progenies (table 36), and for these lots not every plant was noted at the time when it was possible to determine the anther color positively. When some anthers have become dry and weathered, it is impossible to tell whether they were pink or green when fresh. Less difficulty is experienced with purple anthers, which hold their color much longer. Unfortunately, the records of the three F_2 families were not made early enough for positive identification of anther color of all plants. Of 162 purple plants, 117 had purple anthers and 33 had green anthers, while 12 were not recorded. Of 50 sun red plants, 21 had pink anthers and 12 had green anthers, with 17 not recorded. In these two lots the plants with purple and pink anthers were together about three times as numerous as those with green anthers, thus suggesting a simple monohybrid relation between colored and green anthers.

Working hypothesis.— If the genetic factor which is responsible for green anthers of purple and sun red plants be assumed to cause, in the case of dilute purples and dilute sun reds, not merely the anthers but the whole plant — leaves, sheaths, husks, glumes, stalk, and so forth — to be green, a satisfactory working hypothesis is afforded. The factor concerned here has been found to be the well-known aleurone-color factor *R*, or else some factor very closely linked with it. Some of the evidence on which this statement is based is presented later in this paper (pages 80, 98). It may be pointed out in passing that the relation between anther color and aleurone color here noted was studied by Webber (1906) some years before the several aleurone-color and plant-color factors had been determined.

Since aleurone color is not primarily concerned in the present account, it might be less confusing if the case were regarded as one of complete linkage, and if some other symbol for anther color were used and all reference to the *R* factor omitted in this paper. Until recently there was nothing known of aleurone-color behavior that made necessary the assumption of more than the simple factor pair, *R r*. The plant-color behavior, on the other hand, as becomes apparent later, necessitates the assumption of a group of multiple allelomorphs responsible in turn for diverse combinations of colors of leaves, sheaths, anthers, silks, and other plant parts. The commonest combinations in the writer's cultures are

strong pink anthers with deep red silks, lighter pink anthers with reddish or pinkish silks, green anthers with green silks, and so on, but there exist also such combinations as strong pink anthers with green silks, green anthers with reddish silks, and the like. Moreover, different intensities of dilute sun red in leaf blades, glumes, and other parts are sometimes combined with various silk-color and anther-color combinations. There is evidence that at least several of these combinations behave as would be expected if each were a definite unit allelomorphic to any one of the others.

Perhaps the most remarkable feature of this series of allelomorphs — or supposed allelomorphs — is the fact that a single unit behaves as a dominant with respect to the color of one plant part and as a recessive with respect to that of another part. Thus, a combination of dominant pink anthers with recessive green silks is common in the writer's cultures. The wholly green plants used in the crosses here under consideration are recessive for green silks, anthers, glumes, sheaths, husks, and other parts, and dominant for colored aleurone. Since the aleurone-color symbols $R\,r$ have long been employed in the usual way, R as the dominant and r as the recessive allelomorph, this usage is adhered to in this paper. The effect of these factors on plant color is indicated by superscripts. Thus, both R^r and r^r are dominant allelomorphs with respect to pink anthers and reddish silks, while both R^g and r^g are recessive for green anthers, silks, and so on. In the crosses here considered it is known that r^r and R^g are the pair concerned. With respect to plant color, therefore, as contrasted with aleurone color, r^r is dominant and R^g is recessive. While it is realized that this usage may tend to confuse the hasty reader, the use of any other symbols that have so far suggested themselves would result in greater confusion ultimately, particularly when the interrelations of plant color and aleurone color are taken up.

To return to the F_2 behavior of crosses of green IVg with brown, the following notation should express the F_2 results obtained, provided the proposed hypothesis is tenable:

Phenotypes	Plant color	Anther color
81 — $A\,B\,Pl\,r^r$ — *Ia*	Purple	Purple
27 — $A\,B\,Pl\,R^g$ — *Ig*	Purple	Green
27 — $A\,B\,pl\,r^r$ — *IIa*	Sun red	Pink
9 — $A\,B\,pl\,R^g$ — *IIg*	Sun red	Green
27 — $A\,b\,Pl\,r^r$ — *IIIa*	Dilute purple	Purple

Phenotypes	Plant color	Anther color
9 — $A\,b\,Pl\,R^g$ — *III g*	Green	Green
9 — $A\,b\,pl\,r^r$ — *IV a*	Dilute sun red	Pink
3 — $A\,b\,pl\,R^g$ — *IV g*	Green	Green
27 — $a\,B\,Pl\,r^r$ — *V*	Brown	Green
9 — $a\,B\,Pl\,R^g$ — *V*	Brown	Green
9 — $a\,B\,pl\,r^r$ — *VI a*	Green	Green
3 — $a\,B\,pl\,R^g$ — *VI a*	Green	Green
9 — $a\,b\,Pl\,r^r$ — *VI b*	Green	Green
3 — $a\,b\,Pl\,R^g$ — *VI b*	Green	Green
3 — $a\,b\,pl\,r^r$ — *VI c*	Green	Green
1 — $a\,b\,pl\,R^g$ — *VI c*	Green	Green
256		

The theoretical numerical relation between the several color combinations, in the order given above except that all greens are included in the last class, is 81:27:27:9:27:9:36:40, total 256.

The distribution of the 353 individuals of the three F_2 progenies for which anther records were made (table 36, page 146) is compared below with the theoretical distribution. In order that all plants may be included, the few purple and sun red plants whose anther colors were not noted are arbitrarily distributed to the colored-anther and green-anther classes in a 3:1 ratio. The fit of observation to hypothesis is so good that there are three chances in five that the deviations may be due to errors of random sampling, P equaling 0.60.

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple Ia	Green Ig	Pink IIa	Green IIg	Purple IIIa	Pink IVa	Green V	Green IIIg, IVg, VI	
Observed.....	126	36	34	16	39	10	42	50	353
Calculated.....	112	37	37	12	37	12	50	55	352
Difference.....	+14	−1	−3	+4	+2	−2	−8	−5	+1

When the six F_2 progenies listed in table 35, for three of which no records of anther color were made, are grouped without reference to anther color, the comparison of observed and calculated numbers are as given below. For the six progenies there is practically an even chance that the deviations may be due to errors of random sampling, P equaling 0.48. It will be recalled that when these same progenies were compared with the dis-

tribution calculated on the basis of the three-factor hypothesis, the fit was very poor, P equaling 0.0002 (page 76). Comparison of the observed distribution with the distribution calculated on the four-factor basis follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI	Total
Observed	309	100	67	19	88	98	681
Calculated	287	96	72	24	96	106	681
Difference	+22	+4	—5	—5	—8	—8	0

Relation of aleurone color to plant color.— It is evident from the comparisons already given that the four-factor hypothesis fits well the F_2 data, which is of course to be expected since it was invented for that purpose. But this fact alone is far from a substantiation of the hypothesis. The genetic tests ordinarily available are the behavior of the several F_2 types in later generations and in intercrosses. Since aleurone color as well as plant color is involved in these crosses, still another test can be employed. The six F_1 plants whose F_2-progenies are recorded in table 35 produced from self-pollination a total of 955 seeds, of which 388 had colored and 567 colorless aleurone. This obviously approaches closely a 27:37 ratio, the percentage of colorless seeds being 59.4 ± 1.1 while the theoretical percentage is 57.8 (Emerson, 1918). The deviation from expectation, 1.6 ± 1.1 per cent, is such as might be expected by chance once in three trials, P equaling 0.33. Evidently, therefore, the aleurone factors *A*, *C*, and *R* are concerned in these crosses. Since *A* and *R* are assumed by the hypothesis to be plant-color factors also, there is afforded opportunity of comparing the plant-color classes from colored with those from colorless seeds. Since colored aleurone requires the interaction of *A*, *C*, and *R*, colored seeds should never produce brown plants nor green plants of type VI, both of which are *a a*. As seen from the data given below, no brown plants came from colored seeds but a few wholly green plants appeared. Greens of type IVg are of course to be expected from seeds homozygous for R^g. Owing to the fact that a larger percentage of colorless than of colored seeds produced plants, the theoretical distribution with respect to plant color, given below, was calculated separately for colored and for colorless seeds. For the colored seeds there are nearly two chances in

five (P equaling 0.58), and for the colorless seeds only about one chance in fourteen (P equaling 0.07), that the observed deviations may be due to errors of random sampling. The comparisons follow:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI	Total
Colored seeds:							
Observed	148	51	25	8	0	23	255
Calculated	143	48	32	11	0	21	255
Difference	+5	+3	—7	—3	0	+2	0
Colorless seeds:							
Observed	161	49	42	11	88	75	426
Calculated	136	45	39	13	104	89	426
Difference	+25	+4	+3	—2	—16	—14	0

It is noteworthy that the ratio of purples and sun reds to dilute purples and dilute sun reds is considerably greater for plants grown from colored seeds than for those from colorless seeds. This is to be expected from the fact that R must be present in all colored seeds, while some of the colorless seeds here concerned were doubtless $r\,r$. Hence, $R^g\,R^g$ should have occurred more frequently in the colored than in the colorless seeds, and should, by the hypothesis here under test, have reduced the numbers of dilute purples and dilute sun reds, causing these plants to appear as greens, types IIIg and IVg. If the 23 green plants grown from colored seeds are added to the dilute purples and dilute sun reds, the ratio of strong to dilute purples and sun reds approaches closely the ratio observed for the plants from colorless seeds.

It is even more instructive to note the relation of aleurone color to plant color in the case of the three F_2 lots for which anther colors were recorded (table 36, page 146). For this comparison the few purple and sun red plants whose anther colors were not recorded have been distributed to the colored-anther and green-anther classes in approximately the ratio in which these anther colors were found to occur in the cases in which anther colors were recorded. Since a larger proportion of colorless than of colored seeds produced plants, the theoretical distribution has been calculated separately for the two classes of seeds. The comparisons follow:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple Ia	Green Ig	Pink IIa	Green IIg	Purple IIIa	Pink IVa	Green V	Green IIIg, IVg, VI	
Colored aleurone:									
Observed.....	48	25	11	12	16	4	0	10	126
Calculated.....	47	24	16	8	16	5	0	10	126
Difference.....	+1	+1	—5	+4	0	—1	0	0	0
Colorless aleurone:									
Observed.....	78	11	23	4	23	6	42	40	227
Calculated.....	62	10	21	4	21	7	55	47	227
Difference.....	+16	+1	+2	0	+2	—1	—13	—7	0

In view of the rather large number of plant-color classes and the comparatively small number of individuals concerned here, the fit of the observed to the theoretical distribution is remarkably good. The deviations are such as might be expected by chance seven times in ten trials for the colored-seeded lot (P = 0.70), and about once in four trials for the colorless-seeded lot (P = 0.26). In addition to this comparison of the lot as a whole, it should be noted that, while among the purple and sun red plants as a whole the expected relation of colored (purple and pink) anthers to colorless (green) anthers is 3:1, for the colored-seeded lot it is 2:1 and for the colorless-seeded lot it is 6:1. The observed relations were 59:37 and 101:15, or about 1.6:1 and 6.7:1, respectively. On the whole, therefore, this comparison, involving aleurone color as well as plant color, supports the suggested factorial interpretation.

Later behavior of F_2 purple I.— Only three F_2 purples with purple anthers were tested in F_3. One of these, 2960–9, resulted in purple plants with purple, Ia, and green, Ig, anthers, and sun red plants with pink, IIa, and green, IIg, anthers, in the respective numbers 14:9:6:3. A purple plant of the genotype $A\ A\ B\ B\ Pl\ pl\ R^g\ r^r$ should give these four classes in the relation 18:6:6:2. The observed deviations might be expected twice in five trials, P equaling 0.41.

Another F_2 purple plant, 2958–8, gave F_3 progeny consisting of the same eight color types as were seen in F_2 in table 36 (page 146). Evidently the F_2 purple plant was $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$. The deviations from expectation are such as might occur by chance in about seventeen out of any twenty such trials, P equaling 0.86. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	V	IIIg, IVg, VI	
Observed	28	13	11	3	7	3	16	11	92
Calculated	29	10	10	3	10	3	13	14	92
Difference	—1	+3	+1	0	—3	0	+3	—3	0

The third purple-anthered F_2 purple tested, 2961–3, gave in F_3 all the color types except dilute purple, IIIa, and dilute sun red, IVa. A purple plant of the genotype $A\,a\,B\,B\,Pl\,pl\,R^g\,r^r$ should give the color types observed. The observed deviations from expectation might occur by chance about once in seven trials, P equaling 0.15. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Green	Green	
	Ia	Ig	IIa	IIg	V	VI	
Observed	37	11	5	2	12	3	70
Calculated	30	10	10	3	10	8	71
Difference	+7	+1	—5	—1	+2	—5	—1

A single green-anthered F_2 purple, 2960–7, gave four F_3 color types, purple, sun red, brown, and green, all with green anthers. This behavior is to be expected from an F_2 genotype $A\,a\,B\,B\,Pl\,pl\,R^g\,R^g$. One of the F_3 purples, 4956–1, repeated this behavior in F_4. The F_3 and F_4 progenies are shown together in the following comparison, for which P = 0.60:

Color types	Purple	Sun red	Brown	Green	Total
	Ig	IIg	V	VI	
Observed	84	27	35	7	153
Calculated	86	29	29	9	153
Difference	—2	—2	+6	—2	0

It is of interest to note in this connection that a plant of the genotype $A\,a\,B\,B\,Pl\,pl\,R^g\,R^g$ could not exhibit a 27:37 fatio of colored to colorless aleurone, as was the case for some of the plants dealt with earlier.

For $A\ a\ R^g\ R^g$ the aleurone-color ratio must be either 9:7 or 3:1, depending on whether the third aleurone-factor pair is $C\ c$ or $C\ C$. The F_2 purple plant 2960–7 showed a 9:7 aleurone-color ratio with 86 colored and 74 colorless seeds, $A\ a\ C\ c\ R\ R$, while the F_3 plant 4956–1 exhibited a 3:1 ratio with 213 colored and 67 colorless seeds, $A\ a\ C\ C\ R\ R$. Another purple plant of the same F_3 progeny, 4956–32, exhibited a 3:1 aleurone-color ratio and threw only green-anthered purple and sun red plants. Its genotype must have been $A\ A\ B\ B\ C\ c\ Pl\ pl\ R^g\ R^g$. Thus it is often possible, from behavior in the following generation, to know the genotype not only with respect to plant color but for aleurone color as well. This is particularly true when the B factor is present.

Of the twenty-four sorts of behavior possible, according to hypothesis, for F_2 purples of the cross under consideration, four sorts have been exhibited in F_3 and a fifth shown in F_4. This is far from an adequate study of the F_2 purples. All that can be claimed, therefore, is that, so far as they go, the results are in accord with the hypothesis.

Behavior of other F_2 color types.— Only one F_2 sun red plant with pink anthers, 2961–4, was tested in F_3. It produced sun reds with pink and sun reds with green anthers, dilute sun reds, and greens. Since anther color was noted for only a part of the plants, it has to be disregarded in classifying the F_3 progeny. The color types sun red, dilute sun red, and green occurred in the numerical relation 114:23:57. Of the eight possible genotypes of pink-anthered sun red, only three could throw these three color classes — $A\ a\ B\ b\ r^r\ r^r$, $A\ A\ B\ b\ R^g\ r^r$, and $A\ a\ B\ b\ R^g\ r^r$. From the first genotype a 9:3:4, from the second a 12:3:1, and from the third a 36:9:19, relation should exist between the F_3 classes. The poor fit of observed numbers to the 9:3:4 relation makes it improbable that the first genotype is concerned, there being only about one chance in twenty-two that the observed deviations are due to errors of random sampling, P equaling 0.045. The comparison follows:

Color types	Sun red	Dilute sun red	Green	Total
	IIa	IVa	VIa, c	
Observed	114	23	57	194
Calculated	109	36	49	194
Difference	+5	—13	+8	0

A more conclusive reason for throwing out the first genotype is the fact that the plant had some seeds with colored aleurone, which would have been impossible if it were *r r*. The second genotype is discarded because of the extremely poor fit of observed numbers to the 12:3:1 relation. There is an almost inconceivably small chance that the observed deviations may be due to errors of random sampling, χ^2 equaling 180. (When $n' = 3$ and $\chi^2 = 29$, $P = 0.000001$. Higher values of χ^2 when $n' = 3$ are not listed in Pearson's tables.) The comparison follows:

Color types	Sun red	Dilute sun red	Green	Total
	IIa, g	IVa	IVg	
Observed	114	23	57	194
Calculated	146	36	12	194
Difference	—32	—13	+45	0

The elimination of the first two genotypes leaves the third genotype as the only one that can be concerned here. The fit of observed numbers to the 36:9:19 relation is very close, χ^2 equaling 0.84. (Values of P are not listed in Pearson's tables for values of χ^2 less than 1; when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$.) The comparison follows:

Color types	Sun red	Dilute sun red	Green	Total
	IIa, g	IVa	IVg, VIa, c	
Observed	114	23	57	194
Calculated	109	27	58	194
Difference	+5	—4	—1	0

This comparison leaves little doubt that the genotype of the F_2 plant concerned is $A\,a\,B\,b\,R^g\,r^r$. There are, moreover, other considerations which go far toward identifying the genotype as given here. The fact that some sun red plants of F_3 had green and others pink anthers is evidence for the constitution $R^g\,r^r$. Since dilute sun red plants appeared in F_3, there can be no question as to *B b*. The F_2 plant showed a 9:7 aleurone-color segregation, and therefore, in addition to *R r*, it must have been

either $A\ a$ or $C\ c$. An F_3 sun red plant with green anthers, $R^g\ R^g$, had 97 colored and 20 colorless seeds, again indicating either $A\ a$ or $C\ c$. If it was $A\ A\ B\ b\ C\ c\ R^g\ R^g$, both colored and colorless seeds should have given sun red and green plants in a 3:1 ratio; if it was $A\ a\ B\ B\ C\ C\ R^g\ R^g$, the colored seeds should have given sun red and the colorless ones green plants only, the plant-color ratio again being 3:1; but if it was $A\ a\ B\ b\ C\ C\ R^g\ R^g$, the colored seeds should have produced sun red and green plants in a 3:1 ratio and the colorless seeds green plants only, the ratio of sun reds to greens in the two lots together being 9:7. Actually the colored seeds resulted in 23 sun red and 10 green plants and the colorless seeds in 10 green plants only, the ratio of sun reds to greens being 23:20, thus approaching 9:7. There is, therefore, considerable assurance that the F_3 plant was $A\ a\ B\ b\ C\ C\ R^g\ R^g$, that the F_2 plant was $A\ a\ B\ b\ C\ C\ R^g\ r^r$, and that the F_3 numerical relation of plant colors was 36:9:19, as originally suggested by the closeness-of-fit test.

A single dilute purple plant of F_2, 2960–4, was tested in F_3 and found to give 38 dilute purple and 39 green plants. Of the eight possible genotypes for F_2 dilute purples, the only ones that could give only dilute purples and greens in F_3 are $A\ A\ b\ b\ Pl\ Pl\ R^g\ r^r$, $A\ a\ b\ b\ Pl\ Pl\ r^r\ r^r$, and $A\ a\ b\ b\ Pl\ Pl\ R^g\ r^r$. The first two should give a 3:1, and the third a 9:7, F_3 ratio. The plant had colored aleurone, which throws out of consideration the second genotype with $r\ r$. The F_3 plant-color ratio fits fairly well a 9:7 but not at all a 3:1 expectation, the observed numbers being 38:39 and the calculated numbers 43:34 and 58:19, with deviations of 5 and 20, and probable errors of 2.6 and 2.9, respectively. The deviation from a 9:7 ratio might occur by chance once in five trials, P equaling 0.20, but that from a 3:1 ratio not more than twice in about a million trials, P equaling 0.000002. The genotype $A\ a\ b\ b\ Pl\ Pl\ R^g\ r^r$ is therefore decidedly favored by these results. The aleurone-color record shows that this genotype is possible, since there were 57 colored and 56 colorless seeds, a relation about halfway between the 9:7 and the 27:37 ratio due to $A\ a\ C\ C\ R\ r$ and $A\ a\ C\ c\ R\ r$, respectively.

Intercrosses of F_2 color types

It is realized that the tests of F_2 types by studies of their behavior in later generations as reported above, are markedly inadequate to serve

as a demonstration of the hypothesis suggested to account for the F_2 behavior of the cross of brown, type V, with green, type IVg. It is noteworthy, however, that no results have been found that do not agree with the hypothesis. Fortunately, several intercrosses of the types found in F_2 afford additional evidence.

Purple Ig x green VIc.— Green-anthered purples, $A\ B\ Pl\ R^g$, crossed with greens of type VIc, $a\ b\ pl\ r^r$, should give F_2 results identical with those found from the original cross of brown, $a\ B\ Pl\ r^r$, with green of type IVg, $A\ b\ pl\ R^g$, since F_1 in either case should be $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$. Two such crosses are recorded in table 37, group 1 (page 146). The F_1 plants were both purple, with purple anthers. In F_2 the same eight types were noted as in F_2 of the cross of brown with green IVg (table 36). The anther color was not recorded, however, for many of the plants, so that only six color classes are shown, as in table 35. While all the expected color types are present, the fit of observed to calculated numbers is so poor that the observed deviations should not occur by chance more than once in thirty trials, P equaling 0.033. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia, g	IIa, g	IIIa	IVa	V	IIIg, IVg, VI	
Observed....	80	13	9	9	20	27	158
Calculated...	66	22	17	6	22	25	158
Difference...	+14	—9	—8	+3	—2	+2	0

If, notwithstanding the poor fit shown above, the F_1 was $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$, a backcross of F_1 with green of type VIc, $a\ b\ pl\ r^r$, should result in the same six major plant-color types, but no green-anthered purples or sun reds should occur. Such crosses are listed in group 2 of table 37. All the purple plants had purple anthers and all the sun red plants had pink anthers. Moreover, the six color classes appeared in so very nearly the expected relation of 1:1:1:1:1:3 that deviations as great as those observed might be expected to occur by chance perhaps ninety-nine times in one hundred trials, χ^2 equaling 0.85 (when $\chi^2 = 1$ and $n' = 6$, $P = 0.96$). The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VI	
Observed.....	36	29	31	31	31	95	253
Calculated.....	31.6	31.6	31.6	31.6	31.6	94.9	252.9
Difference.....	+4.4	—2.6	—0.6	—0.6	—0.6	+0.1	+0.1

If an F_1 supposedly $A\ a\ B\ b\ Fl\ pl\ R^g\ r^r$, be backcrossed to dilute sun red, type IVa, $A\ b\ pl\ r^r$, color types Ia, IIa, IIIa, and IVa should appear, none of them with green anthers. Such crosses are presented in group 3 of table 37. The anthers thruout were purple or pink, and the several color types appeared in approximately equal numbers, as expected, there being more than two chances in five that the observed deviations may have been due to errors of random sampling, P equaling 0.42. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed.....	115	97	95	111	418
Calculated.....	104.5	104.5	104.5	104.5	418
Difference.....	+10.5	—7.5	—9.5	+6.5	0

If the same F_1 genotype, $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$, be backcrossed with green of type IVg, $A\ b\ pl\ R^g$, there should occur five major color types, brown not appearing, and both green and colored anthers should be found in both the purple and the sun red plants. The records of such a cross are given in group 4 of table 37. The seven expected color types occurred in numbers near enough to expectation so that there are nearly three chances in ten that the deviations may have been due to errors of random sampling, P equaling 0.29. The most pronounced deviations are the excess of dilute sun reds and the deficiency of greens. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	IIIg, IVg	
Observed	10	13	7	8	10	15	13	76
Calculated.....	9.5	9.5	9.5	9.5	9.5	9.5	19	76
Difference.....	+0.5	+3.5	—2.5	—1.5	+0.5	+5.5	—6	0

In conclusion it seems safe to say that the cross of green-anthered purple, Ig, with green of type VIc, has given results similar to those yielded by the cross of brown, V, with green of type IVg. Since this was to have been expected from the hypothesis suggested by the F_2 generation of the latter cross, the results just discussed lend support to that hypothesis.

Purple Ig x dilute sun red IVa.— In accordance with the hypothesis under consideration, green-anthered purple is $A\ B\ Pl\ R^g$ and dilute sun red is $A\ b\ pl\ r^r$. F_1 of the cross should be $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$, and F_2 should consist of the five major color types, purple, sun red, dilute purple, dilute sun red, and green of types IIIg and IVg, with both green-anthered and colored-anthered subclasses of purples and sun reds. The F_1 plants were purple-anthered purples, as expected. Three F_2 progenies are recorded in table 38, group 1. Anther color could not be recorded in all cases, but in each of the three F_2 progenies both green and colored anthers were noted for both purple and sun red plants. In one progeny, 5042–5045, of a total of 57 purples and sun reds, 41 had colored and 16 had green anthers, which is not far from the expected 3:1 relation. The 415 F_2 plants were so distributed among the five color classes that the chances are nearly three in five that the deviations observed may have been due to errors of random sampling, P equaling 0.58. A comparison of observed and theoretical distributions follows:

Color types	Purple Ia, g	Sun red IIa, g	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed	243	71	59	22	20	415
Calculated	234	78	58	19	26	415
Difference	+9	—7	+1	+3	—6	0

An F_1 of the cross here considered, 6557–12, $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$, was backcrossed to a dilute sun red, $A\ b\ pl\ r^r$. Four color types occurred in the progeny, as expected, and all the plants had colored anthers. The deviations from expectation were such as might occur by chance in considerably more than one out of any two such trials, P equaling 0.56. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	43	43	35	48	169
Calculated	42	42	42	42	168
Difference	+1	+1	—7	+6	+1

Purple Ia x green IVg.— The cross between purple Ia and green IVg should have given results identical with those expected from the cross of green-anthered purple with dilute sun red. The parents are supposed to have been $A\ B\ Pl\ r^r$ and $A\ b\ pl\ R^g$, and the F_1, therefore, $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$. The F_1's were purple-anthered purples. Two F_2 progenies are listed in table 38, group 2. All the expected color-types occurred, but the observed frequency distribution was such as might be expected to occur by chance only about once in eleven trials, P equaling 0.09. If these progenies are grouped into five classes, anther color being disregarded, the fit is somewhat better, P equaling 0.16. The comparison of observed and theoretical frequencies follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Green	Total
Anther color	Purple Ia	Green Ig	Pink IIa	Green IIg	Purple IIIa	Pink IVa	Green IIIg, IVg	
Observed	26	14	17	3	9	2	1	72
Calculated	31	10	10	3	10	3	5	72
Difference	—5	+4	+7	0	—1	—1	—4	0

The F_2 of this cross exhibited, as expected, practically the same results as were obtained from the cross of green-anthered purple with dilute sun red. Unlike that cross, the one under consideration here was checked by the behavior of some of its F_2 types in later generations.

A single F_2 purple-anthered purple produced in F_3 16 plants (table 39, group 1), including only purple, sun red, and dilute purple in the relation 9:4:3. Of both the purples and the sun reds, some plants had colored and some had green anthers. Obviously two other types, dilute sun red and green, should occur in such an F_3 and doubtless would have been found had a larger number of plants been grown, for the F_2 plant, in order to have produced the color types recorded, must have been $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$.

Only one plant of each of the missing classes was to have been expected, and the distribution as a whole was not far from expectation, P equaling 0.59. Both the types lacking in F_3 occurred in F_4, a pink-anthered sun red F_3 producing sun reds and dilute sun reds, while green-anthered purples produced in one instance purples, sun reds, and greens, and in another instance purples and greens only, all with green anthers. This F_3 lot may consequently be regarded as $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$, and therefore equivalent to the F_2 lot from which it came, and its F_4 progenies equivalent to F_3 progenies.

A second F_2 purple-anthered purple was backcrossed to green plants of types IVg and VIc (group 1, table 39). From the backcross with green of type IVg, $A\ b\ pl\ R^g$, five major color types appeared and both the purple and the sun red types contained subtypes with colored and with green anthers. While all the classes expected from an F_2 of the genotype $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$ occurred, the frequency distribution was so far from expectation that there is only one chance in five hundred that the observed deviations may have been due to errors of random sampling, P equaling 0.002. The expected and observed distributions are as follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Green	Total
	Ia, g	IIa, g	IIIa	IVa	IIIg, IVg	
Observed	15	15	5	1	9	45
Calculated	9	9	9	9	9	45
Difference	+6	+6	—4	—8	0	0

Whether the discrepancy is genetically significant or was due to some accident of pollination cannot now be determined. A backcross of the same F_2 plant with green of type VIc, $a\ b\ pl\ r^r$, yielded only four color types, as expected (group 1, table 39), the anthers being colored in all cases. The excess of purples and deficiency in two other classes makes the deviations from expectation fairly great, so that there is only about one chance in seven that they may have been due to errors of random sampling, P equaling 0.14. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	27	19	15	14	75
Calculated	19	19	19	19	76
Difference	+8	0	—4	—5	—1

A third purple-anthered purple, an F_3 plant of the lot regarded as equivalent to F_2's, gave in the next generation purple-anthered purples and pink-anthered sun reds in the relation 31:7 (group 2, table 39). From the genotype $A\,A\,B\,B\,Pl\,pl\,r^r\,r^r$, these two phenotypes should appear in a 3:1 ratio. The deviation from expectation was 2.5 ± 1.8, or only such as might be expected about once in three trials, P equaling 0.34.

Two green-anthered purples of F_2 and two of the equivalent F_3 lot noted above were tested by a later generation. Two of the four yielded three color types, purple, sun red, and green, all with green anthers (group 3, table 39). Such behavior is expected from the genotype $A\,A\,B\,b\,Pl\,pl\,R^g\,R^g$. The 9:3:4 relation is approached so closely that the value of P cannot be determined from Pearson's tables, x^2 equaling 0.36. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	37	11	14	62
Calculated	36	12	16	64
Difference	+1	—1	—2	—2

The same two green-anthered purples were backcrossed with green of type IVg, and one of them and a sib of the other with green of type VIc, with results as shown in group 3 of table 39. The crosses with type IVg, $A\,b\,pl\,R^g$, gave the same three classes as did the self-pollinations, and the frequency distribution differed from expectation by values that might occur by chance about once in two trials, P equaling 0.49. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	34	32	53	119
Calculated	30	30	60	120
Difference	+4	+2	—7	—1

The backcrosses of these green-anthered purples with green of type VIc, *a b pl* r^r, as was to be expected, gave very different results. There were produced four instead of three phenotypes, all with colored (purple or pink) instead of green anthers. The deviations from the theoretical frequency distribution are such as might be expected about once in five trials, P equaling 0.21. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	44	48	33	52	177
Calculated	44	44	44	44	176
Difference	0	+4	—11	+8	+1

The other two green-anthered purples that were tested yielded only two phenotypes, green-anthered purple and green, in the relation 56:18 (group 4, table 39). The genotype *A A B b Pl Pl* R^g R^g should give these two phenotypes in a 3:1 ratio. The deviation from expectation was therefore 0.5 ± 2.5. One of the same plants backcrossed to green of type IVg gave 28 green-anthered purples and 27 greens where equality was expected.

Of the twelve kinds of behavior expected of F_2 purples of the cross of purple-anthered purple with green IVg, only four have been demonstrated. So far as they go, however, the results are quite in accord with the hypothesis under test. In addition to the F_2 purples, sun reds and dilute purples also were tested by later generations, as detailed below.

Three pink-anthered sun reds gave sun reds and dilute sun reds only, all with pink anthers (table 40, group 1). These three plants are therefore regarded as *A A B b pl pl* r^r r^r. The ratio observed was 97:26. The deviation from the expected 3:1 ratio was 4.75 ± 3.24, or such as might

occur by chance once in three trials, P equaling 0.32. One of these three sun reds, when crossed with a dilute purple, $A\ b\ Pl\ r^r$, gave 71 purples and 77 dilute purples, all with purple anthers, where equal numbers were expected.

Three other F_2 pink-anthered sun reds produced nothing but sun red plants in F_3, 228 in all (group 2, table 40). Some plants of each progeny had pink and some had green anthers. Small plantings of each lot were made in the garden and larger plantings in the field. Anther color was noted in the case of the garden plants only. The records show 44 with pink and 16 with green anthers, a deviation from a 3:1 ratio of only 1.0 ± 2.3. The F_2 sun reds are therefore assumed to have been $A\ A\ B\ B\ pl\ pl\ R^g\ r^r$. One of these F_2 plants was backcrossed to green, both of type IVg and of type VIc, resulting in a total of 108 sun red plants (group 2). Altho no counts were made for anther color, it was noted that the cross with green IVg, $A\ b\ pl\ R^g$, gave both pink- and green-anthered plants, while the cross with green VIc, $a\ b\ pl\ r^r$, gave pink anthers alone. Only two of the six possible genotypes of F_2 sun reds were demonstrated.

Only one dilute purple F_2 plant was tested further (group 3, table 40). From self-pollination it yielded 46 dilute purple and 9 dilute sun red plants, all with colored (purple or pink) anthers. The deviation from a 3:1 ratio, 4.75 ± 2.17, is such as might be expected by chance about once in seven trials, P equaling 0.14. The same F_2 plant when backcrossed to green of types IVg and VIc (group 3) gave 85 dilute purples and 82 dilute sun reds where equality was expected. Evidently this F_2 was $A\ A\ b\ b\ Pl\ pl\ r^r\ r^r$.

No F_2 dilute sun red or green plants were tested further. One F_3 dilute sun red, however, was found to breed true, producing an F_4 of 30 pink-anthered dilute sun reds. Likewise, eight F_3 and F_4 greens gave a total of 126 green plants in the next generation.

In so far as tests have been made, therefore, the cross of purple-anthered purple with green IVg has behaved as expected on the basis of the hypothetical genotype assigned to F_1, namely, $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$.

Purple Ig x green IVg.— Green-anthered purples are assumed to be $A\ B\ Pl\ R^g$, and green IVg to be $A\ b\ pl\ R^g$. The F_1 genotype is therefore, theoretically, $A\ A\ B\ b\ Pl\ pl\ R^g\ R^g$, and F_2 should consist of the three color types purple, sun red, and green, all with green anthers. Eight such F_2 progenies are recorded in table 41, group 1. The three types

occurred in so nearly the expected relation of 9:3:4 that the observed deviations might be expected by chance considerably more than once in three trials, P equaling 0.37. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	293	105	150	548
Calculated	308	103	137	548
Difference	—15	+2	+13	0

The F_2 greens of this cross are assumed to consist of the genotypes $A\ b\ Pl\ R^g$ and $A\ b\ pl\ R^g$, which, if r^r had been present instead of R^g, would have been dilute purples and dilute sun reds, respectively. In substantiation of this assumption, crosses of F_1's, all green-anthered purples, with dilute sun red, $A\ b\ pl\ r^r$, and with green VIc, $a\ b\ pl\ r^r$, are recorded in group 2 of table 41. As expected, the result was the four classes purple, sun red, dilute purple, and dilute sun red, all with colored anthers. The expected numerical equality of the four classes was so closely approached that deviations such as those observed might be expected by chance in nearly three out of four trials, P equaling 0.74. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	58	61	62	70	251
Calculated	63	63	63	63	252
Difference	—5	—2	—1	+7	—1

Still another F_1 was crossed with a pink-anthered sun red, $A\ B\ pl\ r^r$, and gave 68 purples and 67 sun reds, all with colored anthers, where equal numbers were expected.

So far as tested, therefore, the cross of green-anthered purple with green IVg has given the results expected on the basis of the hypothesis under test.

Purple Ig x brown V.—A cross of green-anthered purple, $A\ B\ Pl\ R^g$, with brown, $a\ B\ Pl\ r^r$, gave in F_1 49 purple-anthered purples, presumably

A a B B Pl Pl R^g r^r. An F_2 progeny was grown from only one F_1 plant, 6653–6, resulting in two major color types, purple and brown, in approximately a 3:1 ratio. The purples were, as expected, of two subtypes, one with purple and the other with green anthers. The theoretical relation of 9:3:4 was realized so closely that the observed deviations might be expected by chance in at least two out of three trials, χ^2 equaling 0.76 (when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$). The comparison follows:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Brown V	Total
Observed	23	5	9	37
Calculated	21	7	9	37
Difference	+2	—2	0	0

A second F_1 plant, 6653–2, was backcrossed with green IVg, *A b pl R^g*, resulting in 39 purple plants, 21 with purple and 18 with green anthers, where equal numbers were expected, the deviation from expectation being 1.5 ± 2.1. The same F_1 plant was crossed with a heterozygous dilute sun red, *A a b b pl pl r^r r^r*, resulting in 45 purple-anthered purples and 18 browns, the deviation from the expected 3:1 ratio being 2.25 ± 2.32.

Purple Ig x dilute purple IIIa.— Crosses of green-anthered purple, *A B Pl R^g*, with dilute purple, *A b Pl r^r*, gave in F_1 purple-anthered purple, *A A B b Pl Pl R^g r^r*. The F_2 should consist of purple-anthered and green-anthered purples, dilute purples, and greens, the three major color types appearing in the relation 12:3:1. In F_2 from a single F_1 plant, 5263–3, both purple-anthered and green-anthered purples were noted, but detailed counts based on anther color were not made. The deviations from the expected numbers for the three major types were such as might occur by chance in nine out of twenty such trials, P equaling 0.45. The comparison follows:

Color types	Purple Ia, g	Dilute purple IIIa	Green IIIg	Total
Observed	36	11	5	52
Calculated	39	10	3	52
Difference	—3	+1	+2	0

A second F_1 plant backcrossed with green IVg, *A b pl* R^g, gave the expected four types. The deviations from the equal frequency expected for the several types was such as might occur by chance somewhat more than once in four trials, P equaling 0.27. The comparison follows:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Dilute purple IIIa	Green IIIg	Total
Observed...	59	67	80	77	283
Calculated..	71	71	71	71	284
Difference..	—12	—4	+9	+6	—1

Dilute purple IIIa x green IVg.—A single cross of dilute purple, *A b Pl* r^r, with green IVg, *A b pl* R^g, gave dilute purple, *A A b b Pl pl* R^g r^r, in F_1, and three phenotypes, dilute purple, dilute sun red, and green, in F_2 (table 42, group 1, page 150). The observed frequencies were 23:8:10, which is the nearest possible approach to the expected 9:3:4 relation for a total of 41 individuals. One F_2 dilute purple gave similar results in F_3, indicating the same genotype as the F_1 dilute purples. The F_4 progenies of this F_3 lot may be regarded as equivalent to F_3's, and are therefore grouped with the F_3 in table 43. Three F_3 and F_4 progenies (table 43, group 1A) approached the 9:3:4 relation so closely that the observed deviations might occur by chance in nearly three out of five trials, P equaling 0.59. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed.....	143	48	73	264
Calculated.....	149	50	66	265
Difference.....	—6	—2	+7	—1

The green plants of these F_3 and F_4 lots, as well as those of the F_2 lot listed in group 1 of table 42, are assumed to be *A b Pl* R^g and *A b pl* R^g, and consequently to differ from the dilute purples and dilute sun reds only in having R^g R^g in place of R^g r^r or r^r r^r. That the *R r* pair is thus concerned in these results can be shown by a comparison between the plant-

color phenotypes resulting from seeds with colored aleurone and those from seeds with colorless aleurone. The F_2 progeny came from a plant that produced from self-pollination colored and colorless seeds in the relation 60:24. This close approach to a 3:1 ratio indicates that the F_1 plant could have been heterozygous for only one of the aleurone-factor pairs *A a*, *C c*, or *R r* (Emerson, 1918). A cross with a *C* tester, *A c R*, resulted in 43 colored and no colorless seeds, while a cross with an R tester, *A C r*, gave 46 colored and 32 colorless seeds, thus indicating *R r* as the factor pair concerned. The colorless seeds must therefore have been *r r*, presumably $r^r r^r$, and in accordance with the hypothesis under test should have produced no green plants. Some of the colored seeds, on the contrary, should have been *R R*, supposedly $R^g R^g$, and these should have given green plants. For the most part, the colored and the colorless seeds were planted separately. The 9:3:4 relation of the three plant-color types is theoretically made up of a 6:2:4 relation from colored seeds and a 3:1:0 relation from colorless seeds. Actually, from colorless seeds there appeared dilute purple and dilute sun red plants in the ratio 69:15. The deviation from expectation, 6.0 ± 2.7, might be expected to occur about once in seven trials, P equaling 0.14. From colored seeds the deviation from the theoretical distribution was such as might occur thru errors of random sampling almost once in four trials, P equaling 0.23. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed	92	42	70	204
Calculated	102	34	68	204
Difference	—10	+8	+2	0

Aleurone is in some cases self-colored and in some cases mottled. Mottled aleurone ordinarily occurs only when the *R* factor is heterozygous, but not all heterozygous individuals are mottled (Emerson, 1918). Mottled seeds of the cross under discussion, just as colorless ones, since they are presumably $R^g r^r$, should produce no green plants. In the case of some of the progenies noted above, the colored seeds were sorted into self-colored, mottled, and colorless. Since usually about one-third

of the colored seeds are mottled, the 9:3:4 relation of plant-color types observed in this cross should be made up of a 3:1:0 relation from colorless seeds, 3:1:0 from mottled seeds, and 3:1:4 from self-colored seeds. Of the progenies for which the seeds were sorted in this way, the colorless seeds produced dilute purple and dilute sun red plants in the relation 60:14, with a deviation from 3:1 of 4.5 ± 2.5, the mottled seeds gave the same plant-color types in the relation 30:12, with a deviation of 1.5 ± 1.9, and the self-colored seeds yielded dilute purple, dilute sun red, and green in the relation 48:19:64 (the theoretical distribution for a total of 131 individuals is 49:16:66), the deviations being such as might occur by chance perhaps three times in four trials, χ^2 equaling 0.64. On the whole, therefore, these crosses, and particularly the interrelations of aleurone and plant colors, afford strong evidence in support of the hypothesis under test.

Before presenting further F_3 results from these crosses, it may be well to consider other crosses of dilute purple with green IVg which, so far as plant color alone is concerned, have given results quite like those presented above but which exhibit a wholly different relation between plant color and aleurone color. The green plants concerned in these other crosses were *C* testers for aleurone color (Emerson, 1918), and were therefore known to be *A c R*, presumably $A\ c\ R^g$. The dilute purple plants concerned were homozygous for aleurone color, and were consequently *A C R*, presumably $A\ c\ R^r$. These crosses differ, then, from the ones discussed above in having R^r in place of r^r and *c* in place of *C*. Since the *C c* pair is supposed not to have any relation to plant color, the results for plant color should be quite like those for the other cross and there should be no relation between plant color and aleurone color. The results for F_2 are presented in table 42, group 2, and the F_3 results in table 43, group 1B. The three plant-color types appeared in F_2 in the relation 328:113:148, and in F_3 in the relation 40:14:23. Considered together these lots deviated very slightly from expectation, χ^2 equaling 0.31. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed	368	127	171	666
Calculated	375	125	166	666
Difference	—7	+2	+5	0

The seeds from which these plants were grown consisted of colored and colorless in approximately a 3:1 ratio, as is expected when the *C* factor alone is heterozygous. The deviations from the expected 9:3:4 relation for plants from colored seeds was such as might occur by chance more than once in three trials, P equaling 0.36, and for plants from colorless seeds such as might occur once in six trials, P equaling 0.17. The comparisons follow:

Plant-color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Colored seeds:				
Observed	215	58	89	362
Calculated	204	68	90	362
Difference	+11	—10	—1	0
Colorless seeds:				
Observed	65	32	32	129
Calculated	73	24	32	129
Difference	—8	+8	0	0

The results presented for plant color alone and in relation to aleurone color in these crosses are therefore quite in keeping with the hypothetical constitution assigned to the F_1 plants, namely, *A A b b Pl pl* $R^r R^g$ *C c*, just as the results from the other crosses were in keeping with the assumed genotype *A A b b Pl pl* $R^g r^r$ *C C* for their F_1 plants.

A single F_1 plant was backcrossed with green IVg, *A b pl* R^g, with results as shown in table 42, group 3. The three color types dilute purple, dilute sun red, and green, occurred in the relation 46:45:86. The expected distribution for a total of 177 individuals is 44:44:89, showing almost a perfect fit, χ^2 equaling 0.21.

For both the lots of crosses under discussion, further tests are afforded by the behavior in F_3 and F_4. As already shown, some of the F_2 dilute purples had the same genetic constitution as the F_1 plants (table 43, groups 1A and 1B). The progenies of two other dilute purples, one of F_2 and the other of an equivalent F_3, produced dilute purple and dilute sun red plants only (group 2, table 43), in the relation 82:23. The devia-

tion from a 3:1 ratio is 3.25 ± 2.99. From their behavior and in view of the crosses in which they occurred, one of these plants is assumed to have been *A A b b Pl pl* r^r r^r and the other *A A b b Pl pl* R^r R^r.

A single dilute purple of an F_3 lot equivalent to an F_2 gave dilute purple and green plants only (group 3, table 43). The two color types appeared in the ratio 62:16, a deviation from 3:1 of 3.5 ± 2.6. The F_3 plant is therefore assumed to have been *A A b b Pl Pl* R^g r^r. Colorless and mottled seeds produced dilute purple plants only, as was expected. From self-colored seeds there resulted dilute purple and green plants in the relation 26:16, a deviation of 2.0 ± 2.0 from the expected 2:1 ratio.

Two dilute sun red plants gave progenies of dilute sun reds and greens in the relation 63:22, a deviation from a 3:1 ratio of 0.75 ± 2.69 (group 4, table 43). Presumably these plants were *A A b b pl pl* R^g r^r and *A A b b pl pl* R^r R^g. Four other dilute sun red plants bred true in the next generation (group 5, table 43), producing a total of 197 dilute sun red plants. These plants are therefore assigned the genotype *A A b b pl pl* r^r r^r.

Seven green plants likewise bred true (group 6, table 43), producing a total of 130 green plants. These plants were presumably *A b pl* R^g and *A b Pl* R^g.

To summarize, all types of behavior were observed in F_3 and equivalent F_4 generations of the cross of dilute purple with green IVg except true-breeding dilute purples. Only eight dilute purples were tested, and only one in nine is expected to breed true.

Sun red IIg and IIa and dilute sun red IVa x green IIIg and IVg.— Two crosses of green-anthered sun red with green IVg gave green-anthered sun red plants in F_1, theoretically *A A B b pl pl* R^g R^g. The parent types only appeared in F_2 (table 44, group 1). The observed numbers of green-anthered sun reds and greens were, respectively, 216 and 77. The deviation from the expected 3:1 ratio was 3.7 5± 5.00.

A cross of pink-anthered sun red with green IVg gave pink-anthered sun red in F_1, theoretically *A A B b pl pl* R^g r^r. F_1 plants backcrossed with green IVg, *A b pl* R^g, gave three major plant-color types (group 2, table 44) — sun red, dilute sun red, and green — with the sun reds appearing in two subtypes, one pink-anthered and the other green-anthered. Theoretically the four types should have been represented by an equal number of individuals. The deviations from this expectation were such

that there is considerably more than an even chance that they might have been due to errors of random sampling, P equaling 0.56. The comparison follows:

Color types	Sun red, pink anthers IIa	Sun red, green anthers IIg	Dilute sun red IVa	Green IVg	Total
Observed.....	105	90	105	109	409
Calculated.....	102	102	102	102	408
Difference.....	+3	—12	+3	+7	+1

Crosses of dilute sun red with green IVg gave 54 dilute sun red plants in F_1, $A\ A\ b\ b\ pl\ pl\ R^g\ r^r$. In F_2 (group 3, table 44) there resulted from a self-pollinated F_1, dilute sun red and green plants in the relation 55:22, a deviation from the expected 3:1 ratio of 2.75 ± 2.56. An F_1 back-crossed with green IVg gave the same two color types in equal numbers, 30 each, exactly as expected. Numerous other crosses of this sort have been observed in connection with studies of the interrelations of aleurone-color and plant-color factors. Since these data are to be presented in a later paper and since they are wholly in accord with the data given in group 3 of table 44, they are not discussed here.

In an earlier section of this paper dealing with the factor pairs *A a*, *B b*, and *Pl pl* only (page 29), it was shown that the green plants there noted are of three kinds, namely, *a b pl*, *a B pl*, and *a b Pl*. Thruout the present section of the paper, which deals with the relation of the multiple-allelomorph series containing R^g, r^r, R^r, r^g, it has been assumed that plants which in the presence of r^r or R^r are dilute purple or dilute sun red, are green in the presence of homozygous R^g. The data presented are wholly in accord with this interpretation, thereby giving considerable assurance of the probable correctness of the hypothesis. The reported interrelations of plant color and aleurone color when the latter was known to involve the *R r* pair, have still further strengthened this assurance. It remains now to present even more direct evidence, namely, that obtained from crosses of green plants encountered in this study, with sun red and dilute sun red plants. These green plants are assumed to be $A\ b\ Pl\ R^g$, type IIIg, and $A\ b\ pl\ R^g$, type IVg.

Certain F_3 and F_4 progenies consisting of green-anthered purples and greens in a 3:1 relation are listed in table 39, group 4. These green plants

were all, presumably, $A\ b\ Pl\ R^g$. Green plants of a later generation, grown from these greens, when crossed with sun red plants, type IIa, gave 64 purple-anthered purples and no other types (table 45, group 1). Another green crossed with dilute sun red resulted in 4 dilute purples. Obviously the same results would have been obtained had the green plants used in these crosses been $a\ b\ Pl\ r^g$, instead of $A\ b\ Pl\ R^g$ as they are supposed to have been. As a matter of fact, however, one of these green plants had homozygous colored aleurone, and therefore must have been $A\ C\ R$. The other two greens, while they had colorless aleurone, came from lots known, from their 3:1 aleurone-color ratios and from crosses with aleurone testers, to be heterozygous for C alone, and therefore $A\ c\ R$. Moreover, the green plants from lots consisting of purples and greens in a 3:1 relation could not have been $a\ a$, for the parents of such lots, if heterozygous for A, must have produced purples and browns rather than purples and greens. The green plants could therefore have been nothing other than $A\ b\ Pl\ R^g$.

Similarly, progenies consisting of green-anthered purples and sun reds, and greens, in a 9:3:4 relation, are listed in table 39, group 3. Green plants of these lots and their green descendants might be either $A\ b\ Pl\ R^g$ or $A\ b\ pl\ R^g$, or might be heterozygous for Pl. Six such green plants were crossed with dilute sun reds (table 45, group 2). None of these greens could have been of the types discussed in the earlier section of this paper, namely, $a\ b\ Pl\ r^r$ and the like, for they were shown by appropriate tests (Emerson, 1918) to be $A\ c\ R$ and some of them have even been used as C testers for aleurone color. Two of these green plants crossed with dilute sun reds gave dilute sun reds only, 59 in all, and are consequently regarded as being $A\ b\ pl\ R^g$. Two others by similar crosses gave dilute purples and dilute sun reds in the relation 20:30, a deviation of 5.0 $\pm$2.4 from the expected equality from plants of the genotype $A\ A\ b\ b\ Pl\ pl\ R^g\ R^g$. Two other greens were crossed with heterozygous dilute sun reds, $A\ A\ b\ b\ pl\ pl\ R^g\ r^r$, and gave dilute purples, dilute sun reds, and greens in the relation 69:54:106. The theoretical distribution among these three classes for a total of 229 individuals, based on the assumption that the green parent plants were $A\ A\ b\ b\ Pl\ pl\ R^g\ R^g$, is 57:57:115, a deviation that might occur by chance about once in five trials, P equaling 0.19.

Progenies consisting of dilute purples, dilute sun reds, and greens in a 9:3:4 relation are listed in table 43, group 1A. Descendants of one of

these green plants were crossed with dilute sun reds which were F_1's of crosses between dilute sun red and green IVg. The results were dilute purple and green plants in the relation 328:338 (table 45, group 3), a deviation from a 1:1 ratio of 5.0 ± 8.7. Since the heterozygous dilute sun red plants were $A\ A\ b\ b\ pl\ pl\ R^g\ r^r$, the green plants crossed with them are assumed to have been $A\ b\ Pl\ R^g$. That this assumption is correct appears the more evident from the fact that the green plants were homozygous for colored aleurone, and hence $A\ C\ R$.

Green IVg x *green VIc.*— Twelve crosses between green plants of type IVg and green plants of type VIc gave a total of 159 F_1 plants, all dilute sun red. With respect to aleurone color, all the type IVg plants concerned in these crosses were known to be $A\ c\ R$, and, in fact, were in general use as C testers for aleurone color. With respect to plant color, therefore, they are assigned the constitution $A\ b\ pl\ R^g$. Of the type VIc greens, four were known to be A testers for aleurone color, and were therefore, with respect to aleurone color, $a\ C\ R$. Their plant-color constitution is accordingly set down as $a\ b\ pl\ R^r$. Six of the type VIc greens had an aleurone-color constitution of $a\ C\ r$, their plant-color genotype being accordingly $a\ b\ pl\ r^r$. The other two VIc greens were certainly $a\ b\ pl$, but whether they were R^r or r^r is unknown.

In F_2, dilute sun red and green plants were present in the ratio 420:291 (table 46, group 1, page 154). From an F_1 of the genotype $A\ a\ b\ b\ pl\ pl$ plus $R^g\ r^r$ or $R^g\ R^r$, a 9:7 ratio of dilute sun red to green is to be expected in F_2, since both A and r^r or R^r are assumed to be necessary for the production of anthocyanic pigment, which distinguishes dilute sun red from green. The theoretical ratio for a total of 711 individuals is 400:311. The observed deviation from this ratio, 20.0 ± 8.9, is such as might occur by chance about once in eight trials, P equaling 0.13.

Two F_1 plants backcrossed to green VIc, $a\ b\ pl\ R^r$, gave 66 dilute sun red and 58 green plants, and two backcrosses with green IVg, $A\ b\ pl\ r^g$, gave 96 dilute sun reds and 96 greens, equality of the two classes being expected in the case of both crosses (group 2, table 46).

That the two parent types of green occurred in F_2 is shown by their relations to aleurone and pericarp color. In the case of every cross, green plants were produced from both colored and colorless seeds. Those from colored seeds could have been only $A\ b\ pl\ R^g$. Since some seeds were colorless because of $a\ a$ and some because of $c\ c$, both parent types of green should have been present in the lots grown from colorless seeds.

In one cross there was present the pericarp factor P, which with A gives a red and with $a\ a$ a brown pericarp. All the F_2 green plants from colored seeds had red pericarp, and of those from colorless seeds the majority had brown pericarp. From the colorless seeds there should have occurred also a combination type of green, $a\ b\ pl\ R^g$, but no tests were made for the identification of this type.

Ten dilute sun reds of F_2 were tested by their F_3 behavior. Three of these (table 47, group 1) gave dilute sun red and green plants in the relation 108:77, a deviation from a 9:7 ratio of 4.0 ± 4.6. Five other F_2 plants (group 2) gave the two color types in the relation 187:66, a deviation from a 3:1 ratio of 3.0 ± 4.6. Two F_2's (group 3) bred true dilute sun red, producing 78 dilute sun red and no green offspring. Theoretically, of 9 F_2 dilute sun reds, there should occur in F_3, true-breeding, 3:1, and 9:7 progenies in the numerical relation 1:4:4. The observed relation between these three sorts of behavior for the ten F_2's tested was 2:5:3. Deviations such as these might occur by chance about once in two trials, P equaling 0.49.

Green IVg x green VIa.— Certain crosses of green IVg with green VI have given sun red plants in F_1. The type VI greens belonged to families in which the B factor was known to be present. They were therefore doubtless $a\ B\ pl$ plus r^r or R^r, and the F_1's were probably $A\ a\ B\ b\ pl\ pl$ plus $r^r\ R^g$ or $R^r\ R^g$. F_2 consisted of the three major color types sun red, dilute sun red, and green (table 48, group 1) in the relation 586:161:348. Obviously this is not a 9:3:4 relation, for the deviations from such expectation, −30, −44, +74, could not be expected to occur thru errors of random sampling once in a million such trials, χ^2 equaling 30.9 and P equaling .000000+. As a matter of fact, an F_1 of the genotype suggested above should give in F_2 the three color types observed in the relation 36:9:19. The observed frequencies of the several classes fit this expectation so closely that the deviations from it might occur by chance in about one out of five trials, P equaling 0.19. The comparison of observed and expected frequencies follows:

Color types	Sun red	Dilute sun red	Green	Total
	IIa, g	IVa	IVg, VIa, c	
Observed	586	161	348	1,095
Calculated	616	154	325	1,095
Difference	—30	+7	+23	0

Not only were the frequencies of the major color types fairly close to expectation, as indicated above, but the expected subclasses of sun red with pink anthers and with green anthers were observed. Counts of anther color were made in the case of only 65 individuals. These plants were distributed to the four color classes, pink-anthered sun red, green-anthered sun red, dilute sun red, and green, in the order 24:9:10:22. The theoretical distribution of 64 individuals being 27:9:9:19, the deviations are such as might occur by chance perhaps twice in three trials, χ^2 equaling 0.91 (when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$).

Only three F_2 sun reds were tested in F_3. One of them (group 2, table 48) bred true sun red, but segregated with respect to anther color. It was therefore presumably *A A B B pl pl* r^r R^g. Two other F_2 sun reds (group 3) gave sun red and green offspring in the ratio 229:71, a deviation of only 4.0 ± 5.1 from a 3:1 ratio. One of these two F_2 plants was crossed with a dilute sun red, resulting in 55 sun red plants. The two F_2 plants, therefore, were presumably *A a B B pl pl*. Anther color was not determined, but the fact that the green plants of F_3 all came from colorless seeds is conclusive evidence for the presence of *A a* and against the presence of r^r R^g. The genotype of the F_2 plants is accordingly set down as *A a B B pl pl* r^r r^r.

Green IIIg x green VIc.— Green plants known to be of type VIc, *a b pl* r^r, were crossed with greens which were known to be R^g R^g and which from their parentage might have had *Pl*. The result in F_1 was dilute purple, supposedly *A a b b Pl pl* r^r R^g. Two F_2 lots (table 49, group 1) consisted of dilute purples, dilute sun reds, and greens in the relation 109:37:135. From the assumed genotype of F_1, there should occur in F_2 the observed color types in the relation 27:9:28. The observed frequencies deviated from the theoretical ones by amounts such as might occur by chance once in three trials. P equaling 0.33. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg, VIb, c	Total
Observed	109	37	135	281
Calculated	119	40	123	282
Difference	—10	—3	+12	—1

The dilute purples of F_2 were presumably all $A\ b\ Pl\ r^r$ and the dilute sun reds all $A\ b\ pl\ r^r$. Of the F_2 greens there should theoretically have been six types, namely, $A\ b\ Pl\ R^g$, $A\ b\ pl\ R^g$, $a\ b\ Pl\ r^r$, $a\ b\ pl\ r^r$, $a\ b\ Pl\ R^g$, and $a\ b\ pl\ R^g$. The relation of these plant colors to aleurone color and to a pericarp color known as cherry, present in these families, affords an opportunity of checking some of these hypothetical formulae. Cherry pericarp is a bright reddish purple, somewhat variable in intensity. In the parent of one of these F_2 progenies it was sufficiently light to make possible the determination of the underlying aleurone color. The F_2 seeds consisted of colored and colorless aleurone in the ratio 140:171, a deviation from a 27:37 ratio of 9.0 ± 5.9, or such a deviation as might occur by chance three times in ten trials, P equaling 0.30. The F_1 plants were known to be $A\ a\ R\ r$, and in order to give a 27:37 ratio with respect to aleurone color they must have been also $C\ c$. Cherry pericarp is of such a nature that it never develops except in the presence of *Pl*. With *A* and *Pl* it is cherry, but with *a* and *Pl* it is brownish. It had been regarded by the writer as due to a factor, *Ch*, but recently Dr. E. G. Anderson has shown (by unpublished data) that the writer's *Ch* is apparently another allelomorph of *R*, and at present it is known to exist only in the form r^{ch}. Since all dilute purples of the lots under consideration here are assumed to be $A\ b\ Pl\ r^{ch}$, they should all have cherry pericarp. Again, since dilute sun reds are *pl pl*, they should all have colorless pericarp. Furthermore, since all green plants from colored seeds are supposed to be $R^g\ R^g$, their pericarp should likewise be colorless. Finally, since the colorless seeds may lack color because of either *a a*, *r r*, or *c c* alone, or because of both *a a* and *r r*, some green plants from colorless seeds should have colorless pericarp, $a\ R^g$ or $A\ c\ R^g$, and some should have brownish pericarp, $a\ Pl\ r^{ch}$. Of course all green plants with *pl pl* also must have colorless pericarp.

The observed results are wholly in accord with these suppositions. In one F_2 progeny, pericarp color was determined for all except a few plants. From seeds with colored aleurone, all the dilute purples had cherry pericarp and all the dilute sun reds and greens had colorless pericarp. These three classes of plant and pericarp color showed frequencies deviating from the theoretical 27:9:18 relation by quantities such as might occur by chance almost once in four trials, P equaling 0.23. From seeds with colorless aleurone, all dilute purples had cherry pericarp, all dilute sun

reds had colorless pericarp, and greens had in part brownish and in part colorless pericarp. The deviations from the expected 27:9:18:20 relation of these four color classes were such as might occur thru errors of random sampling in more than seven out of any ten such trials, P equaling 0.72. The comparisons follow:

Plant color	Dilute purple	Dilute sun red	Green	Green	Total
Pericarp color	Cherry IIIa	Colorless IVa	Brownish VIb	Colorless IIIg, IVg, VIc	
Colored aleurone:					
Observed....	43	10	0	35	88
Calculated...	44	15	0	29	88
Difference...	—1	—5	0	+6	0
Colorless aleurone:					
Observed....	38	11	32	28	109
Calculated...	40	13	27	29	109
Difference...	—2	—2	+5	—1	0

Further tests of the factorial composition, with respect to *Pl*, of some F_2 green plants of this cross are afforded by crosses between them and sun red and dilute sun red plants. One F_2 green crossed with sun red gave 27 purple plants (table 49, group 2). Since the green parent plant came from a colored seed, it is assumed to have been $Pl\ Pl\ R^g\ R^g$ plus $A\ A$ or $A\ a$. Two other greens crossed with dilute sun red gave 39 dilute purple plants, and were therefore *Pl Pl* (group 2, table 49). Since one of these green plants had brownish and the other had colorless pericarp, they are assumed to have been also r^{ch} and $R^g\ R^g$, respectively. A fourth F_2 green crossed with sun red gave purple and sun red plants, and a fifth green crossed with dilute sun red gave dilute purple and dilute sun red plants, indicating *Pl pl* (group 3, table 49). The first of these two had brownish and the second had colorless pericarp. They must therefore have been r^{ch} and $R^g\ R^g$, respectively. A sixth F_2 green crossed with dilute sun red gave only dilute sun red plants, and so must have been *pl pl* (group 4).

Green IIIg x green VIa.— In the sections immediately preceding this, it has been shown that intercrosses of greens may give dilute sun reds (page 104), dilute purples (page 106), or sun reds (page 105) in F_1, the particular color type depending on the genotypes of the greens chosen for crossing. It remains to be shown that purple Ia can be produced by intercrosses of greens. A cross of green VIa, $a\,B\,pl\,r^r$, with green IIIg, $A\,b\,Pl\,R^g$, should give this result, F_1 being $A\,a\,B\,b\,Pl\,pl\,R^g\,r^r$. Such a cross has been made, with results as expected.

A stock of green plants was isolated from a cross of brown V, $a\,B\,Pl\,r^r$, with green VIc, $a\,b\,pl\,r^r$, and was shown, by crosses with aleurone testers and with dilute sun red IVa, to be type VIa, $a\,B\,pl\,r^r$. Another lot of greens arose from a cross of purple Ig with green IVg. The purple Ig parent was from a lot consisting of purple Ia, purple Ig, dilute purple IIIa, and green IIIg, coming from a cross of purple Ig with dilute purple IIIa heterozygous for $R^g\,r^r$. It was therefore $A\,A\,B\,b\,Pl\,Pl\,R^g\,R^g$. The green IVg plant with which it was crossed was known to be $A\,b\,pl\,R^g$. The F_1 of this cross consisted, as was expected, of purples and greens only. The purples were type Ig and must have been heterozygous for $B\,b$ and $Pl\,pl$, and the greens must have been type IIIg and heterozygous for $Pl\,pl$, or $A\,A\,b\,b\,Pl\,pl\,R^g\,R^g$. Two of these F_1 greens were crossed with one of the greens of type VIa mentioned above. The two crosses, 9659 and 9660, resulted as expected in purple-anthered purples, type Ia, and pink-anthered sun reds, type IIa, in the relation 18:20. It has been demonstrated, therefore, that by crossing wholly green plants of appropriate genotypes it is possible to produce purple-anthered purples, the most highly colored type known, a type that is dominant to all other types.

Green IIIg x purple Ia.— A green plant with homozygous purple aleurone and belonging to a family (table 39, group 4) consisting of green-anthered purples and greens only, and therefore theoretically being $A\,b\,Pl\,R^g$, was crossed with a purple-anthered purple, $A\,B\,Pl\,r^r$. A purple-anthered purple F_1, $A\,A\,B\,b\,Pl\,Pl\,r^r\,R^g$, 5350–9, was backcrossed with green IVg of the genotype $A\,b\,pl\,r^g$, with the result that in the next generation there appeared four color types, purple-anthered purple, green-anthered purple, dilute purple, and green, in the relation 28:22:21:29. The deviations from the expected equal distribution of the 100 individuals were such as might occur by chance in considerably more than half of

such trials, P equaling 0.57. It will be recalled that results like these were obtained from a cross of green-anthered purple with dilute purple (page 96), and of course the same results were to be expected since the F_1 in both cases is supposed to have been $A\ A\ B\ b\ Pl\ Pl\ r^r R^g$.

The cross now under consideration has interest from the standpoint of the relation of aleurone color to plant color, and also for certain linkage relations. The F_1 was known to be, with respect to aleurone color, $A\ A\ R\ r$. Whether it was $C\ C$ or $C\ c$ was not known, since a strong red pericarp made aleurone counts impracticable. The green plant on which the F_1 was backcrossed, was determined by appropriate tests to be $C\ C$, so that the relation of the F_1 purple to C is immaterial. The backcross resulted in approximately equal numbers of seeds with and without aleurone color, there being 109 colored and 110 colorless seeds. The colorless seeds must have been $A\ B\ C\ Pl\ r^r\ r^g$ and $A\ b\ C\ Pl\ r^r\ r^g$, and should therefore have produced purple-anthered purples and dilute purples only; while the colored seeds must have been $A\ B\ C\ Pl\ R^g\ r^g$ and $A\ b\ C\ Pl\ R^g\ r^g$, and should correspondingly have produced green-anthered purples and greens only. The results were quite in accord with expectation, as is shown in the following comparison:

Color types	Purple, purple anthers	Purple, green anthers	Dilute purple	Green	Total
	Ia	Ig	IIIa	IIIg	
Colored seeds.....	0	22	0	29	51
Colorless seeds....	28	0	21	0	49

It has been shown earlier in this paper (page 63) that a linkage exists between the factor pair $B\ b$ and a factor pair, $Lg\ lg$, for normal or liguleless leaf, the percentage of crossing-over being about 30. It happens that the F_1 of this cross was $Lg\ lg$ as well as $B\ b$, $B\ lg$ having come from one parent and $b\ Lg$ from the other, and that the green plant used in the backcross was $b\ lg$. There is no question here that the purple-anthered purples and dilute purples produced from colorless seeds differed with respect to the $B\ b$ pair only. Their linkage with liguleless leaf, as indicated by the percentage of crossing-over, was 29.4, or a deviation from 30 of 0.6 ± 2.0. Practically the same linkage relation was found for the plants from colored seeds, green-anthered purples and greens. In this case the percentage of crossing-over was 27.5, a deviation from 30 of

2.5 ± 2.1, or such as might occur by chance about twice in five trials, P equaling 0.42. It is to be assumed, therefore, that the same difference exists between green-anthered purples and greens as between purple-anthered purples and dilute purples, namely, a difference with respect to the factor pair *B b*. This in turn is merely additional evidence that plants which in the presence of r^r are dilute purples, *A b Pl*, appear as greens in the presence of $R^g r^g$, which is the hypothesis under test thruout this section of the paper.

Purple Ia x green-anthered dilute sun red

A purple-anthered purple, known from appropriate aleurone-color tests to be *R R* and hence *A B Pl* R^r, was crossed with a dilute sun red which differed from most dilute sun reds in showing much less anthocyanic pigment, particularly in early stages of growth, than is usual in plants of that type, and in having little, if any, color in its anthers. The F_1's, 2975, were purple-anthered purples. F_2 was expected to show the four color types, purple, sun red, dilute purple, and dilute sun red, commonly found in crosses of purple Ia with dilute sun red IVa. As a matter of fact, the single F_2 progeny grown was found to consist of these four color types as major classes, but each class was found to have colored-anthered (purple or pink) and green-anthered subclasses. The difference between the two subclasses for purple and sun red was sharp, just as is the case in crosses of purple Ia with green IVg, but it was often difficult to separate green-anthered dilute purples from green-anthered dilute sun reds. Ordinarily, anther color (purple or pink) is the surest means of distinguishing between dilute purple and dilute sun red. When both have green anthers the separation must be based on the relative amount of pigment in other plant parts — a difference that is usually not very marked until late in the life of the plants, when dilute purples usually show materially more pigment, especially in parts not exposed to the sun, than do dilute sun reds. It will be recalled that in crosses of purple Ia with green IVg, both colored and green-anthered purples and sun reds appear, but that all the dilute purples and dilute sun reds have colored anthers, the green-anthered individuals appearing as wholly green in all plant parts except perhaps the pericarp. But in the cross here considered, no wholly green plants were found.

The natural supposition is that there is here concerned still another form of the R factor, such that, while it does not allow color to develop in the anthers, does nevertheless result in the development of some anthocyanic pigment in other parts of the plant. The dilute sun red plant used as one parent of this cross was found to be $A\ c\ R$ with respect to aleurone. The factor particularly concerned in the behavior here reported is therefore assigned the designation R^{rg}. The F_1 plants are accordingly assumed to have been $A\ A\ B\ b\ Pl\ pl\ R^r\ R^{rg}$. The frequency distribution for the eight color types observed in F_2 approached the theoretical distribution so closely that deviations of the magnitude observed might occur by chance nearly three times in any ten such trials, P equaling 0.72. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute purple	Dilute sun red	Dilute sun red	Total
Anther color	Purple	Green	Pink	Green	Purple	Green	Pink	Green	
Observed...	212	77	66	22	66	23	22	3	491
Calculated .	207	69	69	23	69	23	23	8	491
Difference..	+5	+8	—3	—1	—3	0	—1	—5	0

One F_2, a green-anthered purple, was tested in F_3. This plant bred true, producing 128 green-anthered purples and no other types.

It is unfortunate that the relation of aleurone color to plant color in this cross afforded no check on the assumption that the observed behavior with respect to anther color of dilute purples and reds was due to a factor belonging to the allelomorphic series R^r, R^g, r^r, r^g. True, the F_1 plant tested was heterozygous with respect to aleurone color, but this was known to be due to $C\ c$. Since no further tests have been made, the only evidence in support of the assumption of a factor R^{rg} is the very close fit of observed with theoretical frequency distributions, the fact that colored and green anthers in purple and sun red types of many other crosses have been found to be due to the R factor, and the demonstrated presence of R in the green-anthered sun red plant used in the cross.

Summary of results involving the allelomorphic series R^r, R^g, R^{rg}, r^r, r^g, r^{ch}

Crosses of brown with green of type IVg have been shown to result in purple F_1's, and in eight color types in F_2 in a numerical relation approximating 81:27:27:9:27:9:36:40, or in six major color types, anther color being disregarded, in approximately the relation 108:36:27:9:36:40.

It has been noted that these results are wholly unlike those for crosses of brown with green reported in an earlier section of this paper, and are similar in general, tho with marked differences in detail, to previously discussed crosses of brown with dilute sun red. As an interpretation of these results, it has been assumed that, in addition to the three pairs *A a*, *B b*, *Pl pl*, a fourth pair — members of a multiple-allelomorph series, such as $R^r R^g$, $r^r R^g$, or $R^r r^g$ — is concerned. It has been assumed further that R^r or r^r is necessary ordinarily for the development of dilute purple and dilute sun red and for the appearance of purple and pink anthers in purples and sun reds, respectively, while $R^g R^g$ or $r^g r^g$ is necessary for green anthers of purples and sun reds and for the conversion of dilute purples and dilute sun reds into wholly green plants. Similarly, the appearance of green-anthered dilute purples and dilute sun reds in a single cross has been ascribed to $R^{rg} R^{rg}$. The relation of the *R* allelomorph to both aleurone color and plant color has afforded reliable tests of the hypothesis. Other tests have consisted of the behavior in later generations of the several F_2 color types and the results of intercrosses between these types. Neither of these tests has been carried to the point of exhausting all the possibilities, but in all a considerable number of tests have been made and all have given results in support of the hypothesis. A single linkage test, involving the *B b* pair with leaf type, *Lg lg*, has afforded added support. On the whole, therefore, the hypothesis has been, if not substantiated, at least rendered highly probable.

RELATION OF ALEURONE FACTORS *C c* AND *Pr pr* TO PLANT COLOR

The relations of the aleurone factors *A* and *R* to plant color have been noted repeatedly in this account. A single observation suggests a relation between the aleurone-factor pair *C c* and leaf color. Culture 2909 came from colored seeds of a selfed ear showing a 3:1 ratio of colored to white seeds, and therefore heterozygous for a single pair of aleurone-color factors. Several ears in the resulting progeny also gave 3:1 ratios. Tests of four plants with aleurone testers gave conclusive evidence that the *C c* pair was the one concerned. One selfed plant of the lot, 2909–32, had 318 colored and 105 white seeds. Both the colored and the white seeds produced only sun red plants, some with green and some with pink anthers, indicating the genotype $A\ A\ B\ B\ C\ c\ pl\ pl\ R^r\ R^g$. All the plants showed strong sun red pigment in the sheaths and the outer husks, but

there was distinctly more red color in the leaves of the plants from colored seeds than in the leaves of the plants from white seeds. Particular attention has not been given to a possible effect of the *C* factor on mature plant colors of other color types. Many cultures of dilute sun reds and greens have afforded opportunities for observing any effect of *C* and *c* on red color in the leaves of seedlings, but no effects have been noted. No particular attention was paid to the matter at the time when the seedlings were under observation, but if the *C c* pair had exerted any marked influence it would probably have been noted.

Numerous cultures of dilute sun red seedlings have been noted with respect to possible effects of the aleurone-factor pair *Pr pr*, but no effect has been observed, the purple and the red seeds having produced seedlings with apparently the same intensity of red color. Likewise, no influence of *Pr pr* on mature plant color has ever been observed in the case of either sun red or dilute sun red. With purple and dilute purple plants, however, a distinct effect is noticeable. Purple and dilute purple plants from seeds with purple aleurone have purple anthers, while those from seeds with red aleurone have reddish purple anthers (Plate I, 1 and 3, and Plate II, 1 and 3). A similar effect is often seen also in the color of the inner husks. In neither the anthers nor the husks is the effect always sufficiently distinct to make possible an accurate separation of plants from purple and from red seeds if they are growing in mixed cultures. In some cases, however, the difference is very distinct. And when the seeds are separated with respect to purple and red aleurone, the two lots of plants resulting usually show fairly distinct differences in anther color and often in husk color as well.

EXPRESSION OF PLANT-COLOR AND ALEURONE-COLOR FACTORS

The mode of expression of the several plant-color factors has been discussed in detail in this paper, and similar discussions of aleurone-color factors are available in numerous other papers. Since aleurone colors and certain plant colors — the purple-red series — are doubtless anthocyanins, it seems natural to expect close interrelations between them. Many such relations have been noted in this account. There are certain matters, however, which need to be brought together in a summary discussion.

It will be recalled (Emerson, 1918) that for the development of any aleurone color, the presence of three dominant factors, *A*, *C*, and *R*, and also of a duplex recessive factor pair, *i i*, is necessary. The *Pr pr* pair has no visible expression except when associated with this combination of the other factors, and then it determines whether the color shall be purple or red. So far as is now known, the plant-color situation with respect to complementary factors is not quite so complex. Something of the same sort is seen, however, in the fact that no anthocyanic pigment ordinarily develops except either in the presence of *A* and R^r, r^r, or r^{ch}, or in the presence of *A*, *B*, and R^g R^g or r^g r^g. With the first of these combinations, the pairs *B b* and *Pl pl* determine the particular color type of the purple-red series. Two of these types, purple and dilute purple, are modified further by *Pr pr*, and the intensity of their color depends also on the member of the *R* series present, r^{ch} exerting a more pronounced effect than R^r or r^r. One type at least, sun red, is influenced somewhat by *C c*. With the second combination, *A*, *B*, and R^g R^g or r^g r^g, the pair *Pl pl* determines whether the type shall be purple or sun red. For the formation of the non-anthocyanic (flavonol) pigment, brown, the interaction of *a a* with either *B* or *Pl* is essential, and usually very little color develops except when both *B* and *Pl* are present. Brown is made more intense by the presence of r^{ch}.

Of the factors concerned with plant colors of maize, the *A a* pair is one of the most fundamental, since it differentiates sharply the anthocyanins of the purple-red series, *A B Pl*, *A B pl*, *A b Pl*, *A b pl*, from the non-anthocyanic brown, *a B Pl*, and the slightly brown or green *a B pl* and *a b Pl* and the wholly green *a b pl*. Without *A* no anthocyanin shows in either the aleurone or the other parts of the plant. A second fundamental pair is *Pl pl*, which differentiates the sun colors from those that develop in local darkness. Purple (*A B Pl*), dilute purple (*A b Pl*), and brown (*a B Pl*) are all able to develop in darkness; while sun red (*A B pl*), dilute sun red (*A b pl*), and the slight brown sometimes seen in *a B pl*, do not develop except in the presence of light. Whether or not the slight brown sometimes present in *a b Pl* forms in darkness has not been determined. To the *Pr pr* pair is due a definite qualitative difference in the colors formed which is presumably associated with a difference in chemical composition of the pigments. In the presence of *Pr* aleurone color is purple, and with *pr* it is red, and a similar difference, tho not always

so sharp a one, is seen in the effects of *Pr pr* on the anther and husk color of purples and dilute purples. The factors R^g and r^g on the one hand, both recessive with respect to plant color, and R^r and r^r on the other hand, both dominant for plant color, apparently always differentiate between colored and colorless anthers and silks in the purple-red series of plant colors, and, when *B* is absent, determine whether or not anthocyanin forms in any part of the plant. The pair *B b* influences mainly the intensity of pigmentation. Thus, purple, *A B Pl*, is more strongly colored than is weak purple, $A\ B^w\ Pl$, which in turn is more strongly colored than is dilute purple, *A b Pl*. The same relation holds between sun red, *A B pl*, weak sun red, $A\ B^w\ pl$, and dilute sun red, *A b pl*. Brown color shows very little in *a b Pl* but is strongly developed in *a B Pl*. A similar difference, however, exists between the slight brown of *a B pl* and the full brown of *a B Pl*. In the one case in which an effect of *C c* has been noted, *C* acted as an intensifier of color.

There are somewhat marked differences between the several factor pairs with respect to the stage of plant development at which their influence is expressed. Seedlings of purple, sun red, dilute purple, and dilute sun red normally exhibit no characteristic differences in intensity or extent of pigmentation. The *B b* and *Pl pl* pairs, which differentiate these color types so sharply at a later stage of growth, do not, therefore, come into expression early. All of these types are more highly colored late in their growth period than they are as seedlings, but the later changes are much more pronounced, for instance, in dilute purple than in dilute sun red, and somewhat more so in purple than in sun red. Apparently, *Pl* exerts its influence comparatively late, but under the intensifying influence of *B*, even *Pl* expresses itself fairly early.

The several factor pairs differ more or less with respect to the particular plant parts affected. Differences in the expression of *B*, B^w, and *b* are more apparent in the husks and the sheaths, particularly the upper sheaths, than elsewhere. When plants of the genotype *a B pl*, commonly classed as green, show any brown, the color is limited to the sheaths and the outer husks. The difference between purple (*A B Pl*) and sun red (*A B pl*) on the one hand, and dilute purple (*A b Pl*) and dilute sun red (*A b pl*) on the other, is more pronounced in the husks and the sheaths than elsewhere. Little difference is apparent between the two groups with respect to the color of anthers, glumes, silks, and the like. The pair

Pl pl is perhaps expressed most definitely in the color of anthers, tho the expression is by no means limited to them. Purple (*A B Pl*) and dilute purple (*A b Pl*) differ from sun red (*A B pl*) and dilute sun red (*A b pl*), not merely in having purple rather than pink anthers, but also in the coloration of their inner husks, their culms, and the like. What little brown color is seen in *a b Pl* is limited almost wholly to the staminate inflorescence. The staminate inflorescence of purples, *A B Pl*, and of browns, *a B Pl*, is strongly colored, but that of dilute purple, *A b Pl*, except for anther color, is not very different from what is seen in dilute sun red, *A b pl*. The *Pl* factor, when associated with r^{ch}, is expressed in the pericarp as cherry in purple and in dilute purple, and as brownish in brown and in green of the genotype *a b Pl*.

Factors *B b* and *Pl pl* are not known to be concerned with aleurone color. All the other factors affecting plant color are aleurone-color factors also. Of these the pair *Pr pr* influences anther color of purple and dilute purple, and to some degree the husk color as well. The pair *C c* has been observed to affect the leaf color of mature plants of the sun red type. The pair *A a* is expressed to some degree in all such parts as culms, sheaths, husks, glumes, anthers, and silks. The pericarp, if a pericarp factor *P* is present, is red with *A* and brown with *a*, or if r^{ch} and *Pl* are present, it is cherry with *A* and brownish with *a*. The *R* series of factors influences many plant parts. With duplex R^g or r^g, no color develops in any part of the plant, except the aleurone, provided *B* is absent. With *B* these factors give colorless anthers and silks merely. Factors R^r and r^r, if *A* also is present, affect practically all plant parts in which anthocyanic pigments ever develop, but are not known to have any influence on the color of the pericarp. The factor r^{ch} is, however, concerned with pericarp color provided *Pl* also is present. This factor has a marked influence on the amount of color that forms in the leaves, particularly of dilute purple and dilute sun red.

It is of no little interest that the *R* series of factors, which behaves as a group of multiple allelomorphs with regard to plant color, usually acts as a simple pair in respect to aleurone color.[6] Moreover, some of these factors act as dominants with respect to aleurone color and as recessives with respect to plant color, while the dominance of others is

[6] There is some evidence that at least one aleurone-color pattern is dependent on an allelomorph of *R r*, the three thus constituting a group of triple allelomorphs affecting aleurone-color development.

the reverse of this. For example, r^r and r^{ch} are recessive for aleurone and dominant for plant color, and R^g is dominant for aleurone and recessive for plant color, while R^r is dominant and r^g recessive for both aleurone and plant colors.

SUMMARY

In this account, six major plant-color types of maize, purple, sun red, dilute purple, dilute sun red, brown, and green (colorless), together with the subtypes, weak purple, weak sun red, green-anthered purple, green-anthered sun red, and five genotypes of green, are described and illustrated, and their environmental and genetic relations are discussed.

The sun red and dilute sun red types are shown to be dependent on light for the development of their color, while the purple, dilute purple, and brown types develop their characteristic colors in darkness. Diversities of temperature and of soil moisture are shown to have no direct effect on the formation of maize plant colors but to have an indirect relation to them thru their influence on soil fertility, which in turn bears a definite relation to the development of the purple-red series of plant color, anthocyanins, but little or no relation to brown. Sun colors particularly are shown to be markedly intensified by infertile soil. It is noted that the several types of the purple-red series are sharply differentiated when grown on fertile soil, but that their characteristic differences are largely masked by growth on infertile soil, while the brown-green series is most readily distinguished from the purple-red series, especially in the seedling stage, if grown on infertile soil. It is suggested that the effect of infertile soil may be due to a deficiency of nitrogen, and perhaps of phosphorus. Observations indicating a close connection between the accumulation of carbohydrates and strong coloration are reported, and the inference that the effect of infertile soil is brought about thru checking growth without inhibiting photosynthesis, thus allowing an accumulation of carbohydrates, is discussed.

In an attempt at a genetic analysis of the several plant-color types, data accumulated during a period of some ten years, and involving an examination of approximately 680 progenies and not less than 48,000 individual plants, are reported. As an interpretation of the results obtained from the more complex crosses, the allelomorphic pairs $A\ a$ and $Pl\ pl$, and the multiple allelomorphs B, B^w, b^s, b, and R^r, R^g, R^{rg},

r^r, r^g, r^{ch}, are assumed and genetic formulae are assigned to the several color types as follows: purple, *A B Pl*; sun red, *A B pl*; dilute purple, *A b Pl*; dilute sun red, *A b pl*; brown, *a B Pl*; green, *a B pl*, *a b Pl*, *a b pl*; all these having in addition R^r, r^r, or r^{ch}. The factor R^{rg} is assumed to be the causal factor for green anthers and silks in purple, sun red, dilute purple, and dilute sun red types, and R^g and r^g are assumed to have the same effect on purple and sun red and to insure colorlessness (green type) thruout in what would otherwise be dilute purple and dilute sun red, the *R* series having no effect on brown, except for r^{ch}, which intensifies brown as well as purple and dilute purple. Of the *R* series, R^r is dominant and r^g is recessive for both plant and aleurone color, r^r and r^{ch} are dominant for plant and recessive for aleurone color, R^g is recessive for plant and dominant for aleurone color, and R^{rg} is dominant for aleurone color and also for plant color except of the anthers and the silks, for which it is recessive. The *A a* pair is concerned with both aleurone and plant color, and the aleurone pairs *C c* and *Pr pr* are assumed to exert a modifying effect on certain plant colors.

The principal hypotheses involved are shown to be in keeping with observed facts when subjected to practically all the available genetic tests, such as backcrosses of F_1 with multiple recessives, behavior of F_2 types in later generations, intercrosses of the several F_2 types, relation of aleurone color to plant color, linkage of certain plant-color types with normal- and liguleless-leaf types and of other plant-color types with yellow and white endosperm. Approximately 32 per cent of crossing-over is reported between *B b* and *Lg lg* and about 20 to 30 per cent between *Pl pl* and *Y y*.

LITERATURE CITED

Collins, G. N. Gametic coupling as a cause of correlations. Amer. nat. 46:569–590. 1912.

Czartkowski, Adam. Anthocyanbildung und Aschenbestandteile. Deut. bot. Gesell. Ber. 32:407–410. 1914.

East, E. M., and Hayes, H. K. Inheritance in maize. Connecticut Agr. Exp. Sta. Bul. 167:1–142. 1911.

Emerson, R. A. Genetic correlation and spurious allelomorphism in maize. Nebraska Agr. Exp. Sta. Ann. rept. 24:58–90. 1911.

——— The inheritance of the ligule and auricles of corn leaves. Nebraska Agr. Exp. Sta. Ann. rept. 25:81–88. 1912.

——— A fifth pair of factors, *A a*, for aleurone color in maize, and its relation to the *C c* and *R r* pairs. Cornell Univ. Agr. Exp. Sta. Memoir 16:225–289. 1918.

Gernert, W. B. The analysis of characters in corn and their behavior in transmission, p. 1–58. (Published by the author, Champaign, Illinois.) 1912.

Knudson, Lewis. Influence of certain carbohydrates on green plants. Cornell Univ. Agr. Exp. Sta. Memoir 9:1–75. 1916.

Lindstrom, E. W. Chlorophyll inheritance in maize. Cornell Univ. Agr. Exp. Sta. Memoir 13:1–68. 1918.

Sando, Charles E., and Bartlett, H. H. The occurrence of quercetin in Emerson's brown-husked type of maize. Journ. agr. research. 1921. (In press.)

Webber, Herbert J. Correlation of characters in plant breeding. Amer. Breeders' Assoc. 2:73–83. 1906.

Wheldale, M. On the formation of anthocyanin. Journ. genetics 1:133–158. 1911.

Memoir 37, *A Modified Babcock Method for Determining Fat in Butter*, the second preceding number in this series of publications, was mailed on December 10, 1920.

APPENDIX

TABLE 1. F_1 PROGENIES OF PURPLE Ia x GREEN VIc

Pedigree nos.		Number of F_1 plants (Purple Ia)
P_1	F_1	
724–1 x 722–1	857	18
1121–8 x 1122–7	1420, 1512, 2022	40
1122–5 x 1121–2	1419, 1511	36
1525–5 x 1546–5	2056	17
Total, 4 progenies		111

TABLE 2. F_2 PROGENIES OF PURPLE Ia x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	1419– 1	1513	94	22	26	12	20	23
	1511– 1	2018	61	19	13	4	13	9
	1512–12	2020	54	16	23	7	21	7
	2022– 3	4012, 4013	7	6	6	3	4	1
	2056– 6	2415, 2416, 4284	39	13	17	4	16	10
	–11	2417, 2418, 2553–2559, 4001–4007	96	22	24	3	26	8
	–16	2412, 4066, 4067	17	3	11	1	8	7
	Total, 7 progenies		368	101	120	34	108	65
2	1514–24	2054	20	7	8	1	5	2
	–31	2055	22	4	4	2	2	6
	2000– 8	2419, 4065	92	29	21	8	19	25
	2019–28	4281	24	8	4	2	4	6
	–34	4282	21	6	4	4	7	4
	2906– 1	5303	17	7	5	2	6	3
	2907– 1	5290–5293, 7050, 7051	93	26	34	7	34	23
	– 7	5299, 5300, 7054, 7055	105	46	30	10	38	31
	2981– 2	5066, 5067	17	4	5	1	8	3
	– 5	5068, 5069	20	6	2	1	2	3
	4020– 7	5712, 6810	109	44	26	12	31	33
	4032– 1	5739	16	5	3	2	3	2
	– 3	5084	15	7	5	4	4	3
	– 4	5087	13	5	4	1	7	7
	Total, 14 progenies		584	204	155	57	170	151
	Total, 21 progenies		952	305	275	91	278	216

TABLE 3. F_2 PROGENIES OF PURPLE x GREEN BACKCROSSED WITH GREEN (Ia x VIc) x VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1 x VIc	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	1420– 1 x 1430– 3	1514.....	12	19	15	16	14	45
	1511– 1 x 1516– 1	2019.....	18	8	12	8	18	50
	1512–12 x –14	2021.....	23	18	16	10	13	44
	2056–16 x 1995– 6	2413, 4068	4	10	8	6	8	18
	Total, 4 progenies.....		57	55	51	40	53	157
2	2867–69 x 4032– 1	5740.....	7	4	6	3	4	10
	2906– 1 x 2887–10	5305.....	7	5	2	8	3	9
	2907– 1 x –22	5296,7052, 7053...	10	11	10	11	9	26
	– 7 x 4032–41	5301, 5302	16	16	16	19	25	47
	4020– 7 x 2888–13	5714.....	2	9	9	4	4	18
	4032– 2 x 2921– 4	5094.....	8	6	18	12	15	33
	3 x 2888– 5	5086.....	19	16	21	12	18	46
	3 x 2922–16	5085.....	14	10	22	16	8	34
	4 x 2888– 1	5089.....	5	15	12	17	18	45
	4 x 2921– 4	5090–5092	25	13	19	18	15	54
	Total, 10 progenies.....		113	105	125	120	119	322
	Total, 14 progenies.....		170	160	176	160	172	479

TABLE 4. F_1 PROGENIES OF DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_1 plants			
	P_1	F_1	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2025–23 x 2192–14..	2333, 4314.....	25	.....	.....	.....
	2029– 8 x 1945–11..	2304, 3596.....	30	.....	.....	.....
	– 8 x 2013–19..	2311.....	17	.....	.....	.....
	– 8 x 2014– 8..	2310, 4034.....	5	.....	.....	.....
	2031–10 x 1945–10..	2309.....	16	.....	.....	.....
	–32 x 2012– 1..	2322.....	20	.....	.....	.....
	2948–16 x 4042– 2..	5168, A108, A120....	79	.....	.....	.....
	4253– 2 x 4299– 2..	5528, 6748A.....	46	.....	.....	1
	4305– 5 x 4042– 2..	5193, 5194.....	24	.....	.....	.....
	Total, 9 progenies.....		262	.....	.....	1
2	2018–69 x 2192–18..	2386, 4301.....	30	35	.....	.....
	2030–13 x –14..	4319.....	7	6	.....	.....
	2031–20 x 2012– 1..	2325, 2326, 2543, 2544, 2950, 2951..	55	55	.....	.....
	2043– 2 x 2026–17..	2347, 4326.....	15	18	.....	.....
	2049–14 x 2192–14..	2336, 4327.....	24	21	.....	.....
	2473– 3 x 2341– 1..	4029.....	4	2	.....	.....
	4370– 5 x 3000– 2..	4746, 4747.....	8	10	.....	.....
	Total, 7 progenies.....		143	147	.....	.....
3	2023–19 x 2192–12..	2332, 4311.....	19	.....	26	.....
	–23 x –12..	2330, 4310.....	15	.....	16	.....
	2027– 9 x –14..	2334, 4316.....	15	.....	18	.....
	2410– 4 x 2417– 2..	2993, 2994.....	9	.....	6	.....
	– 6 x – 1..	2995–2998.....	23	.....	32	.....
	5500– 5 x 5130– 1..	A65.....	24	.....	25	.....
	Total, 6 progenies.....		105	.....	123	.....
4	2025–10 x 2192–14..	4315.....	1	2	6	3
	2029–27 x 2012– 1..	2319, 4055.....	4	3	5	5
	–32 x – 1..	2316, 4318.....	3	5	6	3
	–34 x 2014– 8..	2314, 4054.....	1	1	2	6
	Total, 4 progenies.....		9	11	19	17

TABLE 5. F_2 PROGENIES OF DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	2310– 2..	4036, 4037.	15	7	6	3	3	7
	2332– 1..	2999, 3000.	31	9	8	1	15	7
	2950– 1..	5036, 5037.	36	12	12	2	10	9
	– 4..	5030, 5031.	37	15	13	3	8	13
	–17..	5034, 5035.	32	5	14	6	13	9
	–19..	5032, 5033.	39	12	10	3	12	5
	2995– 7..	5000–5007.	75	24	20	5	21	17
	2996– 1..	5008, 5009.	150	50	58	20	48	45
	4029– 2..	5095.....	61	23	11	5	22	11
	4034– 1..	5098, 5099.	46	12	19	7	17	7
	– 2..	5104.....	42	20	17	8	13	21
	5193– 1..	A135.....	20	5	4	3	4	1
	5194– 5..	A136.....	10	3	12	1	4	7
	5528– 8..	6748B.....	49	11	14	4	12	18
	Total, 14 progenies....		643	208	218	71	202	177
2	2973– 5..	5056–5062.	55	23	21	6	17	17
	2974– 9..	5063–5065.	75	24	23	10	18	22
	4046– 3..	5157, 5158.	20	11	6	5	7	4
	5173– 4..	A128.....	19	5	8	1	9	9
	S17–19...	7762.....	35	11	5	1	14	4
	Total, 5 progenies		204	74	63	23	65	56
	Total, 19 progenies....		847	282	281	94	267	233

TABLE 6. F_2 PROGENIES OF DILUTE SUN RED x BROWN BACKCROSSED WITH GREEN (IVa x V) x VIc

Pedigree nos.		Number of F_2 plants					
F_1 x VIc	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
2310– 1 x 2411– 6..	4035.....	3	4	3	6	2	17
2922–13 x 4029– 2..	5652, 5653..	22	13	19	24	27	75
4029– 2 x 2921–10..	5096.....	9	18	12	8	13	51
4034– 1 x 2922–16..	5100–5103..	10	13	17	11	9	33
– 2 x 2921–68..	5105.....	12	5	5	4	4	16
5813–25 x 5528– 8..	6749.....	3	0	2	4	1	9
A129–12 x A108– 6..	A243, A244.	25	19	20	15	23	48
To al, 7 progenies.....		84	72	78	72	79	249

TABLE 7. F_2 PROGENIES OF PURPLE x GREEN AND DILUTE SUN RED x BROWN BACKCROSSED WITH DILUTE SUN RED (Ia x VIc) x IVa, AND (IVa x V) x IVa

Group	Pedigree nos.		Number of F_2 plants			
	F_1 x IVa	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2056–16 x 1992–13	2414, 4069, 4070	18	16	21	15
	2889–54 x 4032– 1	5741–5744	24	27	21	24
	Total, 2 progenies		42	43	42	39
2	6730 – 9 x 6748A– 5	7467, 7828	87	79	75	71
	6748A–16 x 6751 –22	7229	40	32	42	41
	–18 x –22	7230	28	28	26	35
	–19 x – 1	7231	40	33	30	36
	–20 x – 1	7232	30	25	32	20
	A121– 6 x A108– 8	A241, A242, A461, A462	28	25	38	45
	L188– 1 x 5528 – 8	6786, 82	4	5	3	4
	Total, 7 progenies		257	227	246	252
	Total, 9 progenies		299	270	288	291

TABLE 8. F_3 PROGENIES OF SELFED AND BACKCROSSED F_2 PURPLE PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
1	1513–41	2045, 4008, 4009	32	14	8	3	6	(VIa,b,c) 8
	–68	2048, 2475, 4010, 4011	61	14	21	7	18	10
	2018– 2	4268	15	7	5	0	6	4
	– 9	4271	13	8	6	1	3	3
	2020– 1	4275	16	8	6	2	7	3
	4065– 6	5210	9	3	3	0	1	1
	–62	5213	25	7	6	2	4	1
	–63	5214	22	5	5	1	12	4
	Total, 8 progenies		193	66	60	16	57	34
	2020-117 x 2043-11	4279	4	4	11	4	4	18

TABLE 8 (*continued*)

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
2	1513 – 35	2046	11	4	6	1	.....	.....
	–138	2052	16	6	1	2	.....	.....
	2018 – 6	4270	25	9	5	5	.....	.....
	4066 – 3	5216, 5217	38	14	13	5	.....	.....
	6748B– 41	7400	12	3	4	0	.....	.....
	Total, 5 progenies		102	36	29	13	.....	.....
3								(VIa)
	1513– 59	2047	20	6	.....	.....	5	3
	– 92	2053	24	6	.....	.....	3	3
	–133	2049	16	4	.....	.....	9	2
	4037– 5	5136, 5137	35	15	.....	.....	6	7
	Total, 4 progenies		95	31	.....	.....	23	15
	2020–46 x 2200– 8	4283	5	1	.....	.....	3	3
	2411– 4 x 2412– 2	2981–2983	8	6	.....	.....	2	10
	2443– 2 x – 2	2984–2986	7	8	.....	.....	7	4
	2922–12 x 4037– 5	5138–5140	34	43	.....	.....	32	36
	Total, 4 progenies		54	58	.....	.....	44	53
4								(VIb)
	2018–27	4280	19	.....	5	.....	9	1
	2020–15	4276	19	.....	3	.....	9	3
	–30	4277	29	.....	7	.....	6	4
	4001–12	5079	11	.....	4	.....	4	1
	4005– 5	5010–5013	195	.....	77	.....	71	29
	4066– 5	5218	29	.....	12	.....	6	3
	5099–22	A78	16	.....	6	.....	6	1
	Total, 7 progenies		318	.....	114	.....	111	42
5	1513– 2	2050	19	3	.....	.....	.....	.....
	–110	2051	16	6	.....	.....	.....	.....
	2018– 92	4273	31	13	.....	.....	.....	.....
	–119	4269	33	9	.....	.....	.....	.....
	2412– 1	4033	40	13	.....	.....	.....	.....
	Total, 5 progenies		139	44	.....	.....	.....	.....

TABLE 8 (*concluded*)

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
5 (*continued*)	2411–5 x 2412–1	4032	4	1	.....	.....	.....	.....
	2434–1 x –1	4019, 4020	8	8	.....	.....	.....	.....
	Total, 2 progenies		12	9	.....	.....	.....	.....
6	4006– 1	5014, 5015	126	.....	37	.....	.....	.....
	4065–14	5209	42	.....	12	.....	.....	.....
	Total, 2 progenies		168	.....	49	.....	.....	.....

TABLE 9. F_4 PROGENIES OF SELF-POLLINATED PURPLE PLANTS OF F_3 LOTS CONSISTING OF COLOR TYPES Ia, IIIa, V, AND VIb

Group	Pedigree nos.		Number of F_4 plants			
	F_3	F_4	Purple Ia	Dilute purple IIIa	Brown V	Green VIb
1	5010– 7	7020, 7021	51	15	12	8
	– 9	7022, 7023	53	19	22	6
	–11	7024, 7025	46	17	26	5
	5011– 4	7028, 7029	35	17	14	1
	Total, 4 progenies		185	68	74	20
2	4276–32	5181, A170	46	12	.....	.....
	5010– 2	7092	14	2	.....	.....
	5011– 6	7091, 6837	28	14	.....	.....
	Total, 3 progenies		88	28	.....	.....
3	5011–2	7026, 7027	67	.....	21	.....

TABLE 10. F_3 PROGENIES OF F_2 SUN RED PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Sun red IIa	Dilute sun red IVa	Green
					(VIa, c)
1	1513–152	2038, 2474, 4292	38	11	11
	2018– 4	4286	19	7	*16
	– 39	4287	30	12	11
	– 44	4288	9	4	6
	– 56	4289	30	8	11
	Total, 5 progenies		126	42	55
	1513–100 x 1516–20	2039, 4293	7	8	†23
	2018– 56 x 2043–11	4290	3	1	7
	2020–118 x –11	4291	4	9	20
	Total, 3 progenies		14	18	50
2	4037–2	5126, 5127	23	9	.....
					(VIa)
3	4037–24 x 2921–15	5128, 5129, 7074	50	.....	43

* Plus one brown V plant.
† Plus one purple Ia plant.

TABLE 11. F_3 PROGENIES OF F_2 DILUTE PURPLE PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Dilute purple IIIa	Dilute sun red IVa	Green
					(VIb, c)
1	2018–18	4296	14	6	12
	4037– 9	5117, 5118	38	9	16
	5099– 7	A77	35	15	19
	A120– 13	A229	8	1	3
	Total, 4 progenies		95	31	50
	2922–16 x 4037–9	5119–5121	21	25	57
2	4066–9	5219	57	21	.....
					(VIb)
3	4037–14	5122, 5123	16	.....	5
	5095–29	A63	9	.....	1
	5290–12	7056, 7057	60	.....	14
	Total, 3 progenies		85	.....	20
4	4065–50	5212	21	.....	.....

TABLE 12. F_3 PROGENIES OF F_2 DILUTE SUN RED PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Dilute sun red IVa	Green VIc
1	4036–9	5115	16	6
	6750–4	7247, 7399	34	8
	A120–8	A228	12	3
	Total, 3 progenies		62	17
2	4036–8	5116	27	.....
	4042–2	5166	65	.....
	Total, 2 progenies		92	.....
	2922–18 x 4042–2	5169–5171	69	.....

TABLE 13. F_3 PROGENIES OF F_2 BROWN PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Brown V	Green
				(VIa, b, c)
1	1513–12	2025, 4313	33	35
	2020– 8	4309	16	13
	–47	4305	23	*11
	–98	4307	16	8
	4065–12	5211	8	7
	Total, 5 progenies		96	74
				(VIa, b)
2	1513– 16	2030	21	6
	– 39	2026	23	10
	–143	2027	30	9
	–194	2023	32	9
	2018– 69	2539, 2540, 4299, 4300	94	25
	– 96	2338, 4302	64	20
	2020– 57	4306	29	9
	4037– 6	5130, 7076	46	12
	6748B–37	7401	15	4
	Total, 9 progenies		354	104
	4037–6 x 2922–6	5131–5133	34	41

* Plus one sun red IIa plant.

TABLE 14. PROGENIES OF F_2 AND F_3 BROWN PLANTS, OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V, CROSSED WITH DILUTE SUN RED IVa PLANTS

Group	Pedigree nos.		Number of F_3 plants			
	F_2 x IVa	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2018–69 x 2192–18..	2386, 4301.....	30	35	.....	.....
	4370– 5 x 3000– 2..	4746, 4747.....	8	10	.....	.....
	Total, 2 progenies.....		38	45	.....	.....
2	2410–4 x 2417–2....	2993, 2994.....	9	.....	6	.....
	–6 x –1....	2995–2998.....	23	.....	32	.....
	Total, 2 progenies.....		32	.....	38	.....
3	5095–20 x L170–1 ..	S17.....	15	.....	.....	.....
	F_3 x IVa	F_4	Number of F_4 plants			
4	2025–10 x 2192–14..	4315.....	1	2	6	3
5	2030–13 x 2192–14..	4319.....	7	6	.....	.....
	2043– 2 x 2026–17..	2347, 4326.....	15	18	.....	.....
	Total, 2 progenies.....		22	24	.....	.....
6	2023–19 x 2192–12..	2332, 4311.....	19	.....	26	.....
	–23 x –12..	2330, 4310.....	15	.....	16	.....
	2027– 9 x –14..	2334, 4316.....	15	.....	18	.....
	5500– 5 x 5130– 1..	A65.....	24	.....	25	.....
	Total, 4 progenies.....		73	.....	85	.....
7	2025–23 x 2192–14..	2333, 4314.....	25	.....	.....	.....
	4253– 2 x 4299– 2..	5528, 6748A.....	*46	.....	.....	.....
	4305– 5 x 4042– 2..	5193, 5194.....	24	.....	.....	.....
	Total, 3 progenies.....		95	.....	.....	.....

* Plus one dilute sun red IVa plant.

TABLE 15. F_3 PROGENIES OF SELFED AND BACKCROSSED GREEN PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree Nos. F_2	Pedigree Nos. F_3	Number of F_3 plants (Green)
			(VI)
1	1513 - 42	2033	22
	-106	2036	18
	-111	2032	13
	4036 - 6	5114	22
	4037 - 29	5124, 5125	42
	4066 - 4	5215	32
	5095 - 30	A62	8
	674SB- 11	7402	22
	Total, 8 progenies		179
2	1514- 9	2034	20
	-37	2035	19
	-47	2037	18
	6749- 1	7242	19
	- 4	7243	20
	Total, 5 progenies		96
			(VIa)
3	2019- 40	2364, 4356	*26
	- 63	2356, 4355	24
	- 92	2384	10
	- 98	2374	10
	-106	2357	15
	Total, 5 progenies		85
			(VIb)
4	2019-33	2349, 4354	29
	-57	2373, 4353	34
	-73	2379	10
	-84	2383	14
	Total, 4 progenies		87
			(VIc)
5	2019-17	2395	14
	-25	2348, 4357	29
	Total, 2 progenies		43

* Plus one brown V plant.

TABLE 16. F_1 PROGENIES OF CROSSES OF GREEN VIa, VIb, AND VIc WITH DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_1 plants		
	P_1	F_1	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2047–25 x 2192–14	2392	16	.....	.....
	2049–12 x –14	2393	20	.....	.....
	4300–14 x 4364– 1	5198	52	.....	.....
	4307– 9 x 4042– 2	5183, 5184	60	.....	.....
	Total, 4 progenies		148	.....	.....
2	2036–9 x 2192–14	4320	.....	9	.....
	4725–2 x 5095–30	A96, A97	.....	67	.....
	Total, 2 progenies		.....	76	.....
3	2025–12 x 2192–14	2335	.....	.....	24
4	2019– 29 x 1946– 4	2398, 2399	30	.....	19
	– 40 x 2192–18	2365, 4340	5	.....	5
	– 63 x –18	2358, 4349	11	.....	10
	– 92 x 1945–10	2385	13	.....	12
	– 98 x –10	2375	11	.....	12
	–104 x 2012– 1	2363	13	.....	12
	–106 x 2192–18	2359, 4351	27	.....	15
	Total, 7 progenies		110	.....	85
5	2019–33 x 2192–18	2352, 4342	.....	5	4
	–51 x 1946– 4	2361, 4347	.....	19	15
	–57 x 2192–18	2369, 2370, 4345	.....	8	14
	–73 x 1945–11	2377, 2378	.....	2	6
	–84 x –10	2382, 4352	.....	22	26
	Total, 5 progenies		.....	56	65
6	2019–17 x 1945–11	2396, 2397	.....	.....	43
	–19 x –11	2381	.....	.....	19
	–25 x –11	2351, 4344	.....	.....	44
	Total, 3 progenies		.....	.....	106

TABLE 17. F_2 AND BACKCROSS PROGENIES OF DILUTE SUN RED IVa x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Dilute sun red IVa	Green VIc
1	1983–34	4502, 4503	27	11
	2854– 7	4677–4679	199	73
	2866– 1	6471, 6472	43	15
	Total, 3 progenies		269	99
2	F_1 x VIc			
	2854–13 x 2887–69	6325, 6326	87	96
	–16 x –69	6319–6321	42	45
	2861– 1 x –41	4686–4688	93	100
	2866– 2 x 2888– 2	5748–5750, 6485–6487	90	74
	4707–82 x 4685– 1	6533–6535	45	43
	Total, 5 progenies		357	358

TABLE 18. F_1 PROGENIES OF INTERCROSSES BETWEEN GREEN PLANTS, VIa, VIb, AND VIc

Group	Pedigree nos.		Number of F_1 plants	
	P_1	F_1	Brown V	Green VI
1	2019–25 x 2019–106	2354	.....	23
2	2019–25 x 2019–33	2350, 4343	.....	22
3	2019– 40 x 2019– 63	2367	.....	25
	– 98 x – 40	2376	.....	25
	–104 x –106	2362	.....	22
	Total, 3 progenies		.....	72
4	2019–57 x 2019–51	2371, 4346	.....	24
5	2019– 33 x 2019–63	2355	6	19
	– 40 x –33	2366, 4341	8	28
	– 57 x –98	2372, 4350	14	26
	– 73 x –40	2380	7	16
	–106 x –51	2360	5	16
	Total, 5 progenies		40	105

TABLE 19. F_2 PROGENIES OF CROSSES BETWEEN BROWN V AND GREEN VIc

Pedigree nos.		Number of F_2 plants	
F_1	F_2	Brown V	Green VIa, b, c
1514–12	2029	19	16
–23	2031	22	13
–38	2028	25	16
2983– 7	5071, 5072	40	44
–11	5070	15	11
2986– 4	5078	21	8
– 9	5077	46	36
4035–35	5110	14	6
4068– 4	5225	53	23
–10	5227	24	20
–11	5226	38	30
Total, 11 progenies		317	223

TABLE 20. F_3 PROGENIES FROM F_2 BROWN PLANTS OF THE CROSS BROWN V x GREEN VIc

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Brown V	Green VI
1	2031–28	4323	19	.....
	–32	2323	10	.....
	Total, 2 progenies		29	.....
2	2031–20	2324, 2541, 2542, 2948, 2949	82	34
	–29	2327, 2328	18	6
	Total, 2 progenies		100	40
3	2029–27	2320, 4321	17	20
	–34	2315, 4322	22	19
	Total, 2 progenies		39	39

TABLE 21. F_2 PROGENIES OF THE CROSSES SUN RED IIa x GREEN VIc AND DILUTE SUN RED IVa x GREEN VIa

Group	Pedigree nos.		Number of F_2 plants		
	F_1	F_2	Sun red IIa	Dilute sun red IVa	Green VIa, c
1	1514-32	2040, 4294	53	16	19
	-76	2041, 4295	40	14	23
	2083- 1	4336, 4337	24	10	11
	- 2	4338, 4339	26	4	11
	2981- 3	4992, 4993	91	42	45
	- 4	4994-4996	203	55	84
	4014- 1	5554-5557	83	33	33
	- 3	5559-5563	47	13	13
	4019- 2	5691, 5692	28	6	18
	- 4	5685, 5686	20	2	12
	4020- 1	5708	28	12	10
	4035- 3	5111-5113	49	21	24
	4040- 2	5148, 5149	14	5	13
	6661- 9	7379	35	16	21
	6662- 1	7381	44	9	29
	- 8	7380	42	10	17
	Total, 16 progenies		827	268	383
2	2398- 2	4426, 4427	28	9	12
	4029- 1	5097	31	18	21
	4776- 1	6951-6953	127	38	71
	4780- 9	6960, 6961	92	25	42
	-11	6954-6956	65	30	33
	Total, 5 progenies		343	120	179
3	1416- 1 x 1430- 1	1494, 2074	39	39	92
	2888-22 x 4019- 2	5694B, 5695A	16	14	22
	2922-18 x 4014- 3	5563-5565	30	26	68
	4014- 1 x 2922- 1	5558	3	3	10
	4019- 2 x 2888- 1	5697, 5698	15	14	22
	- 4 x - 1	5689, 5690	24	13	31
	4020- 1 x 2887-69	5709	7	14	22
	Total, 7 progenies		134	123	267
4	2921-15 x 4029- 1	5654-5656	28	37	80
	4774- 1 x 4710-45	6945, 6946	78	71	151
	4781- 2 x 4707-35	6967, 6968	54	76	132
	4782- 5 x -18	6972, 6973	103	88	195
	-13 x -15	6974-6978, 7667, 7668	80	101	191
	4789- 4 x -19	6989, 6990	50	43	108
	6661- 9 x 6690-17	7328, 7329	17	17	38
	6790- 5 x 6809-18	7293	32	32	67
	Total, 8 progenies		442	465	962

TABLE 22. F_2 PROGENIES OF THE CROSSES DILUTE PURPLE IIIa x GREEN VIc AND DILUTE SUN RED IVa x GREEN VIb

Group	Pedigree nos.		Number of F_2 plants		
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c
1	1514–61	2044, 2560, 2561	44	14	16
	2019–10	2425, 2931, 2932	19	3	6
	2072– 1	4333, 4334	38	12	10
	– 9	4335	22	13	7
	2956– 2	4899–4904	153	58	73
	4035–33	5107	50	16	24
	4068– 6	5222	46	18	26
	–17	5223	44	15	11
	Total, 8 progenies		416	149	173
2	2361– 1	4424, 4425	14	4	4
	4070– 6	5235, 5236	133	51	52
	–11	5237, 5238	62	21	19
	5269– 3	6696, 6697	30	11	15
	A96–14	A416, A417	15	6	4
	A97–29	A407, A408	30	9	13
	Total, 6 progenies		274	102	107
	6790–1 x 6809–8	7292	26	20	56

TABLE 23. F_2 PROGENIES OF THE CROSS SUN RED IIa x BROWN V

Pedigree nos.		Number of F_2 plants			
F_1	F_2	Purple Ia	Sun red IIa	Brown V	Green VIa
5192–1	A99	14	4	5	1
–2	7767	37	5	9	2
–3	7766, S23	69	20	23	7
Total, 3 progenies		120	29	37	10

TABLE 24. F_2 PROGENIES OF THE CROSS SUN RED IIa x DILUTE SUN RED IVa

roup	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Sun red IIa	Dilute sun red IVa
1	413- 1	1298	40	13
	617-11	1235	15	4
	1520- 9	2017	31	8
	2065- 1	4330	14	5
	- 2	2431, 4331	48	15
	2414- 2	2987-2992	36	9
	2975- 4	4983-4986, 7001, 7002	373	123
	4028- 3	5643-5646	22	7
	4040- 3	5150, 5151	41	8
	4332-26	5491-5493	55	16
	4787- 4	6779-6782	166	50
	5165- 2	A114	55	20
	7224- 4	8118, 8119	43	12
	7359- 1	8170, 8171	9	3
	7854- 1	8094, 8095	35	15
	A119- 4	A227	15	6
	Total, 16 progenies		998	314
2	F_1 x IVa			
	2065- 1 x 2043- 2	4329	27	30
	- 2 x - 2	2432, 4332	6	13
	4714-11 x 4774- 1	6943, 6944, 7676, 7677	173	133
	7224- 9 x 7225- 7	8115, 8116	196	180
	7354- 1 x 7315- 5	8250, 8251	86	96
	7770- 1 x 7768-172	8731	16	14
	- 5 x -172	8732	17	11
	A140-14 x A105- 6	A252, A468	92	87
	L1773-15 x L2049- 11	8741	46	37
	-20 x - 10	8742	41	39
	L1844-14 x L2048- 24	8743	37	41
	L2063- 5 x - 8	8746	56	48
	-26 x L2049- 3	8745	7	7
	L2064- 2 x L2048- 22	8744	11	6
	Total, 14 progenies		811	742

TABLE 25. F_3 PROGENIES OF F_2 SUN RED AND DILUTE SUN RED PLANTS OF THE CROSS SUN RED IIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Sun red IIa	Dilute sun red IVa
1	2990– 1	5776–5778	.....	10
	4133–26	5366	.....	40
	Total, 2 progenies		.....	50
2	2991–1	5779, 5780	10	.....
	–4	5781	9	.....
	Total, 2 progenies		19	.....
	7001–7 x 7002–11	7684, 7685	101	.....
3	1235– 1	1633–1635, 2009	23	10
	1298–14	2011	14	2
	2987– 2	4997, 4998, 6999, 7000	324	111
	– 9	4999	12	4
	Total, 4 progenies		373	127

TABLE 26. F_2 PROGENIES OF THE CROSS DILUTE PURPLE IIIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa
1	483– 3	884	16	5
	848– 2	1574	20	10
	2425– 2	2946, 2947	47	16
	4040– 1	5145–5147	69	26
	4070– 8	5240–5242	65	18
	–15	5234	27	8
	A119– 3	A226	17	4
	Total, 7 progenies		261	87
2	F_1 x IV			
	7317– 6 x 7322– 4	8204, 8205	18	22
	A106– 6 x A140–31	A249, A467	85	95
	A140–12 x A105– 3	A250, A251, A465, A466	83	51
	L1760– 6 x L2026–15	8739	56	63
	L1838–16 x –15	8738	33	32
	Total, 5 progenies		275	263

TABLE 27. F_1 PROGENIES OF THE CROSS SUN RED IIa x DILUTE PURPLE IIIa

Group	Pedigree nos.		Number of F_1 plants		
	P_1	F_1	Purple Ia	Sun red IIa	Dilute purple IIIa
1	1529–18 x 1542–8.....	2057.....	10	.....	.....
	6889– 1 x 6835–1.....	7627.....	14	.....	.....
	Total, 2 progenies.....		24	.....	.....
2	2903–2 x 2947–37.....	4796–4799.....	74	75	.....
3	488– 9 x 730– 3.....	842, 1389.....	18	.....	23
	1529–15 x 1549–35.....	2058.....	10	.....	6
	Total, 2 progenies.....		28	.....	29

TABLE 28. F_2 PROGENIES OF THE CROSS SUN RED IIa x DILUTE PURPLE IIIa

Pedigree nos.		Number of F_2 plants			
F_1 x IVa	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
6650– 9 x 6691– 8.....	7337.....	8	12	13	6
6651–10 x – 8.....	7338.....	7	7	5	6
7700– 4 x 7768–172.....	8723, 8724.....	9	8	6	5
–14 x –172.....	8725, 8726.....	13	10	12	15
7769– 2 x –172.....	8729, 8730.....	8	14	14	12
– 5 x 7315– 10.....	8263, 8264.....	19	22	18	15
– 7 x – 9.....	8261, 8262.....	35	37	36	24
Total, 7 progenies.....		99	110	104	83

TABLE 29. F_2 PROGENIES OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants			
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	478– 3	880	53	18	12	4
	– 4	881	49	20	11	5
	479– 1	883	43	15	12	3
	484–24	907, 1531	39	11	13	5
	–26	828, 1396, 1530	74	25	23	10
	739– 1	1312, 1549	97	27	28	8
	849– 1	1553, 1554	40	10	14	2
	850– 3	1559	10	5	0	1
	851– 2	1563	23	5	3	0
	– 3	1565	16	4	7	1
	852– 1	1566, 1567	14	5	3	1
	– 2	1568	2	0	1	1
	1564–15	4102	13	2	1	0
	2971– 3	4968–4976	65	22	23	8
	4028– 1	5647	17	5	5	0
	– 6	5082, A66	138	41	45	14
	4045– 3	5154	40	10	13	5
	4046– 4	5159, 5160	65	23	18	6
	4070– 4	5239	34	10	9	3
	–12	5232, 5233	7	1	2	2
	5165– 8	A117	40	14	13	5
	5172– 3	A126	17	7	6	1
	5179– 1	A130	42	15	11	7
	– 6	A131	12	1	4	3
	5180– 5	A133	36	11	10	3
	S12–18	A208	27	9	9	2
	Total, 26 progenies		1,013	316	296	100
2	F_1 x IVa					
	740– 2 x 732– 1	1118, 1119	39	33	36	35
	1105– 9 x 849– 3	1557, 1558	15	14	14	15
	–15 x – 1	1561, 1562	11	11	7	8
	–16 x 852– 2	1570, 1571	13	10	12	11
	1106–12 x 848– 1	1572, 1573	9	6	12	9
	1107– 4 x 851– 2	1564	4	6	8	4
	–13 x 850– 3	1560	10	7	12	8
	2922–19 x 4046– 4	5161, 5162, A142, A143	37	34	39	30
	4045– 3 x 2922–18	5155, 5156	23	17	13	17
	4046– 4 x 4042– 2	5164, 5165, A105–A107	26	23	27	26
	4729– 8 x 5165– 8	S12	7	2	5	5
	5812– 3 x 5179– 6	A132	6	9	3	5
	6785– 1 x 6784–18	7429, 7430	10	14	17	9
	– 1 x –26	7431, 7432	31	31	36	26
	7226– 2 x 7268– 2	8111	33	30	32	27
	7263– 9 x 7240–10	8008	14	15	18	14
	A140–18 x A106– 4	A248, A469	35	44	34	40
	Total, 17 progenies		323	306	325	289

TABLE 30. F_3 AND F_4 PROGENIES OF F_2 AND EQUIVALENT F_3 PURPLE PLANTS OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants			
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	271– 9	496, 497, 722	34	11	9	5
	1312–52	1535, 1577	35	13	9	1
	–59	1536, 2002	42	14	10	2
	4102– 2	5177	25	8	8	3
	5082–23	6742, A68	48	24	18	8
	–33	6743, A69	74	32	22	9
	5159– 3	A147	10	3	2	0
	Total, 7 progenies		268	105	78	28
	1312–59 x 1140–18	1575, 1576, 2000, 2001	26	25	24	21
2	271– 5	489, 490	12	5	.....	.....
	1312–87	1537	34	16	.....	.....
	5160– 8	A149	14	1	.....	.....
	Total, 3 progenies		60	22	.....	.....
	148– 1 x 271– 5	478, 479	12	6	.....	.....
	1312–87 x 1140–18	1578	9	13	.....	.....
	4102–13 x 4042– 2	5179, 5180, A113	11	12	.....	.....
	Total, 3 progenies		32	31	.....	.....
3	271– 3	492, 493	49	.....	10	.....
	1312–50	1534	44	.....	18	.....
	–81	1581	43	.....	11	.....
	4102–12	5178	26	.....	9	.....
	Total, 4 progenies		162	.....	48	.....
	271–12 x 80–8	483, 484	17	.....	15	.....
	F_3	F_4	Number of F_4 plants			
4	722– 5 x 720– 1	739, 762, 856, 1550	41	54	.....	.....
	A68–31	A339	13	5	.....	.....
5	722–3 x 719–3	740, 761, 849, 850	40	.....	44	.....
	–3 x 721–7	848	12	.....	8	.....
	Total, 2 progenies		52	.....	52	.....
6	722–1	760, 905, 1121, 1526	69	.....	.....	.....
	724–1 x 722–1	857	18	.....	.....	.....

TABLE 31. F_3 PROGENIES OF SUN RED, DILUTE PURPLE, AND DILUTE SUN RED F_2 PLANTS OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	1312- 4	1579	17	.....	.....
	-36	1542	18	.....	.....
	-55	1543	18	.....	.....
	Total, 3 progenies		53	.....	.....
	1312-38	1580, 2010	24	.....	7
	5159- 8	A148	14	.....	5
	A132- 3	A233	16	.....	7
	A133-12	A193	16	.....	5
	Total, 4 progenies		70	.....	24
2	80- 4	487, 488	.....	30	.....
	271- 4	494	.....	50	.....
	A117-12	A473	.....	17	.....
	Total, 3 progenies		.....	97	.....
	271- 1	491	.....	55	25
	- 7	495	.....	42	16
	1312- 3	1538	.....	46	16
	-65	1539, 1999	.....	36	12
	5234- 1	A86	.....	11	5
	- 8	A87	.....	27	12
	Total, 6 progenies		.....	217	86
3	80- 8	485, 486	.....	.....	19
	1312-11	1544, 1872	.....	.....	27
	A133- 3	A192	.....	.....	26
	Total, 3 progenies		.....	.....	72

TABLE 32. F_2 PROGENIES OF THE CROSS WEAK SUN RED IIb x DILUTE SUN RED IVa

Pedigree nos.		Number of F_2 plants	
F_1	F_2	Weak sun red IIb	Dilute sun red IVa
2187–21	4135, 5371	151	41
–23	4133, 5365	160	59
2189–16	4138, 5377	112	25
2190– 4	5373	122	44
– 4 x 2187– 1	4142, 5374	99	42
– 7 x –23	4143, 5376	176	75
– 7	2391, 4144, 5375, 7072	141	49
4022– 5	5715	17	7
4134–22	5370	35	14
–56	5378	89	27
4162–41	5411	17	3
5364– 6	A58	181	43
Total, 12 progenies		1,300	429

TABLE 33. F_3 PROGENIES OF THE CROSS WEAK SUN RED IIb x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Weak sun red IIb	Dilute sun red IVa
1	4136–43	5384, 6805, 7740	77	.....
2	4136–11	5383, 6802	86	39
	4138–15	5385	22	8
	5365–26	A61	13	5
	5371–23	6798	7	2
	Total, 4 progenies		128	54
3	4143–23	5392, 5393	.....	95

TABLE 34. F_2 PROGENIES OF THE CROSSES WEAK PURPLE Ib x DILUTE PURPLE IIIa, WEAK PURPLE Ib x DILUTE SUN RED IVa, AND WEAK SUN RED IIb x DILUTE PURPLE IIIa

Group	Pedigree nos.		Number of F_2 plants			
	F_1 x IIIa, IVa	F_2	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa
1	A208–15 x A445– 1..	A822.....	4	.....	4	.....
	A452– 4 x 7302– 4..	A789, A790.....	53	.....	57	.....
	–18 x –44..	A791, A792.....	84	.....	102	.....
	Total, 3 progenies.....		141	.....	163	.....
2	7507– 2 x A438– 5..	A793–A796.....	77	86	61	56
	A292–17 x A441– 6..	A788.....	55	58	49	38
	A441– 2 x 7515– 3..	A783.....	76	80	69	108
	– 6 x – 8..	A784.....	64	68	69	88
	– 7 x – 8..	A785.....	68	60	66	53
	–12 x A339–10..	A786.....	64	70	69	103
	–18 x 7515– 4..	A787.....	77	104	77	91
	Total, 7 progenies.....		481	526	460	537
3	S27–2 x 6805–9.....	7773, 7774.....	21	28	22	27

TABLE 35. F_2 PROGENIES OF THE CROSS GREEN IVg x BROWN V

Pedigree nos.		Number of F_2 plants					
F_1	F_2	Purple Ia, g	Sun red IIa, g	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI
2400– 1.....	2958–2961...	19	5	6	1	5	2
2952– 1.....	4844–4860...	59	21	8	1	14	18
–11.....	4861–4871...	43	15	7	4	11	15
–24.....	4872–4884...	42	12	9	2	15	16
–32.....	4885–4898...	62	23	12	3	20	17
2953–10.....	4822–4829...	84	24	25	8	23	30
Total, 6 progenies		309	100	67	19	88	98

TABLE 36. F_2 PROGENIES OF THE CROSS GREEN IVg x BROWN V

Pedigree nos. F_2	Number of F_2 plants									
	Purple			Sun red			Dilute purple	Dilute sun red	Brown	Green
	Purple anthers Ia	Green anthers Ig	? anthers I	Pink anthers IIa	Green anthers IIg	? anthers II	Purple anthers IIIa	Pink anthers IVa	Green anthers V	Green anthers IIIg, IVg, VI
2958–2961	14	5	0	1	1	3	6	1	5	2
4822–4829	61	12	11	10	4	10	25	8	23	30
4844–4860	42	16	1	10	7	4	8	1	14	18
Total, 3 progenies	117	33	12	21	12	17	39	10	42	50

TABLE 37. F_2 PROGENIES OF THE CROSS PURPLE Ig x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
1			(Ia, g)	(IIa, g)				(IIIg, IVg, VI)
	5534–39	6795, 6796	65	11	6	7	15	26
	6655– 6	7376	15	2	3	2	5	1
	Total, 2 progenies		80	13	9	9	20	27
2	F_1 x VIc		(Ia)	(IIa)				(VI)
	6655– 6 x 6690–17	7349	6	13	13	15	17	46
	6808–13 x 6790– 8	7290	30	16	18	16	14	49
	Total, 2 progenies		36	29	31	31	31	95
3	F_1 x IVa							
	6779–2 x 6790–8	7299, 7300	27	25	30	31	.....	.....
	6792–2 x –8	7297	29	29	19	32	.....	.....
	–8 x –8	7296	59	43	46	48	.....	.....
	Total, 3 progenies		115	97	95	111	.....	.....
4	F_1 x IVg		(Ia, Ig)	(IIa, IIg)				(IIIg, IVg)
	6656–9 x 6652–6	7344	23	15	10	15	.....	13

TABLE 38. F_2 PROGENIES OF THE CROSSES PURPLE Ig x DILUTE SUN RED IVa AND PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple Ia, g	Sun red IIa, g	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	2954–3..	5042–5045.	43	14	13	5	7
	2956–3..	4905–4914.	144	42	25	14	7
	–4..	4915–4929.	56	15	21	3	6
	Total, 3 progenies....		243	71	59	22	20
2	2421–1..	2910, 2911.	14	7	5	1	1
	–2..	2908, 2909.	26	13	4	1	0
	Total, 2 progenies....		40	20	9	2	1

TABLE 39. F_3 AND F_4 PROGENIES FROM F_2 AND EQUIVALENT F_3 PURPLES OF THE CROSS PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants				
	F_2 and F_3	F_3 and F_4	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green
1	2909–16.....	5251, 5252	(Ia, g) 9	(IIa, g) 4	3	0	0
	F_2 x IVg 2909–4 x 2884–21	5255.....	15	15	5	1	(IIIg, IVg) 9
	F_2 x VIc 2909–4 x 2887–38	5256, A94.	(Ia) 27	(IIa) 19	15	14	.....
2	5251–6.....	6708.....	31	7	.....	.....	.....
3	2909–9.....	5257, 5258	(Ig) 14	(IIg) 2	.....	.....	5
	5252–1.....	6652.....	23	9	.....	.....	9
	Total, 2 progenies.....		37	11	.....	.....	14

TABLE 39 (*concluded*)

Group	Pedigree nos.		Number of F_3 and F_4 plants				
	F_2 and F_3	F_3 and F_4	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green
3 (*continued*)	F_2, F_3 x IVg		(Ig)	(IIg)			(IIIg, IVg)
	2909– 9 x 2884–21	5259, 5260, 7007, 7008, 7060, 7061.	19	18	.....	.....	34
	4717–71 x 5252– 1	6654A.....	11	8	.....	.....	13
	5252– 1 x 5669– 3	6654B.....	4	6	.....	.....	6
	Total, 3 progenies.....		34	32	.....	.....	53
	F_2, F_3 x VIc		(Ia)	(IIa)			
	2909– 9 x 2887–38	5261, 5262.	14	11	7	11	.....
	4057– 1 x 2909– 9	5534, 6790.	16	10	13	18	.....
	5251– 1 x 5813–18	6655.....	9	16	7	14	.....
	5813–18 x 5251– 1	6656.....	5	11	6	9	.....
	Total, 4 progenies.....		44	48	33	52	.....
4			(Ig)				(IIIg)
	2909–34.....	5253, 5254, 7090.....	26	.....	.....	.....	6
	5251– 7.....	6658, 7015.	30	.....	.....	.....	12
	Total, 2 progenies.....		56	.....	.....	.....	18
	F_3 x IVg						
	4717–20 x 5251–7..	6659, 7014.	28	.....	.....	.....	27

TABLE 40. F_3 AND EQUIVALENT F_4 PROGENIES FROM F_2 AND F_3 SUN REDS AND DILUTE PURPLES OF THE CROSS PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants		
	F_2 and F_3	F_3 and F_4	Sun red	Dilute purple IIIa	Dilute sun red IVa
			(IIa)		
1	2090–20	5278	30	.....	8
	5251– 8	6648	37	.....	10
	–10	6709	30	.....	8
	Total, 3 progenies		97	.....	26
			(IIa, g)		
2	2909– 8	5270–5273	43	.....	.....
	–26	5280–5283	64	.....	.....
	–32	5274–5277	121	.....	.....
	Total, 3 progenies		228	.....	.....
	F_2 x IVg 2909–26 x 2884–35	5284–5287, 7137	41	.....	.....
	F_2 x VIc 2909–26 x 2887–38	5288, 5289	(IIa) 67	.....	.....
	Total, 2 progenies		108	.....	.....
3	2909–21	5265, 5266	.....	46	9
	F_2 x IVg 2909–21 x 2884–35	5267, 5268	.....	44	31
	F_2 x VIc 2887–31 x 2909–21	5269	.....	41	51
	Total, 2 progenies		.....	85	82

TABLE 41. F_2 PROGENIES OF THE CROSS PURPLE Ig x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	5255 - 6	7094, 7095, 7701, 7702	(Ig) 80	(IIg) 24	.....	.....	55
	5259 - 3	7010, 7011	54	22	.....	.....	25
	6654B- 3	7375	23	7	.....	.....	9
	6659 -15	7365	28	12	.....	.....	12
	-22	7366	11	3	.....	.....	5
	-27	7368, 8491	43	17	.....	.....	24
	6660 - 9	7378	21	7	.....	.....	10
	-12	7377	33	13	.....	.....	10
	Total, 8 progenies		293	105	.....	.....	150
2	F_1 x IVa		(Ia)	(IIa)			
	6659-19 x 6691-8	7339	14	9	14	12	.....
	6660- 3 x -8	7340	9	11	12	11	.....
	F_1 x VIc						
	6654A-2 x 6690- 9	7335	20	15	13	10	.....
	B-1 x -17	7336	15	26	23	37	.....
	Total, 4 progenies		58	61	62	70	.....

TABLE 42. F_2 PROGENIES OF THE CROSS DILUTE PURPLE IIIa x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants		
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	2403-1	2962-2966	23	8	10
2	2420- 1	2904, 2905	17	5	9
	2954- 4	5038-5041	63	26	34
	2967- 2	6826, 6827	36	8	17
	-11	6828, 6829	78	32	31
	5263- 4	6669, 6670	31	16	8
	5267- 5	6675-6678	41	14	27
	-12	6679-6682	62	12	22
	Total, 7 progenies		328	113	148
3	F_1 x IVg				
	7322-3 x 7317-4	8210-8213	46	45	86

TABLE 43. F_3 AND F_4 PROGENIES FROM F_2 AND EQUIVALENT F_3 DILUTE PURPLES, DILUTE SUN REDS, AND GREENS, OF THE CROSS DILUTE PURPLE IIIa x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants		
	F_2 and F_3	F_3 and F_4	Dilute purple IIIa	Dilute sun red IVa	Green
					(IIIg, IVg)
1A	2966– 7	5049–5055	50	25	26
	5049–25	6816–6818, 7441	52	13	20
	5050– 6	6822–6824, 7058, 7059	41	10	27
	Total, 3 progenies		143	48	73
1B	6676–12	7383	26	10	16
	6828–12	7658–7660	14	4	7
	Total, 2 progenies		40	14	23
2	5052–7	6825, 7323, 7442	27	9	.....
	6676–8	7382, A266	55	14	.....
	Total, 2 progenies		82	23	.....
					(IIIg)
3	5049–37	6819–6821	62	.....	16
					(IVg)
4	2905–22	2547–2550	.....	21	9
	5053– 1	6875, 6911, 6912	.....	42	13
	Total, 2 progenies		.....	63	22
5	5050– 1	6874	.....	17	.....
	5054–10	6745, 6872, 6873	.....	108	.....
	5055– 2	6871, 7315	.....	51	.....
	– 5	7515	.....	21	.....
	Total, 4 progenies		.....	197	.....
					(IIIg, IVg)
6	2905– 5	5243, 5244	.....	.....	5
	–19	5245, 5246	.....	.....	13
	5049–13	6913, 6914	.....	.....	11
	5052– 3	6833	.....	.....	24
	– 5	85	.....	.....	15
	–12	6832	.....	.....	32
	6829– 9	7655–7657	.....	.....	30
	Total, 7 progenies		.....	.....	130

TABLE 44. F_2 PROGENIES OF THE CROSSES SUN RED IIg x GREEN IVg, SUN RED IIa x GREEN IVg, AND DILUTE SUN RED IVa x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants			
	F_1	F_2	Sun red		Dilute sun red	Green
			Pink anthers IIa	Green anthers IIg	Pink anthers IVa	Green anthers IVg
1	4787–6	6983, 6984	.....	122	.....	52
	5284–3	7003–7006	.....	94	.....	25
	Total, 2 progenies		.....	216	.....	77
2	F_1 x IVg					
	7317–6 x 7318–4	8214–8217	22	31	24	32
	7318–1 x 7317–4	8222–8225	38	25	34	26
	–4 x –6	8218–8221	45	34	47	51
	Total, 3 progenies		105	90	105	109
3	5267–3	6671–6674	.....	.....	55	22
	F_1 x IVg					
	7031–14 x 6857–5	7725, 7726	.....	.....	30	30

TABLE 45. F_1 PROGENIES OF CROSSES OF SUN RED IIa AND DILUTE SUN RED IVa WITH GREEN IIIg AND IVg

Group	Pedigree nos.		Number of F_1 plants			
	P_1	F_1	Purple Ia	Dilute purple IIIa	Dilute sun red IVa	Green
1	IIa x IIIg					
	7097-5 x A159-25...	7710.....	33	.....	.....	.....
	7357-3 x 7356- 1...	8151, 8152.....	31	.....	.....	.....
	Total, 2 progenies.....		64	.....	.....	.....
	IVa x IIIg					
	A9-22 x 7097-1.....	7709.....	.....	4	.....	.....
2	IVa x IVg					
	6860- 8 x 6869-1....	7713.....	.....	.....	28	.....
	A9-14 x 7060-1....	7708, A283, A284	.....	.....	31	.....
	Total, 2 progenies.....		.....	.....	59	.....
	IVa x IIIg					
	6860-13 x 6871-39...	7714.....	.....	11	12	.....
	6861- 2 x 6751- 3...	7711.....	.....	9	18	.....
	Total, 2 progenies.....		.....	20	30	.....
	IVa x IIIg					(IIIg, IVg)
	6861-4 x 6882-5.....	7512, 7513, 7716.	.....	25	11	34
	7039-3 x 7061-1.....	7727, 7728.....	.....	44	43	72
	Total, 2 progenies.....		.....	69	54	106
3	IVa x IIIg					(IIIg)
	7312-8 x 7313-2.....	8183.....	.....	86	.....	92
	7313-2 x 7314-1.....	8184.....	.....	31	.....	19
	7314-1 x 7313-1.....	8200, 8201.....	.....	126	.....	129
	-6 x -2.....	8185.....	.....	85	.....	98
	Total, 4 progenies.....		.....	328	.....	338

TABLE 46. F_2 PROGENIES OF THE CROSS GREEN IVg x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Dilute sun red IVa	Green
				(IVg, VIc)
1	5534-4	6791, 6792	35	29
	6530-1	7179, 7180	51	43
	-2	7181, 7182	32	30
	6531-1	7177, 7178	64	42
	-2	7175, 7176	63	38
	7032-1	7163, 7164	52	39
	7036-3	7169, 7170	60	36
	7037-2	7171, 7172	63	34
	Total, 8 progenies		420	291
2	F_1 x VIc			(VIc)
	7032-7 x 6878-42	7729, 7730	24	24
	7034-5 x -42	7767, 7768	42	34
	Total, 2 progenies		66	58
	F_1 x IVg			(IVg)
	7037-4 x 7049-7	7173, 7174	48	50
	7049-1 x 7037-4	7731, 7732	48	46
	Total, 2 progenies		96	96

TABLE 47. F_3 PROGENIES OF F_2 DILUTE SUN RED PLANTS OF THE CROSS GREEN IVg x GREEN VIc

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Dilute sun red IVa	Green IVg, VIc
1	6791- 3	7148, 7149	23	19
	6792- 6	7154, 7155	69	45
	-11	7159	16	13
	Total, 3 progenies		108	77
2	6791-22	7150, 7151	65	23
	-23	7152, 7153	49	18
	6792- 7	7157	38	12
	-10	7158	23	10
	-13	7160	12	3
	Total, 5 progenies		187	66
3	6792- 5	7156	48	.....
	-25	7161	30	.....
	Total, 2 progenies		78	.....

TABLE 48. F_2 AND F_3 PROGENIES OF THE CROSS GREEN IVg x GREEN VIa

Group	Pedigree nos.		Number of F_2 and F_3 plants		
	F_1	F_2	Sun red	Dilute sun red IVa	Green
			(IIa, g)		(IVg,VIa,c)
1	2400– 2	2902, 2903	7	3	5
	2952– 5	4838–4843	36	3	18
	–22	4830–4837	99	15	57
	2953– 4	4810–4813	88	32	59
	– 7	4814–4817	111	20	62
	–21	4818–4821	92	30	45
	2957– 2	4930, 4931	153	58	102
	Total, 7 progenies		586	161	348
	F_2	F_3			
2	4930–31	6991, 6992	119	.....	.....
			(IIa)		(VIa)
3	2903– 2	4783–4786	99	.....	32
	4930–22	6993, 6994	130	.....	39
	Total, 2 progenies		229	.....	71
	F_2 x IVa				
	2903-2 x 2889–38	4787–4790	55	.....	.....

TABLE 49. F_2 PROGENIES OF THE CROSS GREEN IIIg x GREEN VIc, AND F_1 PROGENIES OF CROSSES OF F_2 GREENS WITH SUN RED IIa AND DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg, VIb, c
1	2907–8	5297, 5298	.....	.....	28	11	38
	5262–5	7085, 7086, 7722, 7723	.....	.....	81	26	97
	Total, 2 progenies		.....	.....	109	37	135
	P_1	F_1	Number of F_1 plants				
2	IIIg x IIa 7085–10 x A159–24	7717	27	.....	.....	.....	.....
	IIIg x IVa 7086–2 x 7102–7	7207	.....	.....	14	.....	.....
	–3 x –8	7719	.....	.....	25	.....	.....
	Total, 2 progenies		.....	.....	39	.....	.....
3	IIIg x IIa 7086–6 x A159–17	7718, A298, A299	28	41	.....	.....	.....
	IIIg x IVa 7086–4 x 7102–8	7720	.....	.....	11	9	.....
4	IVg x IVa 7086–8 x 7102–8	7721	.....	.....	.....	22	.....

ANTHER, GLUME, AND RACHIS COLOR OF PURPLE

1, Purple, type Ia, typical, anthers purple; 2, type Ia with r^{ch}, anthers near-black; 3, type Ia with *pr*, anthers reddish; 4, type Ig, with R^g or r^g, anthers green (Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF DILUTE PURPLE AND GREEN

1. Dilute purple, type IIIa, typical, anthers purple; 2. type IIIa with r^{ch}, anthers near-black; 3. type IIIa with *pr*, anthers reddish
4. Green, types IIIg and IVg with R^g or r^g, green thruout

(Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF SUN RED AND DILUTE SUN RED

1. Sun red, type IIa, intensely pigmented form
2. Dilute sun red, type IVa, intensely pigmented form; 3 and 4, near-green forms, little color in glumes, anthers green with reddish stippling as shown in enlarged anther

(Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF BROWN AND GREEN

1, Brown, type V, intensely pigmented, homozygous form; 2, type V, less intensely pigmented form, heterozygous for *B* or *Pl* or both
3, Green, type VIc; 4, type VIb, green with tinge of brown due to *Pl* and r^{ch}
(Drawings by C. W. Redwood, somewhat diagrammatic)

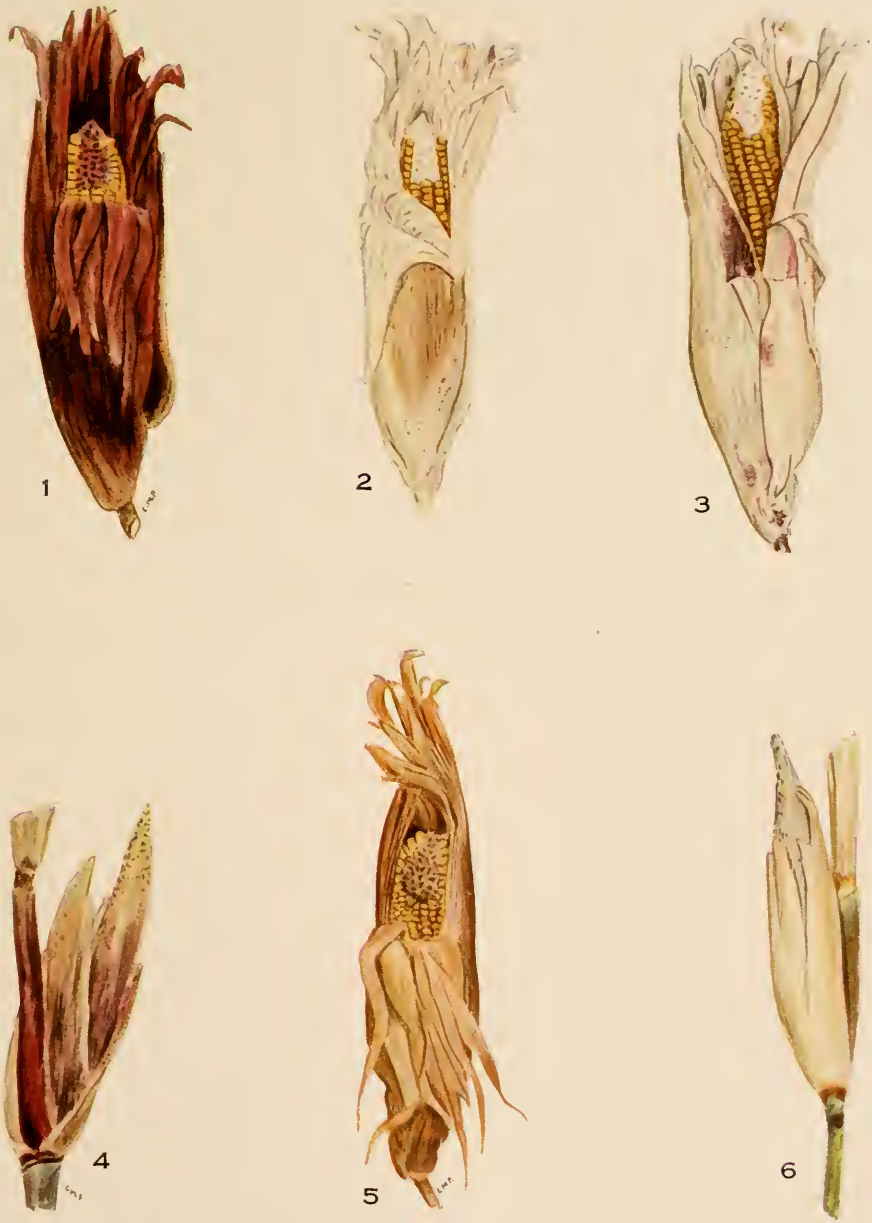
CULM, HUSK, AND SHEATH COLOR OF PURPLE AND SUN RED

1, Purple, type Ia; 2, weak purple, type Ib
3, Sun red, type IIa; 4, weak sun red, type IIb; 5, type IIb, inner husks of lower ear highly colored from exposure to sunlight directly after being torn apart
(Drawings 1 and 3 by C. W. Redwood; 2, 4, and 5 by Bernice M. Branson)

CULM, HUSK, AND SHEATH COLOR OF DILUTE PURPLE, DILUTE SUN RED, BROWN, AND GREEN

1, Dilute purple and dilute sun red, types IIIa and IVa; 2, more highly colored form of types IIIa and IVa
3, Brown, type V
4, Green, types VIb and VIc; 5, type VIa, with some brown in outer husks due to *B*

(Drawings by C. W. Redwood)



MATURE CULM, HUSK, AND COB COLOR

1. Purple, type Ia; 2. sun red, type IIa; 3. dilute purple, type IIIa; 4. more intensely pigmented form of type IIIa; 5. brown, type V; 6. dilute sun red, type IVa

(Drawings by Carrie M. Preston)

DEVELOPMENT OF COLOR IN DARKNESS

Tassels and sheaths developed under black paper bags: 1, purple, type Ia; 2, brown, type V; 3, dilute purple, type IIIa; 4, sun red, type IIa, no red color

(Drawings by Carrie M. Preston)

RELATION OF SOIL FERTILITY TO COLOR DEVELOPMENT

Young plants of dilute sun red, type IVa: 1, plant grown in fertile soil; 2, plant grown in infertile soil

(Drawing 1 by Bernice M. Branson; 2 by Carrie M. Preston)

COLOR DEVELOPMENT IN BROKEN LEAVES

1. Dilute sun red, type IVa, about one week after the leaf was creased; 2. dilute purple, type IIIa with japonica white stripes, about three days after the leaf was creased

(Drawings by Carrie M. Preston)

ABERRANT COLORATION OF BROWN TASSEL

Poorly developed tassels of brown, type V, sometimes exhibit purple in abnormally developed parts

(Drawing by Carrie M. Preston)