INHERITANCE OF COTYLEDON, SEED-COAT, HILUM AND PUBESCENCE COLORS IN SOY-BEANS[1]

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Received May 9, 1921

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INTRODUCTION

All genetic studies thus far made on the soy-bean (*Soja max*) have been concerned with color characters. PIPER and MORSE (1910) noted segregation in some progenies in pubescence and seed-coat colors, though no definite hybridization experiments were conducted. TERAO (1918) reported the results of studies on the inheritance of cotyledon color and the relation of green and yellow seed-coat colors.

The soy-bean is especially favorable in some respects for genetic studies. There is a large number of differential characters exhibited by the many

[1] Papers from the Department of Genetics, Agricultural Experiment Station, UNIVERSITY OF WISCONSIN, No. 28. Published with the approval of the DIRECTOR of the STATION.

now well-established varieties; and the plant sets seed abundantly, is self-fertile, and nearly always self-fertilized. The only difficulty encountered in conducting such studies on this plant is in making crosses, due to the small size of the flower; but after some practice, a fair degree of success is attained.

MATERIALS AND METHODS

In 1912 the Department of Genetics of the UNIVERSITY OF WISCONSIN started an experiment to determine the effect of selection within pure lines of soy-beans on the content and drying quality of the oil. When the writer entered the Department in 1914, this experiment was placed under his direction as well as certain genetic studies then in progress on varietal crosses in soy-beans. To Prof. L. J. COLE the writer is indebted for helpful criticism and inspiration which it is a pleasure to acknowledge.

Most of the varieties used in the pure-line selection experiment were obtained from the Agronomy Department of the WISCONSIN AGRICULTURAL EXPERIMENT STATION. Two of these bore the U. S. Seed and Plant Introduction numbers 20406 and 20854, and were given in our records numbers 8 and 9, respectively. Variety 8 has white or gray pubescence on the stems, leaves and pods, and the hilum, seed coat, and cotyledons are yellow. Variety 9 has brown or tawny pubescence, the hilum is black, and the seed coat and cotyledons are green. The hybrid generations F_1 to F_3 of reciprocal crosses (also F_4 of cross variety 8 ♀ × variety 9 ♂) between these two varieties supply nearly all of the data presented in this paper.

Some additional data also are presented on the segregation of cotyledon color within the Auburn variety, S. P. I. No. 21079A, a sample of which was originally obtained from the U. S. DEPARTMENT OF AGRICULTURE. In the original sample as received, both types of cotyledons were found, though no differences were apparent in other seed characters, such as shape, color of coat, etc. Certain of these seeds, when tested, proved to be heterozygous for yellow cotyledon, and further study of their progenies furnished the data presented elsewhere in this paper.

The difficulty of making artificial crosses in the soy-bean is a real hindrance to the progress of genetic studies in this plant. In making crosses, it is necessary to remove the sepals and petals first, and then to remove the anthers with the point of a needle. In many cases the pistil is severely injured in this operation, and never recovers. Pollination is attended with difficulty, also, (1) because of the scanty supply of pollen in just the right stage of development, and (2) because of the difficulty of applying pollen to the stigmatic surface, which, instead of being upright on a straight style, is directed downward on a curved style. Artificial crossing in the greenhouse is even less successful than in the field because the flowers are usually smaller, and because of the greater scarcity of pollen.

As stated in the beginning, the soy-bean is nearly always self-fertilized. Natural hybrids are rare, but they do occur, as will be shown later in this paper. However, under ordinary field conditions and methods of planting, the number of such hybrids is ordinarily negligible; and this number would likely be still more insignificant when the plants stand farther apart in the row, as was the case in the plantings for these studies. For this reason it was not deemed necessary to bag flowers of hybrid plants. All data, therefore, in the following pages, with the exception of crosses, are from plants grown from seeds which were not protected by bags from possible natural cross-pollination.

A word of explanation is necessary regarding the methods employed in calculating the biometrical constants given in this paper.

The probable errors of Mendelian ratios were calculated according to the formula $\pm .6745 \sqrt{p \times q \times n}$, where n is the total number of individuals in the experiment, p is the percent of one member of the ratio, and q is the percent of the other member of that ratio. Thus, in a 3:1 ratio, $p = 75$ percent (.75) and $q = 25$ percent (.25); and in a 15:1 ratio, $p = 93.75$ percent (.9375) and $q = 6.25$ percent (.0625). The probable errors thus obtained were compared with the deviations of the actual numbers from those expected on the basis of the given ratio.

For tests of goodness of fit in cases where the number of classes was more than two, use was made of the method suggested by HARRIS (1912).

INHERITANCE OF COTYLEDON COLOR

TERAO'S *results*

TERAO (1918) described the types of cotyledon color, yellow and green, found in soy-beans. In his crosses, the cotyledon color of the hybrid progeny was the same as the female parent in every case, and there was no evidence of segregation in succeeding generations. This character was therefore stated to be maternal in inheritance.

To explain these results TERAO suggested that there were two kinds of chlorophyll represented by the two cotyledon colors; one which always remains green, and the other which changes to yellow on the ripening of the beans. The former was designated as (G) and the latter as (Y). If the female parent possessed (G) or (Y), the hybrid progeny, down at least to the F_3 generation,[2] would have green or yellow cotyledons, respectively. As the inheritance thus appeared to be strictly maternal, and the male parent consequently could bring neither (Y) nor (G) into the hybrid, no form could be produced having both types of chlorophyll, and the probable relationship of (Y) and (G) in inheritance could not, therefore, be determined.

In the crossing experiments with soy-beans here reported cotyedon color was found to segregate regularly just as does seed-coat color or any other Mendelian character.

Variety 8 × variety 9. Results of reciprocal crosses

Crosses between varieties 8 and 9 were made reciprocally in the summer of 1916. Two hybrid seeds resulted from variety 9 (♀) × variety 8 (♂) and 8 from the reciprocal cross. All 10 beans had yellow cotyledons, thus indicating that, in this case at least, cotyledon color was not maternal in its inheritance. Rather it indicated that the same condition exists in soy-beans as in the garden pea; namely, that yellow cotyledon is dominant to green.

The two hybrid plants resulting from variety 9 (♀) × variety 8 (♂) were given the progeny No. (471), and were numbered (471)-80 and (471)-81. They were grown in the field in the summer of 1917. The 8 hybrid plants resulting from variety 8 (♀) × variety 9 (♂) were grown in the greenhouse in the early spring of 1917, and were given the progeny No. (399). These plants were small and branchless, and bore few seeds. They were not harvested separately as were the F_1's of the reciprocal; hence the data are given as if from one plant only.

Beans produced by these F_1 plants showed segregation in cotyledon color. The data are given in table 1.

Plants B82a, (1235)-1, and 1234-1, data for which are included in table 1, were natural hybrids between varieties 8 and 9. These varieties were planted in 1918 in a plot by themselves and in such a way that the plants of one variety alternated in the row with those of the other. Such close planting gave opportunity for the branches of adjacent plants to intermingle and to be in contact, thus favoring natural crossing. Among the thousands of beans produced by plants of variety 9 (green cotyledons), 5 were found with yellow cotyledons. These were obviously the result of crossing with variety 8. Three of these beans produced the hybrid plants mentioned above.

The aberrant ratios given by plants (471)-80 and (471)-81 (see table 1) were possibly due to the fact that many of the beans were not well matured.

[2] TERAO did not carry the investigation beyond the F_3 generation.

The fall of 1917 was very unfavorable for the proper ripening of the seeds. Rainfall was excessive, and there was very little sunshine during the whole ripening period. Moreover, frost killed the plants before many of the last-formed pods were fully developed, and, in consequence, the seeds contained in them dried up and retained the green color of the cotyledons shown by all soy-beans prior to the ripening period.

The small number of beans produced by B82a and plants of (399) (see table 1) was due to their being grown in the greenhouse. B82a showed no segregation at all, but this is not surprising considering the small number of seeds produced. That this plant did not breed true will be shown later when the F_3 generation is considered.

TABLE 1

Cotyledon color in the F_2 generation. Data from all crosses, both natural and artificial.

PLANT NUMBER	NUMBER SEED OBSERVED WITH		DEVIATION* (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Yellow cotyledon	Green cotyledon				
(471)–80	115†	28†	19	1.95	9.75	4.1:1
(471)–81	119	16	8	1.89	4.23	7.4:1
(399)	21	1	0	0.78	—	21.0:1
B82A	4	0	0	0.33	—	—
(1235)–1	51	7	29	1.24	23.39	7.3:1
(1234)–1	153	7	3	2.06	1.46	22.0:1
Total........	463	59	26	3.73	6.98	7.85:1

* These deviations are figured on basis of a 15:1 ratio.

† These are corrected figures. Original figures were 109 beans with yellow and 34 with green cotyledons. For explanation see text.

The peculiar and wide ratios shown by (1234)-1 and (1235)-1 (table 1) may also be due to difficulties and errors in classification, as the fall of 1919 was quite similar to that of 1917, there being excessive rainfall and little sunshine. Such errors in judging phenotypes can only be checked up by the breeding test, which for these plants has not yet been made.

It must be admitted that the true nature of the inheritance of cotyledon color in the artificial crosses was not discerned from the F_2 ratios obtained in 1917. Nor, as will be seen later, did an F_3 generation grown in the same year aid at all in interpreting these ratios. It was not until data on progenies grown in 1918 (F_3 of one cross, F_4 of the other) were secured, that it was possible to see the true state of affairs.

The importance of making back-crosses with the recessive type to separate phenotypically similar genotypes was fully appreciated, but crosses in soy-beans are very difficult to make, and if a successful cross is made after many trials and failures, only one, two, three, or at most four seeds are obtained. For these reasons, such test matings were not attempted, and resort was had to growing progenies from different plants separately and in as large numbers as possible.

In view of the above considerations, a large F_3 generation, particularly of one cross (variety 9, green ♀ × variety 8, yellow ♂) was grown in order to determine the meaning of the peculiar F_2 ratios. The number of plants grown and their parentage are given in table 2. More seeds of each cross were planted but many failed to germinate. The seeds with green cotyledons were especially poor in this respect, only 9 plants being raised from 32 seeds of this type planted, or 28 percent, as compared with a corresponding percentage of 83.0 for the yellow-cotyledon seeds. It was unfortunate that so few of the green-cotyledon plants could be tested by their progeny in this way, as such a test would have furnished a good check on the color classification of the beans of each parent plant.

TABLE 2

Showing the number, parentage, etc., of F_2 plants grown to produce the F_3 generation in cotyledon color.

CROSS	PARENT	PROGENY NUMBERS	NUMBER OF PLANTS GROWN FROM		YEAR
			Yellow-cotyledon seeds	Green-cotyledon seeds	
Variety 8 (yellow) ♀ × Variety 9 (green) ♂	(399)	(470)	18	1	1917
Variety 9 (green) ♀ × Variety 8 (yellow) ♂	(471)–80 (471)–81	(801) (803)	(60) 61* 56	(6) 5* 3	1918 1918
Natural cross Variety 9 (green) ♀ × Variety 8 (yellow) ♂	B82a	(1233)	4	–	1919

* Corrected figures. For explanation see text.

The F_3-generation results were interesting for several reasons. In the first place, all plants but one from seeds with green cotyledons bred true for green (table 11).[3] The exception was a plant which bred true for yellow. The bean from which this plant was grown was produced by plant

[3] Tables 11–53, inclusive, are given in the appendix.

(471)-80, in 1917, when, as previously stated, the conditions for properly maturing soy-beans were very poor. All the reliable data from breeding tests show that in soy-beans, green cotyledons are recessive to yellow. Hence, it is believed that the exception above mentioned was caused by an error in the classification, the cotyledons of the parent bean appearing green, but proving themselves to be yellow genetically. Had all the other green-cotyledon seeds of this plant been tested, and had this error been consistent throughout, as may be assumed, then approximately one-sixth, or 6, of the beans classed as having green cotyledons would have behaved in the breeding test as yellows, and therefore, may be added to the yellow class and subtracted from the green. If this is done, the figures are 115 seeds with yellow and 28 with green cotyledons, or an actual ratio (F_2) of 4.1:1. These are the corrected figures for this plant given in table 1.

TABLE 3

Showing relative proportion of the three types of F_2 yellow-cotyledon seed as indicated by the F_3 generation.

TYPE OF F_2 YELLOW	RATIOS IN SINGLE PROGENIES				TOTAL	THEORETICAL NUMBERS ON BASIS OF 7:4:4 RATIO
	(470)	(801)	(803)	(1233)*		
Bred true	10	33	33	2	78	65
Segregated 15:1	5	13	12	2	32	37
Segregated 3:1	3	15	11	—	29	37
Total	18	61	56	4	139	139

$\chi^2 = 5.006$ P = .080147

* Data from natural cross. Parent was B82A (table 1).

In the second place, the plants from F_2 yellow-cotyledon beans were of three types based on their breeding behavior; namely, a type breeding true for yellow, a type segregating in the approximate ratio of 3 yellow to 1 green, and still another type segregating in the approximate ratio of 15 yellow : 1 green, and there were about as many plants belonging to the first type as to both of the others. These results were such as one would expect on the theory of duplicate factors for cotyledon color. The full data from the cross and its reciprocal are presented in detail in tables 12, 13, and 14, but are summarized in table 3.

The F_3 generation from the natural crosses (progeny 1233) consisted of only 4 plants, 2 of which bred true for yellow cotyledon and the other 2 showed segregation in an approximate 15:1 ratio. Individual counts on this progeny are given in table 15 (see appendix). These data conform closely to those secured from the artificial crosses. That no plants in this progeny gave 3:1 ratios is believed to be due to the small number grown, and not to an irregularity in genetic behavior.

Cotyledon color in the F_4 generation, data for which are given in tables 16–34, was obtained only for the cross variety 8, yellow, ♀ × variety 9, green, ♂. Neither the reciprocal nor the natural crosses have as yet been carried beyond the F_3 generation.

Of the nineteen F_2 plants of this cross grown, ten bred true for yellow cotyledon. Only two of these ten plants produced any green-cotyledon seeds at all (table 14), and in each of these plants, (470)-78 and (470)-79, three seeds were found whose cotyledons appeared green, though it was doubtful whether they could be so called. Unfortunately, they could not be tested out, but many seeds with yellow cotyledons were tested and all were found to breed true for yellow. Similarly, many seeds of the other

TABLE 4

Cotyledon color in the F_4 generation. Progeny of yellow-cotyledon beans from plants giving F_3 ratio of 3 yellow : 1 green.

PARENT	(470)-63	(470)-65	(470)-72	TOTAL	THEORETICAL NUMBERS ON BASIS OF 1:2 RATIO
PROGENY NUMBERS	(915)	(909)	(913)		
Bred true	3	6	6	15	13
Segregated, 3:1	5	11	8	24	26
Total	8	17	14	39	39

eight plants were tested, and they also bred true for yellow cotyledon. Individual counts on these F_3 plants are given in tables 24–33, inclusive.

Three F_2 plants, (470)-63, (470)-65, and (470)-72, as seen from table 14, gave approximate 3:1 ratios. Table 4 summarizes the results which are given in detail in tables 21, 22 and 23.

Actual results obtained and expected results are thus shown to be in close agreement.

Plants (470)-60, (470)-70, (470)-71, (470)-75 and (470)-77 gave very diverse and abnormal ratios (see table 14), but it is permissible to place them in the class segregating in a 15:1 ratio because of the progeny tests which are given in detail in tables 16–20. A summary of these results is given in table 5.

The above progenies are comparable to those given in table 3, as they are produced from yellow-cotyledon seeds borne by plants giving 15:1 ratios. Hence, the totals may be added together. When this is done, the grand totals are:

Bred true for yellow cotyledon.................................115; expected, 101
Segregated in 15:1 ratio.................................... 50; expected, 57
Segregated in 3:1 ratio..................................... 50; expected, 57

$\chi^2 = 3.66$ P = .16185

Figure 1 presents these totals graphically.

As might be expected, there was considerable variation in actual ratios among plants showing segregation into the two cotyledon colors. These ratios ranged from 1.73:1 to 24.0:1 but in general they grouped themselves about equally on either side of 3 and 15, respectively. With few exceptions there was no trouble in placing a plant in the former or the latter class. There was one instance of overlapping of these two classes. Plant (470)-77 showed an actual ratio of 4.0:1, though the progeny test (table 17) proved it to belong to the 15:1 ratio class. This low ratio was slightly

TABLE 5

Cotyledon color in the F_4 generation. Progeny of yellow-cotyledon beans from plants giving F_3 ratio of 15 yellow : 1 green.

PARENT	(470)-60	(470)-70	(470)-71	(470)-75	(470)-77	TOTAL	THEORETICAL NUMBERS ON BASIS OF 7:4:4 RATIO
PROGENY NUMBERS	(906)	(920)	(903)	(912)	(907)		
Bred true	7	11	9	4	6	37	36
Segregated, 15:1	4	3	2	6	3	18	20
Segregated, 3:1	6	5	1	7	2	21	20
Total	17	19	12	17	11	76	76

$\chi^2 = .2778$ P = .8906943

exceeded by plants (920)-54 and (915)-98 which belong to the 3:1 group but both of which showed an actual ratio of 4.08:1. That these plants belonged to the 3:1 ratio class is more than probable, particularly plant (915)-98, as its parent was a 3:1-ratio plant and as it was one of a progeny showing only two types (table 23), namely, plants breeding true for yellow, and plants segregating in a 3:1 ratio.

It is significant that the widest 15:1 ratios found were those given by plants grown in 1917. For example, plant (470)-60 gave a ratio of 24 yellow: 1 green; plant (470)-71, 5.3:1; plant (471)-80, 4.1:1, and plant (470)-77 (above mentioned), 4.0:1. In the case of the first plant, there were only 3 green-cotyledon seeds out of a total of 75, and it might be suspected that these were accidental mixtures and that the plant really bred true for yellow, were it not for the fact that the yellows, in the next generation, gave results (see table 16) which proved them to behave as the yellows of a 15:1 ratio. Similarly with regard to the other plants mentioned above, the actual ratio for each was "wide," but on the other side of 15, being closer to a 3:1 than a 15:1; but, in the next generation, they gave results (tables 12, 17, 20) like those given by the yellows of plant (470)-60.

The variation in actual ratio shown by segregating plants of the 15:1 class is represented by the frequency table (table 6). The frequency polygon

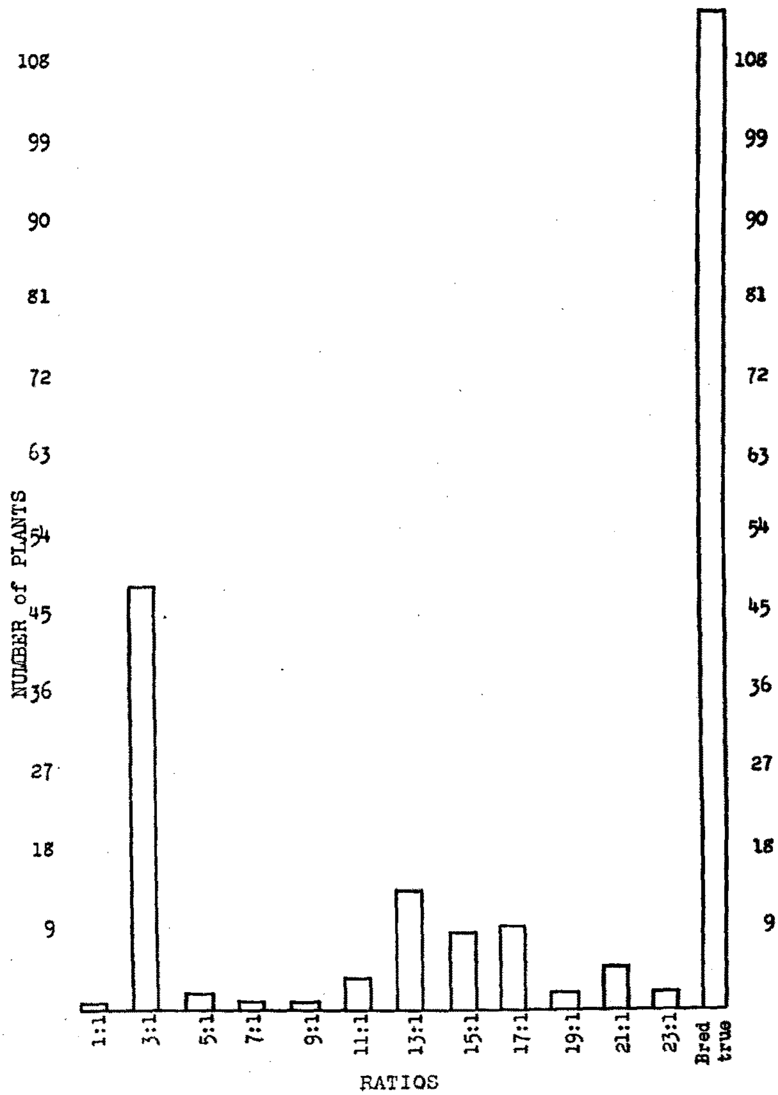

FIGURE 1.—Graphic representation of actual ratios obtained, showing tendency to fall into three groups; namely, (a) those breeding true for yellow; (b) those segregating in 15:1 ratio, and (c) those segregating in 3:1 ratio. Based on tables 3 and 5 combined.

shown in figure 2 is based on the data given in this table. About two-thirds of the total number of plants are included in the three classes, the mid-values of which are the ratios 13:1, 15:1, and 17:1.

The actual ratios for the 3:1 class of segregating plants were much less variable than those for the 15:1 class. The range was from 1.73:1 to 4.08:1. The lowest ratio (1.73:1) was given by plant (470)-65, also grown in 1917. That this is only an aberrant 3:1 ratio is proved by progeny which the seeds with yellow cotyledons produced (table 22). Plants giving the highest ratio, 4.08:1, have been discussed above.

To show the variation of segregating plants (3:1 class) with respect to actual ratio, the following frequency table (table 7) has been prepared.

TABLE 6

Frequency distribution of segregating plants (15:1 class) with respect to actual ratio of yellow- to green-cotyledon seeds.

CLASS RANGE	MID-VALUE OF CLASS	FREQUENCY (NUMBER OF PLANTS)	PERCENT OF TOTAL
2.1:1 to 4.0:1	3:1	1	1.818
4.1:1 to 6.0:1	5:1	2	3.637
6.1:1 to 8.0:1	7:1	3	5.454
8.1:1 to 10.0:1	9:1	1	1.818
10.1:1 to 12.0:1	11:1	4	7.273
12.1:1 to 14.0:1	13:1	14	25.455
14.1:1 to 16.0:1	15:1	9	16.364
16.1:1 to 18.0:1	17:1	10	18.180
18.1:1 to 20.0:1	19:1	2	3.637
20.1:1 to 22.0:1	21:1	7	12.727
22.1:1 to 24.0:1	23:1	2	3.637
Total....................................		55	100.000

Fully two-thirds of the total number of plants are contained in the three classes the mid-values of which are the ratios 2.75:1, 3.0:1, and 3.25:1. The frequency polygon shown in figure 3 is based on data given in this table.

The F_4 generation brought out two other instances of error in classification. In the first case, plant (470)-77, (see table 14), was noted as having produced 18 yellow- and 12 green-cotyledon beans. The progeny of this plant consisted of 12 plants, 10 of which were from seeds with yellow cotyledons, and 2 from seeds supposedly with green cotyledons. One of these 2 plants (907)-74, (table 17), segregated in cotyledon color, thus proving that the cotyledons of the parent seed were genetically yellow, though they appeared green. If, as may be assumed, one-half of the seeds of (470)-77 classed as having green cotyledons are considered as really

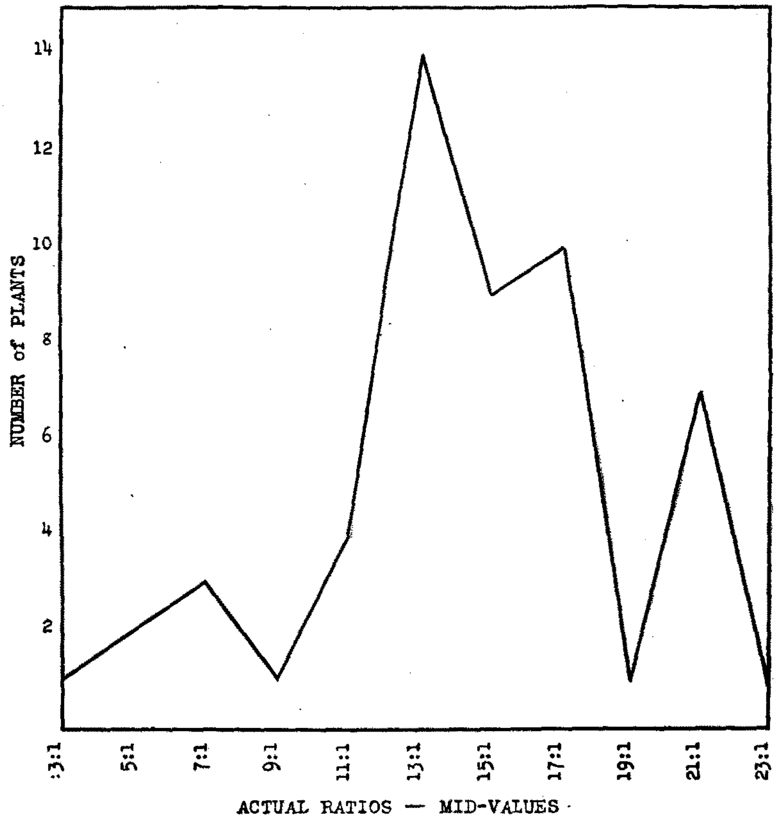

FIGURE 2.—Frequency polygon showing variation of segregating plants (15:1 class) with respect to actual ratio of yellow- to green-cotyledon beans.

TABLE 7

Frequency distribution of segregating plants (3:1 class) showing variation in actual ratio of yellow- to green-cotyledon seeds.

CLASS RANGE	MID-VALUE OF CLASS	FREQUENCY (NUMBER OF PLANTS)	PERCENT OF TOTAL
1.63:1 to 1.87:1	1.75:1	1	1.351
1.88:1 to 2.12:1	2.00:1	0	—
2.13:1 to 2.37:1	2.25:1	2	2.703
2.38:1 to 2.62:1	2.50:1	8	10.811
2.63:1 to 2.87:1	2.75:1	13	17.568
2.88:1 to 3.12:1	3.00:1	19	25.675
3.13:1 to 3.37:1	3.25:1	22	29.730
3.38:1 to 3.62:1	3.50:1	5	6.756
3.63:1 to 3.87:1	3.75:1	2	2.703
3.88:1 to 4.12:1	4.00:1	2	2.703
Total....................................		74	100.000

genetically yellows, then the figures would be 24 yellow and 6 green instead of 18 and 12, respectively.

Similarly, plant (470)-65 was noted as having produced 20 seeds with yellow and 22 with green cotyledons. The progeny of this plant consisted of 15 plants, 7 of which were from seeds with yellow cotyledons and 8 from seeds supposedly with green cotyledons. One of these 8 plants (909)-150, (table 22), segregated, however, instead of breeding true for

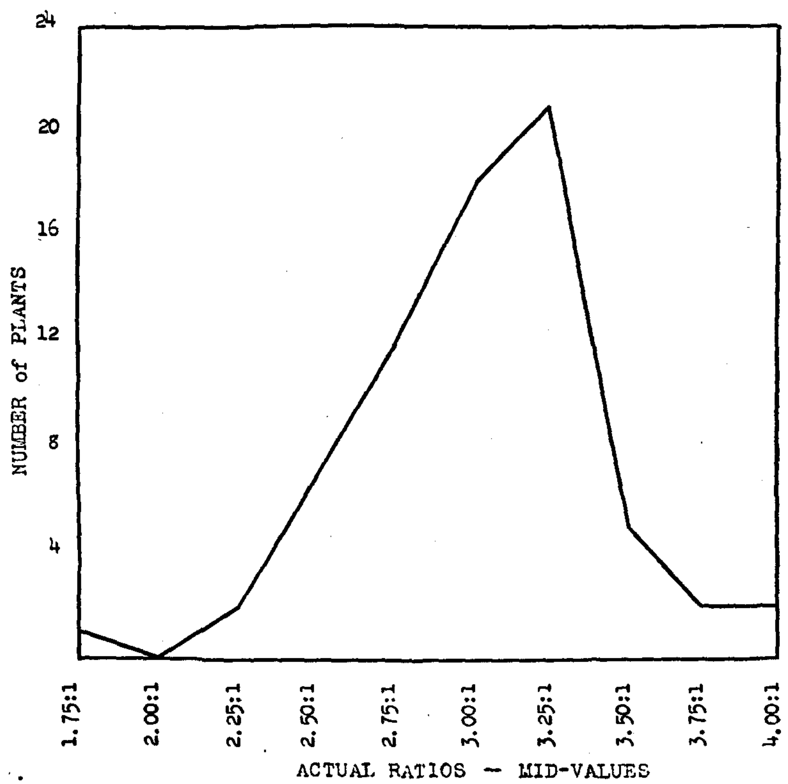

FIGURE 3.—Frequency polygon showing variation of segregating plants (3:1 class) in actual ratio of yellow- to green-cotyledon seeds.

green, thus proving the cotyledons of the parent seed to have been yellow, genetically. A re-examination of the seeds not planted showed there were 12 seeds with yellow and 7 with green cotyledons. These added to the number tested and the number which were planted but failed to germinate, gives a total of 25 yellow- and 16 green-cotyledon seeds. If it be assumed that one of the 7 green-cotyledon seeds not planted should, on being tested, prove to behave genetically as a yellow, then the final figures would be 26 yellow and 15 green, the "corrected" figures for this plant given in table 14. One seed of unknown cotyledon color was lost; hence the total number is one less than as originally given.

In figure 4 a diagrammatic representation is given of the inheritance of cotyledon color in the cross variety 9 ♀ (green cotyledons) × variety 8 ♂ (yellow cotyledons). Figure 5 is a similar diagram for the reciprocal of this cross. A comparison of these two diagrams shows at a glance

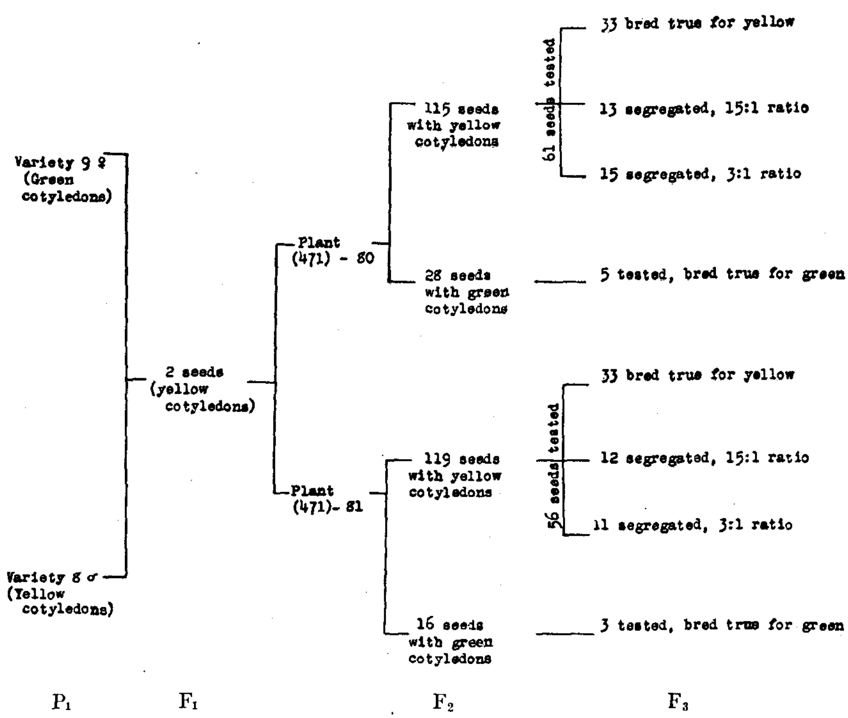

FIGURE 4.—Diagrammatic representation of inheritance of cotyledon color in cross variety 9 ♀ (green) × variety 8 ♂ (yellow).

that the mode of inheritance of cotyledon color is the same irrespective of which variety is used as the female parent.

Unexpected beans

Reference to tables 11, 13, 14, 17, 20, 22, 23, 24, 26, 29, 30, 33, and 34 shows that in plants classed as breeding true for yellow or green cotyledons a few beans with the unexpected cotyledon color were found. The question arises as to how these may be accounted for.

In number, they are few compared with the total number of "expected" beans. All plants classed as breeding true for yellow or green cotyledon produced a total of 123,624 beans. Of these, 110, or one bean in 1123, had the unexpected cotyledon color,—57 yellow and 53 green.

Of the 347 plants here considered, 298, or 86 percent, produced yellow- or green-cotyledon seeds exclusively. In each of 19 plants, or 5 percent of the total, 1 bean was found with the unexpected cotyledon color; in 15 plants, 2 such beans; in 9 plants, 3; in 1 plant, 4; in 4 plants, 5; and in 1 plant, 10.

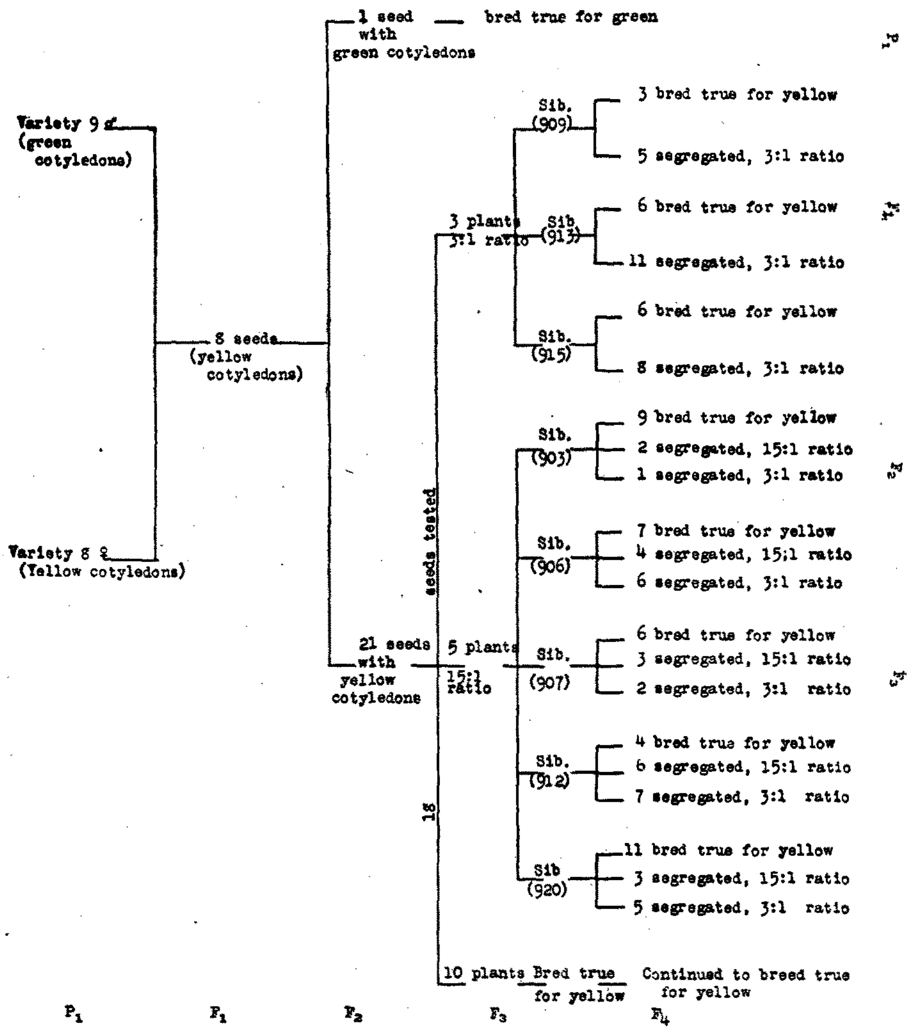

FIGURE 5.—Diagrammatic representation of inheritance of cotyledon color in cross variety 8 ♀ (yellow) × variety 9 ♂ (green).

The occurrence of yellow-cotyledon beans in plants classed as breeding true for green will be considered first. There are at least three ways in which these may be accounted for: (1) crossing; (2) mutation; and (3) seed mixture. The first is the most probable since (a) yellow is dominant, (b) cotyledon color is a seed character, permitting the effect of the cross to become apparent the same season it is made, and (c) it has already been shown (page 490) that crosses do occur occasionally. The occurrence of a dominant mutation, as from green to yellow cotyledon, is a possibility. As to (3), it is very probable that some of these unexpected beans are seed mixtures. It would not be surprising if, in harvesting and threshing so many plants and in cleaning such a large number of seed, a few mixtures should occur in spite of the greatest pains taken to prevent it. Seed mixtures are easily and quickly detected if other seed characters, such as seed-coat color, are also different, but where there are no differences except in color of cotyledon, one cannot be certain whether the unexpected seeds are really mixtures or whether they may not as likely be accounted for by crossing or by mutation. Furthermore, the breeding test would seldom aid in settling this question. Heterozygosity would not serve as a criterion since yellow-cotyledon seeds resulting from crossing or from mutation would probably be heterozygous, as would also the majority of mixed yellow-cotyledon seeds from segregating plants.

Of the 53 green-cotyledon seeds found on plants classed as being homozygous for yellow, 18 were small, shrivelled and immature, and the cotyledons appeared green even though genetically they may have been yellow. In such immature seeds it appears that that stage of ripening is never reached where the green pigment fades out, and so the yellow always remains hidden. If, however, these 18 beans be disregarded because of their immaturity and the consequent doubt as to the color of their cotyledons, there will still remain 35 unexpected seeds to be accounted for.

It is clear that certain considerations involved in the occurrence of unexpected yellow-cotyledon beans do not apply to the unexpected greens. Thus, cross-pollination with the green-cotyledon type would not account for them since yellow is dominant. Nor would "loss" mutations give rise to green-cotyledon seeds unless they occurred in both gametes at once, which, while not impossible, is at least extremely unlikely.

It is believed that, occasionally, genetically yellow-cotyledon beans fail to turn yellow on ripening, but always remain green, though showing a fair degree of maturity in other ways. Such beans may be due to an unfavorable environment for bringing out the proper cotyledon color. The location on the parent plant is of prime importance in this connection. Seeds borne on the lower branches often do not have sufficient sunlight and air; they may even be lying on the ground and often be almost completely covered with soil, and of course they cannot ripen properly. This belief is supported by two or three instances (cited earlier in this paper) of beans, classed as having green cotyledons, breeding like genetic yellows.

Of course, such unexpected seeds cannot be discerned in plants segregating for cotyledon color; they affect the ratios, but so slightly as to be of no significance. As indicated above, in every 1123 beans there was 1 bean with the unexpected cotyledon color. The average number of beans per plant for the plants classed as being homozygous for green or yellow cotyledon was 356. On the average, then, in every 3 plants examined, 1 unexpected bean would be found. If these figures be assumed to apply to segregating plants as well, it is clear that in two-thirds of the plants, the ratio would not be affected at all, and in one-third, it would be affected too slightly to be significant.

It appears likely then that a considerable number of the beans with unexpected cotyledon color are the result of cross-pollination. The rest are due to such factors as unfavorable weather conditions, mutations, and mechanical mixtures. In numbers they are very small in proportion to the total number of beans counted (upwards of a hundred thousand); and therefore, it is felt that they do not affect the validity of the results.

A soy-bean chimera

During the course of these studies, a single bean was found having one yellow and one green cotyledon. The color of each cotyledon was quite normal and distinct, making a striking contrast. A view of the back of the bean opposite the hilum showed a distinct line of demarcation. The seed coat being green and slightly transparent, the difference in color of the cotyledons produced a chromium green effect on one side and a yellowish green on the other.

This bean was borne by plant (909)-160, which produced, in addition, 272 beans with yellow and 91 beans with green cotyledons. The parent plant was, therefore, heterozygous for one factor only.

The plant grown the following year from the chimera proved to be heterozygous, bearing 85 seeds with yellow and 23 seeds with green cotyledons. These two types were distributed over the plant according to chance, just as on any normal segregating plant; hence, the embryo proper of the bean was not affected genetically by whatever caused the abnormal condition of the cotyledons.

The most plausible explanation appears to be that a somatic mutation occurred at a very early stage in the development of the embryo. As all the cells were heterozygous for but one of the factors for cotyledon color, such a mutation would involve a change in only one factor, and would therefore be within the limits of probability. Many other cases of somatic mutation are known, particularly in corn (COLLINS 1919).

Interpretation of inheritance of cotyledon color

BUNYARD (see DARBISHIRE 1911, page 131) has shown that the cotyledons of both yellow- and green-cotyledon varieties of the garden pea (*Pisum sativum*) have both yellow and green pigments while the seeds are still immature. As the peas ripen, the green pigment fades out in yellow varieties, but persists in green varieties. Yellow-cotyledon varieties, therefore, are first green, later turning yellow, and they differ from the greens only in having a factor which causes the green pigment to fade out as the beans mature.

It is probable that in the soy-bean the same situation exists in regard to the green and yellow pigments in the cotyledons. This is indicated by the fact that in immature beans the cotyledons are green irrespective of the variety. Furthermore, on exposing mature beans with green cotyledons to the light for a time, the green color gradually fades out, and the cotyledons become yellow, thus proving that both pigments were originally present, at least potentially. It is probable, therefore, that, as the beans ripen, the green pigment disappears in yellow-cotyledon varieties, but remains in varieties with green cotyledons; and that, as in peas, the yellow-cotyledon varieties differ from the greens only in having a factor which causes the green pigment to fade out at the time of maturity.

In the garden pea WHITE (1916) has assumed that three factors are concerned with the production of cotyledon color; namely, Y, G, and I. Y and G are factors for yellow and green pigments, respectively, both being present in all but one of the varieties with which he experimented; and I is a factor causing the green pigment to disappear at maturity, present only in yellow-cotyledon varieties. Thus, the two cotyledon colors in peas ordinarily differ by a single factor, I, and in crosses the yellow proves dominant, the ratio of 3 yellow to 1 green being obtained in F_2.

WHITE found one yellow-cotyledon variety, "Goldkönig," which evidently lacked both factors G and I; for in crosses with green-cotyledon varieties, green was dominant, and an F_2 ratio of 3 green to 1 yellow was obtained; while in crosses with other varieties with yellow cotyledons, the F_2 ratio of 13 yellow to 3 green was obtained.

Inasmuch as the relation between the two cotyledon colors in soy-beans is probably the same as that in peas, the same factors may be used. So far as known, however, Y and G are present in all varieties of soy-beans; no recessive yellow has been found such as WHITE reports in the Goldkönig pea, though numerous crosses have been made between different yellow-cotyledon varieties. On the contrary, in the cross and its reciprocal reported in this paper, green is recessive to yellow, as also is the case in the Auburn, brief mention of which has been made earlier in this paper, and which will be discussed more fully later. All the data available therefore, have shown that yellow cotyledon in soy-beans is dominant to green.

With regard, however, to factors, such as *I*, that cause the green pigment to disappear at maturity, varieties of soy-beans with yellow cotyledons differ among themselves, as shown by the data which have been presented. Some, perhaps most varieties, as for example, Auburn, possess only one factor of this nature, while others typified by variety 8, possess two such factors. These are duplicates of each other and produce the same effect, as far as cotyledon color is concerned, whether one or both are present.

If *D* be used to symbolize the factor which is the duplicate of *I*, then the factorial composition of variety 8 (yellow cotyledons) is *YYGGIIDD*, and of variety 9 (green cotyledons), *YYGGiidd*. The hybrid between these two varieties would therefore be *YYGGIiDd*. The factorial composition of the F_2 generation and their breeding behavior in F_3 are as follows:

F_2 ratio	*Genotypes*			*Types and proportions in F_3*
15 yellow	(1) *YYGGIIDD*	1	7	Breed true for yellow cotyledon
	(2) *YYGGIIDd*	2		
	(3) *YYGGIiDD*	2		
	(4) *YYGGiiDD*	1		
	(5) *YYGGIIdd*	1		
	(6) *YYGGIiDd*	4	4	Segregate in 15:1 ratio
	(7) *YYGGIidd*	2	4	Segregate in 3:1 ratio
	(8) *YYGGiiDd*	2		
1 green	(9) *YYGGiidd*	1	1	Breeds true for green cotyledon

Lines segregating in a 3:1 ratio carry only one of these factors, *I* or *D*. Whether one or the other is present in a particular line may be determined by making crosses between it and other lines also giving this simple ratio. If, as a result of such crosses, types are obtained which breed true or which again segregate in a 3:1 ratio, the same factor is present in both lines; but if segregation occurs in a 15:1 ratio, different factors are present in the two lines, and *D* can be arbitrarily assigned to one line and *I* to the other. These lines can then be used in crosses with other yellow-cotyledon varieties to determine whether, in the latter, *I* or *D*, or even a different factor is responsible for the yellow cotyledon color.

Another method of determining which factor is carried by a particular line is by means of linkage which exists between one of the factors for yellow cotyledon and the factor, *V*, for green seed coat. This will be considered more in detail in a succeeding section.

As far as could be determined dominance was complete in the case of both *I* and *D*. Furthermore, one factor appears not only as efficient as the other in causing the green pigment to fade on maturity, but either one appears to be as efficient as both together in bringing about this change. Hence, factors, *D* and *I* are considered to be real duplicates of each other, like SHULL's *C* and *D* for obcordate seed capsules in Bursa.

Duplicate factors in other plants

Duplicate factors have been reported by NILSSON-EHLE (1908)for red grains in wheat and (1909) for the presence of a ligule in oats; for endosperm color in corn by EAST (1910), EAST and HAYES (1911), and BURTT-DAVY (1914); for capsule form, leaf lobes and leaf texture in *Bursa bursa-pastoris* by SHULL (1914, 1918, 1920); and for variegation in *Plantago major* by IKENO (1917). In respect to grain color in wheat and endosperm color in corn there is an apparent lack of dominance and a cumulative effect resulting in a greater intensity of color when either factor is homozygous or when both are present in the same zygote. In the other cases mentioned above, dominance is apparently complete, and the several genotypes in F_2 cannot be distinguished except by the progeny test. The factors in all these cases, however, show independence in inheritance (i.e., no linkage).

Auburn variety

It will be recalled that both cotyledon colors were found in a bulk sample of Auburn, a black-seeded variety.

In 1915, a number of plants were grown from both green- and yellow-cotyledon seeds as found in the original sample, but no detailed records were made concerning cotyledon color. Only one plant (115)-184, grown from a seed with yellow cotyledons, was harvested. Of 628 seeds produced by this plant, 480 had yellow and 148 had green cotyledons. This proportion suggests a 3:1 ratio of yellow to green. On the basis of such a ratio the expected numbers would be 471 and 157, respectively.

The following year, 52 plants were grown from the yellow-cotyledon beans and 17 from the green, and counts were made on 50 and 17 plants, respectively. Tables 35 and 36 give the data for each plant.

Of the 50 plants from yellow-cotyledon seeds (see table 36), 38 proved to be heterozygous, and 12 bred true for yellow. On the basis of a 2:1 ratio these numbers should be 33 and 17, respectively.

In 1917, fifteen plants were grown from yellow-cotyledon seeds of plant (211)-390. All but one of these proved to be heterozygous. The ratio, therefore, of heterozygous to homozygous plants was 14:1. No reason is apparent for such a wide divergence from expectation. It may be only a chance deviation, but it may be significant, especially as it falls in line with the case above given in which the homozygous plants were also deficient. There were also five plants grown from green-cotyledon seeds of (211)-390, and they all bred true for green.

As green is recessive all beans with this cotyledon color should breed true. It will be noted from table 35 that in addition to the green some yellow-cotyledon seeds were found in each plant, and that they ranged in number from 3 in plant (210)-310 to 27 in plant (210)-308. In a total of 12,085 beans produced by all plants from green-cotyledon seeds, 11,893 had green cotyledons, and 192, yellow, or a ratio of 62:1.

Among the 12 plants (table 36) classed as breeding true for yellow cotyledons only 4 unexpected seeds were found out of 9864 seeds produced. This is a ratio of 1 to 2466. The disparity in the ratios given by the two types of plants is very striking.

In a preceding section, a discussion was given of ways in which the occurrence of such unexpected beans may be accounted for. Points there brought out apply equally well here. Cross-pollination, for example, would account for many of the yellow-cotyledon seeds found in plants otherwise breeding true for green. Direct proof that natural crossing did occur is at hand. Plant (210)-330 (see table 35), is noted as having 14 seeds with yellow cotyledons and 987 with green. In 1917, twelve plants were grown from the green-cotyledon seeds, and all bred true. From the seeds with yellow cotyledons seven plants were grown, one of which bore seeds with the black seed coat characteristic of the Auburn variety, while the seeds borne by the other six plants had a mottled black and yellow seed coat. All but one of these seven plants showed segregation in cotyledon color in an approximate 15:1 ratio (see table 37), and that plant produced only 23 seeds, most of which were small and immature. Probably all had yellow cotyledons, though this could not be determined with certainty. Plant (210)-330 was growing in the row in close proximity to plant (211)-332 which segregated in a 3:1 ratio in cotyledon color; and in the rows on either side of (210)-330 were types with yellow seed coats, yellow cotyledons, brown hilums and gray pubescence. It is more than probable that the results shown in table 37 can be explained by natural crosses with these adjacent types.

Plant (469)-54 was tested further, and the resulting progeny showed segregation in several plant characters, such as color of seed coat, pubescence and hilum, while with respect to cotyledon color, three types were produced in approximately the expected proportions; namely, a type breeding true for yellow, a type segregating in a 3:1 ratio, and a type segregating in a 15:1 ratio. Among the segregates, moreover, a plant was occasionally found with the self-black seed coat typical of the Auburn variety. It is fairly certain, therefore, that most of the original beans with yellow cotyledons, at first supposed to be mixtures, were the result of crosses with a yellow-cotyledon variety having two factors for cotyledon color.

Plant (469)-53 with its self-black seed coat cannot be explained in this way. If it is the result of a cross with a yellow-coated variety, the seed coat would likely be mottled instead of self-black. The ratio of yellow to green cotyledons shown by this plant is also peculiar; the deviation on a 15:1 basis being nearly 6 times the probable error. It may represent only a 3:1 ratio, and hence be simply the result of a cross with plant (211)-332, or a mixture from a segregating plant of this variety. Further speculation, however, is out of place till this plant has been tested.

A number of seeds of plant (211)-340 (see table 36) were also tested to compare the progenies of certain apparently "intermediate"-cotyledon-colored seeds with those whose cotyledons were a full rich yellow. From the latter type of seeds, 12 plants were grown, all of which bred true for yellow cotyledon. One of these, however, showed the same peculiar seed-coat color as was described above, indicating that the original bean was the result of a cross. From the intermediate seeds, 39 plants were grown, 37 of which bred true for yellow, one segregated in a ratio of 3 yellow: 1 green, and one bred true for green. A mechanical mixture was probably responsible for the last-named plant, while natural crossing would account for the one which segregated, particularly as plant (211)-340 grew in the row adjacent to and in contact with a plant, (211)-338, which segregated in cotyledon color.

In view of the above evidences for the occurrence of natural hybrids in the Auburn variety, it is believed that natural crossing will account for a considerable number of the unexpected beans. A mutative change from green to yellow might also account for some. There are a few beans, it is true, whose occurrence can only be explained, perhaps, by stating that they are the result of mechanical mixtures; but they are thought to be much less numerous than the hybrid beans, and therefore, that they are too few in number to cast any doubt on the ratios herein reported or the conclusions drawn therefrom.

The three green-cotyledon seeds found among plants otherwise breeding true for yellow are very probably not the result of cross-pollination or of mutation. They may be genetic yellows in which the green pigment has not faded out for some reason or other; or they may simply be mixtures from some other plant. The latter is the more probable. If these are considered to be mixtures, then it would be expected that as many more beans with yellow cotyledons should be classed as such. This would mean that 1 in 1233 beans was a mixture, not far from the proportion which was found in plants breeding true for yellow in progenies of the cross variety 8 × variety 9, discussed earlier in this paper.

There is no reason to believe that the proportion of mixed seeds is any greater in the plants breeding true for green. Hence, only a few of the 192 unexpected seeds found in these plants can be accounted for in this way. The evidence points to the conclusion that nearly all of them are the result of cross-pollination, which, for some reason not yet evident, appears to occur much more frequently in the Auburn variety than in varieties 8 and 9.

The data presented above show that the inheritance of cotyledon color in the Auburn variety can be explained by a simple allelomorphic relationship between the two cotyledon colors. Whether *I* or *D* is the factor responsible for yellow cotyledon in this variety is not yet known; but if it be *I*, then the yellow types have the composition *YYGGII* or *YYGGIi*, and the greens, *YYGGii*; but if it be *D*, then this factor should be substituted for *I* in the above formulae. Which factor is involved may be determined by following the same procedure as outlined for this purpose in types arising from the cross variety 8 × variety 9.

INHERITANCE OF GREEN AND YELLOW SEED-COAT COLORS

TERAO'S *results*

TERAO (1918) has already shown that green and yellow seed coats in soy-beans behave as a single allelomorphic pair, green being dominant to yellow and both types recurring in F_2 in a simple 3:1 ratio. This he found to be true no matter which way the cross was made when the female parent had yellow cotyledons, but when the cotyledons and seed coats of the female parent were green, there was no segregation at all, the F_1's and F_2's breeding true to the characters of the female parent.

These peculiar inheritance phenomena were interpreted as follows: The two kinds of chlorophyll, "(Y)" and "(G)" are present in the seed coats as well as in the cotyledons. In the inheritance of the seed coats, however, there is a pair of Mendelian factors (*Hh*) concerned.

"The factor '*H*' inhibits the chlorophyll '(*Y*)' in the seed-coat of the beans with yellow cotyledons from changing to yellow, producing beans with yellow cotyledons and green seed-coat; the absence of the factor '*H*', expressed by '*h*' allows the seed-coat of the bean with yellow cotyledons to remain yellow. The seed-coat of the bean with green cotyledons remains green no matter whether the factor '*H*' is present or absent, because the beans of this kind have the chlorophyll '(G)' which is incapable of changing the color."

However, in the F_2 of the cross green cotyledons, green seed coat ♀ × yellow cotyledons, yellow seed coat ♂, two types were observed, namely, a dark green, and a light green seed coat; and these occurred in a 3:1 ratio. But no plants were produced with yellow seed coats.

Variety 8 × variety 9

The cross variety 9 (green coat) × variety 8 (yellow coat) gave results which in part seemed to confirm those of TERAO. But seeds produced by F_1 plants had green seed coats irrespective of the way the cross was made, and without regard, also, to whether the cotyledon color of the female parent was green or yellow. The F_2 generation consisted of both types in an approximate ratio of 3 green to 1 yellow (see table 38).

F_2 plants with yellow seed coats bred true for this character, as shown by three progenies totaling 58 plants. Of 16 progenies from F_2 plants with green seed coats, 5 bred true for green and 11 segregated again, giving approximately 3 green to 1 yellow. The data for each progeny are given in table 39.

If the F_2 progenies and those of the F_3 which show segregation are added together, the total is 236 green to 87 yellow, a deviation of 6 from expectation.

From the data above presented it appears clear that green and yellow seed coats in soy-beans behave in inheritance as if determined by a single pair of factors (V, v).[4]

RELATION BETWEEN COTYLEDON AND SEED-COAT COLORS

When seed-coat and cotyledon colors are considered together, it is obvious that the two characters are not absolutely independent of each other in inheritance. TERAO (1918) observed this fact, stating that "beans with green cotyledons have always green seed coats." The present author has not observed any variety with green cotyledons beneath *yellow* coats, and PIPER and MORSE (1910) in their descriptions of nearly 300 varieties, mention no such type. Many varieties exist with black seed coats and green cotyledons and a type with green cotyledons and brown coats has recently been isolated in connection with the present investigation. This type also does not seem to occur among established varieties.

Among hybrids of the cross between varieties 8 and 9, a few plants have appeared bearing seeds with green cotyledons and yellow seed coats. When plants of this type appear, they breed true because recessive for both characters.

[4] "V" for virescent.

It is well to repeat here that variety 8 had yellow cotyledons beneath yellow seed coats, and variety 9 had green cotyledons beneath green seed coats. Hence one parent brought into the hybrid one dominant character, and the other parent, the other dominant character. It may not be out of place, also, to mention the well-known fact that the cotyledon color appears a generation ahead of a plant character, such as seed-coat color. In the above cross and its reciprocal, then, the hybrid seeds obtained showed the dominant cotyledon color, yellow, but the coat color of these seeds was yellow or green depending on which parent bore them.

Seeds produced by F_1 plants had green coats, the dominant color, but they were in the proportion of 15 yellow to 1 green, in respect to cotyledon, as pointed out earlier in this paper. From the yellow-cotyledon seeds

TABLE 8

Relation of cotyledon color and seed coat color in inheritance. Observed and corrected figures compared with expected on basis of independence.

COTYLEDON COLOR	COAT COLOR	EXPECTED PROPORTIONS	OBSERVED	CORRECTED	CALCULATED
15 yellow	3 green	45	147	150	160
	1 yellow	15	63	64	53
1 green	3 green	3	18	14	11
	1 yellow	1	0	0	4
Total			228	228	228

$\chi^2 = 7.726$ P = .053104

210 plants were grown, and from the green-cotyledon seeds, 18.[5] Table 8 shows how these plants were distributed among the various classes, and how this distribution compares with that expected on the basis of independence of the characters in inheritance.

A correction is made of the observed figures in table 8 for the reason that cotyledon color segregates on the F_1 plants, and in planting for the F_2 generation, no attempt was made to grow just one-fifteenth as many plants from green- as from yellow-cotyledon beans. Furthermore, if this had been done, the failure of some seeds to germinate would have resulted perhaps in wide departures from the theoretical ratio,—deviation for which segregation and recombination of genetic factors would not have been responsible. The use of such corrected figures is justified, as LINDSTROM (1917) has pointed out, provided (1) that the ratio to which the correction is made has been proved, and (2) that the actual proportions shown by

[5] Included in these figures are F_2 and F_3 plants of like parentage. The individual progenies on which these totals are based are given in table 40.

the observed figures for the other segregating character are maintained in the corrected figures.

The low value of P (table 8), calculated from deviations of the corrected from the expected numbers, points to a strong probability that the deviations were not due to random sampling. Some factor besides chance, therefore, was evidently involved in producing these results. In this connection two points appear significant; (1) not a single plant from green-cotyledon seeds bore yellow-coated seeds, though 4 such plants in 18 were expected; and (2) of the plants from yellow-cotyledon seeds, those bearing yellow-coated beans were in excess and those bearing green-coated seeds were deficient.

These facts become significant when it is remembered that the two types in excess, (a) yellow cotyledon, yellow seed coat, (b) green cotyledons, green seed coat, were the two parental types; and it appeared that a possible explanation for these results is that of linkage between one of the factors for cotyledon color, as *D*, and the factor, *V*, for green seed-coat color.

As stated earlier in this paper, *D* and *I*, the factors for yellow cotyledon color, give every evidence of being absolutely independent in inheritance. If so, then they are located on different pairs of chromosomes; and if *V* is linked, say, with *D*, it is independent of *I*; or if linked with *I*, it is independent of *D*. Obviously, so far as the results are concerned, it makes no difference whether *V* is linked with one or the other cotyledon factor. The linkage is considered arbitrarily, therefore, to exist between *V* and *D*.

The first question which naturally arises is whether the linkage is complete or only partial. If it be assumed for the moment that the linkage is complete, then the expected numbers for the types given in table 8 would be 157, 57, 14, and 0 as compared with the corrected numbers 150, 64, 14, and 0, respectively. In this particular case, then $\chi^2 = 1.172$, and P = .565483. Obviously, this is the closest fit that can be obtained for these data; for, any amount of partial linkage that might be assumed would bring the results nearer those calculated for the independent inheritance of *V* and *D*. Complete linkage, therefore, appears to give a satisfactory explanation as far as these data are concerned.

It has been shown earlier in this paper that the F_2 seeds were of three types as indicated by the F_3 generation in cotyledon color; namely, (1) those which bred true for yellow cotyledon; (2) those which segregated in a 15:1 ratio; and (3) those which segregated in a 3:1 ratio; and further, that these types appeared in the proportions of 7:4:4, respectively. If the cotyledon and seed-coat colors are independent in inheritance, each of these three types of F_2 yellow-cotyledon seeds should produce plants that show the coat colors in the ratio of 3 green to 1 yellow. In table 9, below, are shown the types and their expected proportions together with the actual data obtained.[6]

With the exception of the two types which segregated in cotyledon color, and which had green coats, there is obviously a wide divergence between observed and expected numbers. The deviations are so large that P has no value at all to 5 decimal places, and hence the data strongly support the idea of a linkage relation existing between the two characters concerned.

TABLE 9

Relation of cotyledon color and seed-coat color in inheritance. Observed figures compared with expected on basis of independence.

COTYLEDON COLOR	SEED-COAT COLOR	EXPECTED PROPORTIONS	OBSERVED	EXPECTED
7 Bred true for yellow	3 green 1 yellow	21 7	57 55	73.5 24.5
4 Segregated 15:1	3 green 1 yellow	12 4	45 3	42.0 14.0
4 Segregated 3:1	3 green 1 yellow	12 4	45 5	42.0 14.0
Total		60	210	210.0

$\chi^2 = 56.521$ P = .00000

On the assumption of complete linkage between V and D, no F_2 plants could occur which segregated in cotyledon color and had yellow seed coats. However, there were 8 such plants as shown in table 9, 3 segregating in a 15:1 ratio and 5 in a 3:1 ratio. Hence, the linkage cannot be complete.

It is next in order, therefore, to test out the theory of partial linkage. No direct way of doing this for these data was available. Tables were at hand (Bateson and Punnett 1911, Castle 1916) giving expected proportions of zygotic types in F_2 for any assumed linkage values in cases where only 2 factor pairs were involved; but these tables obviously could not be used for cases involving 3 factor pairs, 2 of which were duplicate.

[6] Individual progenies which furnish these data are given in table 40.

Hence, for such special cases the following formula[7] was developed from EMERSON's (1916) general formula:

$$\overbrace{12\,r^2 + 11\,(s^2 + 2\,rs)}^{\text{a}} : \overbrace{4\,(s^2 + 2\,rs) + 3\,r^2}^{\text{b}} : \overbrace{s^2 + 2\,rs}^{\text{c}} : \overbrace{r^2}^{\text{d}} \tag{1}$$

where

type a = yellow cotyledon, green seed coat,
type b = yellow cotyledon, yellow seed coat,
type c = green cotyledon, green seed coat,
type d = green cotyledon, yellow seed coat,

and

$r : s$ = any assumed gametic ratio.

The following formulae for r and s in terms of types a, b, c, and d, were deduced from the above general formula:

$$r = .25\sqrt{\text{a} + \text{b} + \text{d} + 15\text{c}} \tag{2}$$

$$s = .25\sqrt{\text{a} + \text{b} + \text{c} + \text{d}} - r \tag{3}$$

The values of r and s having thus been found, the percentage of crossing over was calculated by the following formula:

$$\frac{r}{r+s} \times 100 = \text{percent crossing over, repulsion phase.} \tag{4}$$

The application of formulae 2 and 3 to the corrected figures in table 8 gives the value .5 for r and 3.275 for s; in other words, in approximately every 8 gametes formed, 1 is a crossover. Applying formula 4, the percentage of crossing over is found to be 13.25. If, however, the exact corrected figures, 149.625, 64.125, 14.25 and 0 be used in these calculations instead of the whole numbers, 150, 64, 14 and 0, respectively, $r = 0$, and $s = 3.775$. Thus, no crossover gametes are formed, and the linkage is complete. Obviously, no conclusion can be drawn from these data as to the exact amount of linkage.

Fortunately, the data in table 9 throw some light on this problem. For any assumed gametic ratio, the expected zygotic series was determined by substituting for r and s in the following formula:

$$\overbrace{6\,r^2 + 3\,(4\,rs + s^2)}^{\text{a}} : \overbrace{r^2 + 2\,(rs + 2s^2)}^{\text{b}} : \overbrace{4\,r^2 + 2\,(2rs + 2s^2)}^{\text{c}} :$$

$$\overbrace{4\,rs}^{\text{d}} : \overbrace{2r^2 + 2\,(3rs + 2s^2)}^{\text{e}} : \overbrace{2\,r^2 + 3\,rs}^{\text{f}} : \overbrace{2\,rs + s^2}^{\text{g}} : \overbrace{r^2}^{\text{h}} \tag{5}$$

[7] The development of this and the following formulae will be presented in a separate paper.

where

type a = number of plants with all yellow-cotyledon seeds, green seed coats;

type b = number of plants with all yellow-cotyledon seeds, yellow seed coats;

type c = number of plants with 15 yellow- : 1 green-cotyledon seeds, green seed coats;

type d = number of plants with 15 yellow- : 1 green-cotyledon seeds, yellow seed coats;

type e = number of plants with 3 yellow- : 1 green-cotyledon seeds, green seed coats;

type f = number of plants with 3 yellow- : 1 green-cotyledon seeds, yellow seed coats;

type g = number of plants with all green-cotyledon seeds, green seed coats;

type h = number of plants with all green-cotyledon seeds, yellow seed coats;

By comparing the expected zygotic series thus obtained with the corresponding observed numbers, the calculated series giving the closest correspondence was chosen by inspection, and the approximate percentage of crossing over determined from the corresponding gametic ratio. In table 41 are shown the deviations of the observed from the expected proportions based on the given gametic ratios, together with the values of χ^2 and P for each. The gametic ratio of 2:13 appears to give the closest fit. This is a crossover percentage of 13.33, which is quite close to that calculated on the basis of the corrected numbers in table 8. It is very probable, therefore, that a ratio of 1 crossover gamete to 7 non-crossover gametes is not far from the correct ratio. More data are required, however, to determine the correct linkage value.

INHERITANCE OF HILUM COLOR

The two varieties which furnished the foregoing data on cotyledon and seed-coat colors also differed in color of hilum or "eye." In seeds of variety 8, the original hilum color was yellow, the same color as the seed coat, while in seeds of variety 9, the hilum was black, and the color was confined exclusively to the "eye."

Selfed seed borne by the parent plants of both varieties had hilums typical of their respective variety as above described. However, plants grown from these beans produced seed which were not altogether typical. Thus, seeds of variety 9 showed a pattern extending partially over the seed, due, apparently, to the spreading of the black pigment from the hilum as a center. In the case of variety 8, there was a change also, the hilum being brown in later generations, instead of the typical yellow. The seeds, furthermore, showed a similar pattern, except that the superimposed pigment was brown instead of black. The pattern in both cases consisted of blotches, patches, splashes or bands irregular in outline and variable in extent and location even on seeds from the same plant.[8]

The F_1 plants resulting from reciprocal crosses between these two varieties bore seeds with black hilum like that in seeds of variety 9, thus showing this to be the dominant character. These F_1 beans showed the pattern development, as did also those produced by the F_2 and F_3 plants. The pattern color was in every case the same as the hilum color, and there was, in the hybrids, the same variation in extent and location on the seed coats as in the pure-line progeny of the two parents described above.

The two types, black and brown hilums (which is equivalent to saying black and brown patterns), were obtained in the F_2 generation in a 9:7 ratio. The data are given in table 42. As there shown, of 144 plants, 85 had black hilum and 59 had brown. These numbers thus showed a deviation of 4 from expectation.

The 9:7 ratio obtained in the F_2 generation suggests two complementary factors, as B and H, for the production of black hilum. In the absence of either one or the other factor, the hilum is brown, and in the absence of both, the hilum is yellow like that shown by typical seeds of variety 8. On this interpretation, the expected ratio is 9:6:1. It was impossible in this material, however, to distinguish the double recessive and it is consequently included with the browns; hence the ratio, 9:7.[9]

F_2 plants bearing seeds with brown hilum, bred true for this character in F_3. There were in all 19 progenies containing 544 plants, the seeds

[8] The cause of development of the pattern in pure lines of self-colored beans is not at present known. It is a phenomenon of wide occurrence, appearing in a number of yellow and green varieties in many sections where soy-beans are grown. Seeds with such a pattern show no segregation on being tested and hence are not the result of hybridization. There are indications that the causal factors are, in part, physiological rather than genetic in nature, for the following reasons: (1) the wide variation in the extent of the pattern (from self-yellow or self-green to self-brown or self-black) on seeds from the same plant; and (2) the striking similarity in some material in the pattern shown by seeds in the same pod, and the dissimilarity of seeds in different pods though borne by the same plant. The study of the factors involved in the development of the pattern is of great practical importance from the standpoint of the uniformity of soy-bean varieties. It is hoped that investigations now in progress will throw some light on this problem.

[9] Whatever factors were responsible for the encroachment of the pattern in the pure-line progeny of variety 8 also caused its development in the double recessives obtained as segregates in this cross. In this discussion, therefore, the double recessive type is considered a bean with a brown pattern and brown hilum indistinguishable from $BBhh$ or $bbHH$.

of which all had brown hilums. Had it been possible to distinguish the double recessive, many of these progenies would no doubt have shown segregation.

The F_2 plants bearing seeds with black hilum bred differently, as was expected. On the theory of complementary factors, 1 F_2 plant out of 9 should breed true in F_3; 4 should produce blacks and browns in an approximate 3:1 ratio; and the remaining 4 out of 9 should behave like the F_1 plants, giving again an approximate 9:7 ratio. Of 17 progenies, 2 bred true, 7 gave blacks and browns in a ratio of 3:1, and 8 gave these types in a ratio of 9:7, as close an approximation to the theoretical proportions as is possible in 17 progenies. The actual data obtained are presented in table 43.

Data on the F_4 generation were obtained from progenies of single plants of progeny (917). Ofthe 14 plants with black hilum, 11 were tested and gave the results shown in table 44. It will be seen from this table that 4 progenies bred true, 3 gave a 3:1 ratio, and 4, a 9:7 ratio. In 11 progenies, the expected proportions for the three types are 1:5:5. For the actual data, $\chi^2 = 10.00$, and $P = .006738$. The fit is therefore poor, but the numbers are small. Some significance can be attached to the fact that all the types expected were obtained.

In a total of 28 progenies in F_3 and F_4, all from plants with black hilum, 6 bred true for this character, 10 segregated in a 3:1 ratio, and 12 segregated in a 9:7 ratio. On the basis of a 1:4:4 ratio, these numbers should be 3, 12.5 and 12.5, respectively. For these combined data, $\chi^2 = 3.52$, and $P = .177377$.

INHERITANCE OF PUBESCENCE COLOR

Tawny and gray pubescence colors have already been mentioned. They are found to behave in inheritance as a simple allelomorphic pair of characters, tawny being dominant to gray, as PIPER and MORSE (1910) have shown.

Reciprocal crosses between variety 9 (tawny pubescence) and variety 8 (gray pubescence) gave 10 F_1 plants, all of which were tawny. The F_2 generation showed segregation in a simple monohybrid ratio and the results were the same no matter which way the cross was made. Table 45 gives the results obtained.

Progenies were grown from 11 F_2 plants with gray pubescence, and all bred true, giving a total of 273 plants. From F_2 plants with tawny pubescence, 19 progenies were grown and they gave the results shown in table 46.

From this table, it is seen that 7 progenies bred true while 12 segregated. The expected numbers on the basis of a 1:2 ratio are 6 and 13, respectively. The ratios for the individual progenies show considerable variation, and the deviations from the expected 3:1 are, in some cases, quite marked. For example, (907) gave a ratio of 11 tawny to 1 gray; (908) 1 to 1; (917) 17 to 1; (1154) 9 to 1; and (1159) 7.5 to 1. The numbers are small, however, and may be, in consequence, only chance deviations from the expected.

Of the 17 plants in progeny (917) with tawny pubescence, 11 were tested. On the assumption that the above ratio shown by (917) is a 3:1, it would be expected that one-third, or 4, of the plants tested would breed true, and two-thirds, or 7, would again segregate in a 3:1 ratio. As shown in table 47, 6 bred true and 5 segregated. This excess in the number of homozygous tawny plants appears significant though it may not be so. However, the fact that the segregating progenies produced fair 3:1 ratios for such small numbers would seem to indicate mere chance deviation in the case of progeny (917).

Summation of all progenies in F_2, F_3 and F_4, showing segregation, gives 430 plants with tawny and 130 with gray pubescence, the expected numbers being 420 and 140, respectively.

Of 30 progenies, in F_3 and F_4, all from plants with tawny pubescence, 13 bred true for this character while 17 segregated. Based on a 1:2 ratio, these numbers should be 10 and 20, respectively, thus showing a deviation of three.

Hence, in the inheritance of pubescence color, a single pair of factors, *Tt*, is involved.

LINKAGE BETWEEN HILUM AND PUBESCENCE COLORS

One of the parents of this cross (variety 9) had tawny pubescence and black hilum, (*BBHHTT*) and the other parent (variety 8), gray pubescence and yellow hilum (*bbhhtt*).[10] The cross and its reciprocal showed the same results in all hybrid generations.

Plants of the F_1 generation had tawny pubescence and black hilum, these being the dominant characters. In the F_2 generation, the following types were obtained: (a) tawny pubescence and black hilum; (b) tawny pubescence and brown hilum; (c) gray pubescence and brown hilum. Not a single plant was observed with gray pubescence and black hilum. The actual data (table 10) conform fairly well to a 9:3:4 ratio for the three types obtained.

[10] In this discussion, as in the section on hilum color, the double recessive type in hilum color is always included with the browns, being indistinguishable from them.

F_2 plants which had brown hilum and gray pubescence, bred true for these characters as was shown by 11 progenies totaling 273 plants. F_2 plants with brown hilum and tawny pubescence bred true for the former character, and either bred true for tawny pubescence or segregated in a ratio of 3 tawny to 1 gray. The data are given in table 46, which contains F_3 results on the inheritance of pubescence color. Progenies in this table from brown tawny plants are (920), (921), and (1153). Of the 3 progenies, therefore, 2 bred true and 1 segregated.

Plants of the F_2 generation with tawny pubescence and black hilum bred differently in F_3. Some bred true for both characters, some segregated in hilum color alone, and the rest segregated in both characters, but in different proportions, depending on the factorial composition of the parent plant. The actual results are set forth in table 48.

TABLE 10

F_2 generation of black tawny × brown gray.

PROGENY NUMBERS	NUMBER OF PLANTS OBSERVED			
	Black tawny	Black gray	Brown tawny	Brown gray
(470)	10	–	2	7
(801)	40	–	10	16
(803)	35	–	7	17
Total	85	–	19	40
Expected numbers on basis of 9:3:4 ratio	81	–	27	36

$\chi^2 = 3.0115$ P = .22212

Theoretically, the F_2 plants with black hilum and tawny pubescence should consist of the following types (as shown by the F_3) and in the following proportions:

Of 9 black tawny F_2 plants
- (a) 1 should breed true.
- (b) 2 should segregate into 3 black tawny: 1 brown tawny.
- (c) 2 should segregate into 3 black tawny: 1 brown gray.
- (d) 4 should segregate into 9 black tawny: 3 brown tawny: 4 brown gray.

As seen from table 48, 2 F_2 plants belong to class (a), 4 to class (b), 3 to class (c), and 8 to class (d). These numbers are as close to expectation as is possible with 17 progenies. Were one more added to class (c) the actual and expected numbers would correspond exactly.

The totals for the 9:3:4 class show wide departures from the expected numbers, particularly those for the brown tawny and brown gray classes, the former being as much in excess as the latter is deficient. The actual ratio thus resembles more closely a 9:4:3 than a 9:3:4. All but 2 or 3 individual progenies showed such a reversal of ratio. This is peculiar in view of (1) the close correspondence of the F_2 data with the theoretical, and (2) the existence of the 4 types of F_2 plants in expected proportions, as indicated by the F_3 generation; but in the presence of such proof, it is not believed necessary to call in question the theoretical interpretation suggested.

As stated above under the separate discussions of the inheritance of hilum and pubescence colors, 11 plants of (917) with black hilum and tawny pubescence were tested. Their progenies constituted the F_4 generation of this cross with respect to these 2 characters. The data are given in table 49.

This table shows that of 11 progenies, 4 bred true, 2 gave a 3:1 ratio in hilum color, 1 gave a 3:1 ratio of black tawny to brown gray, and 4 gave a 9:3:4 ratio. Theoretically, these numbers should be 1, 2.5, 2.5 and 5, respectively.

Altogether, 28 progenies are represented in tables 48 and 49. Of these, 6 bred true, 6 segregated in a ratio of 3 black tawny to 1 brown tawny, 4 segregated in a ratio of 3 black tawny to 1 brown gray, and 12 segregated in a 9:3:4 ratio. These types should be in the proportions 3:6:6:13. The totals would have been in closer accord with expectation, had the F_4 results not shown such marked deviations.

Summation of all progenies in F_2, F_3 and F_4, giving 9:3:4 ratios, gives the following results:

Black tawny	254; expected,	242
Brown tawny	82; expected,	81
Brown gray	95; expected,	108
Total	431	431

$\chi^2 = 2.1723 \qquad P = .342939$

Summation of all progenies in F_3 and F_4, giving ratios of 3 black tawny to 1 brown tawny, gives the following totals:

Black tawny	99; expected,	100.5	Deviation = 1.5
Brown tawny	35; expected,	33.5	
Total	134	134.0	

Summation of all progenies in F_3 and F_4 giving ratios of 3 black tawny to 1 brown gray, gives the following totals:

Black tawny	83; expected,	85.5	Deviation = 2.5
Brown gray	31; expected,	28.5	
Total	114	114.0	

The data above presented are in accord with the interpretation that one of the factors for hilum color, *B* or *H*, is completely linked with *T*, the factor for tawny pubescence. It is an arbitrary matter whether *B* and *T*, or *H* and *T*, are considered thus linked, as far as the interpretation of the results is concerned. The linkage is therefore taken to exist between *H* and *T*.

On this interpretation, the types obtained in F_2 and their behavior in F_3 when selfed are as follows:

Phenotypic ratio F_2	*Genotypic ratio*	*F_3*
9 Black hilum, Tawny pubescence	1 *BHT . BHT*	Breeds true
	2 *BHT . bHT*	3 black tawny: 1 brown tawny.
	2 *BHT . Bht*	3 black tawny: 1 brown gray.
	4 *BHT . bht*	9 black tawny: 3 brown tawny: 4 brown gray
3 Brown hilum, Tawny pubescence	1 *bHT . bHT*	Breeds true
	2 *bHT . bht*	3 brown tawny: 1 brown gray.
4 Brown hilum, Gray pubescence	1 *Bht . Bht*	Breeds true
	2 *Bht . bht*	Breeds true[11]
	1 *bht . bht*	Breeds true[11]

It is clear from the foregoing that all plants with brown hilum and tawny pubescence carry *H* and *T* but lack *B*; while plants with gray pubescence may lack all three factors or may carry *B* only. Owing, then, to this linkage relation it is possible to determine which of the plants with brown hilum carry *B* and which carry *H*.

As the linkage is complete between *H* and *T*, the combined effects of these two factors may be thought of as due to a single factor which has more than one effect. Thus, *T*, the factor for tawny pubescence, may be thought of as not only being able to change the pubescence color from gray to tawny, but also as acting with *B* to change the hilum color from brown to black. This is perhaps the most convenient way of regarding the situation.

[11] Theoretically, presence and absence of *B* should differentiate between brown and yellow hilum. See p. 516.

Single factors having multiple effects have been established in a number of forms. In *Drosophila melanogaster*, for example, the factor for morula eye is also responsible for "spineless" (BRIDGES 1919). In corn, red grain and red cob are inherited together and apparently both are due to the same factor (EMERSON 1911). In the soy-bean (unpublished data), a purplish stem always accompanies a purple flower. Very likely the same factor causes both effects. Other examples could be cited, all to the same point. Indeed, so many cases of unbroken correlation have been and are being established that every factor, it is believed, has many more effects than simply the one which happens to be most conspicuous and for which it is named.

CHARACTERS INHERITED INDEPENDENTLY

The relationship between hilum and pubescence, and between cotyledon and green seed coat have been discussed above. It next remains to discover what relation, if any, exists between (1) cotyledon and pubescence color, (2) cotyledon and hilum color, (3) seed-coat and pubescence color, and (4) seed-coat and hilum color.

The data are given in tables 50–53. The progenies furnishing these data are F_2's and F_3's of like parentage in plant characters, but F_3's and F_4's of like parentage in cotyledon color. Included in the tables are the expected numbers calculated on the basis of independent inheritance of the factors concerned, and the values of χ^2 and P.

The lowest value for P, 0.634195, was found in table 53, giving the data on seed-coat and pubescence colors; the highest value for P, 0.809799, was found in table 52, for seed-coat and hilum. The chances, therefore, are better than even in each case that the characters concerned are inherited independently of each other.

LINKAGE GROUPS

The inheritance of six factors and their linkages have been discussed in this paper. These factors are grouped as follows:

I. *D*, factor for yellow cotyledon. } About 13 percent
V, factor for green seed coat. } crossing over.

II. *I*, duplicate factor for yellow cotyledon.

III. *B*, factor for brown hilum. Complementary with *H* in producing black hilum.

IV. *H*, factor for brown hilum. } Completely
T, factor for tawny pubescence. } linked.

Y and *G* are factors for yellow and green pigment, respectively, in the cotyledons, but since no soy-beans have yet been found lacking one or the other pigment, except as caused by the action of *I* or *D*, the mode of inheritance of *Y* and *G* cannot be determined.

Studies have been made on the inheritance of other characters in the soy-bean; as, dwarfness, flower color, etc. The data are to be published soon. To date, however, their relations with the characters reported in this paper have not been determined, though some preliminary studies indicate that flower color is independent of both factors *D* and *I* for cotyledon color.

SUMMARY

1. Yellow cotyledon was found to be dominant to green. There was no evidence of maternal inheritance.

2. Cotyledon color in the F_2 generation of certain crosses showed aberrant ratios which were interpreted as 15:1 ratios only in the light of data on later hybrid generations.

3. The F_3 generation consisted of three types of progenies derived from F_2 yellow-cotyledon beans; namely, a type breeding true for yellow; a type segregating according to a 15:1 ratio; and a type segregating according to a 3:1 ratio. The observed numbers of plants belonging to the three types approached closely the expected proportions of 7:4:4.

4. Cotyledon color in the F_4 generation confirmed results obtained in F_3. (a) Progenies from yellow-cotyledon beans which bred true in F_3 continued to breed true in F_4. (b) Progenies from lines giving 3:1 ratios in F_3 were of two types in F_4; namely, a type breeding true, and a type giving 3:1 ratios; and these two types were to each other as 1:2. (c) Progenies from lines giving 15:1 ratios in F_3 gave again the three types and in the same proportions as were obtained in the F_3 generation.

5. With three exceptions the green-cotyledon beans bred true for green. These exceptions are believed to be due to errors in classification, the beans appearing green, though proving themselves to be yellow, genetically.

6. Fourteen percent of the plants classed as breeding true for yellow or green cotyledon bore from 1 to 10 seeds of the unexpected cotyledon color. Cross-pollination, unfavorable weather conditions, mutation, and mechanical mixtures are the factors believed to be responsible for their occurrence. It is felt that they do not occur in proportions large enough to affect the validity of the results.

7. In the Auburn, a black-seeded variety, found to be segregating for cotyledon color, all green-cotyledon beans were found to breed true, but

the yellow-cotyledon beans from segregating plants were of two types in the ratio of 1:2, namely, a type breeding true for yellow, and a type giving a 3:1 ratio,—indicating a simple allelomorphic relationship between the two cotyledon colors.

8. Green seed coat proved to be dominant to yellow seed coat, and in F_2 a ratio of three green to one yellow was obtained.

9. There is an apparent repulsion between green seed coat and yellow cotyledon, and conversely between yellow seed coat and green cotyledon. Evidence available indicated about 13 percent crossing over.

10. Black hilum is dominant to brown hilum, and in F_2 a ratio of 9 black to 7 brown was obtained. This indicates that there are two factors, complements of each other, which are necessary to produce black hilum. In the absence of either one or both, the hilum is brown.

11. Tawny pubescence is dominant to gray pubescence, and in F_2 a ratio of 3 tawny to 1 gray was obtained.

12. Complete linkage was found to exist between the factor for tawny pubescence, and one of the complementary factors for black hilum. No plants were produced with black hilum and gray pubescence.

In the light of these facts the following factors were used to explain the inheritance of the above characters in soy-beans:

Y, factor for yellow pigment in cotyledon.

G, factor for green pigment in cotyledon.

I, factor causing green pigment to fade out at maturity; *i*, green cotyledon, in absence of *D*.

D, duplicate of *I; d*, green cotyledon, in absence of *I*.

V, factor for green seed coat; *v*, yellow seed coat.

T, factor for tawny pubescence; *t*, gray pubescence.

B, factor for brown hilum. Complement of *H*.

H, factor for brown hilum. Complement of *B*. With both *B* and *H* present the hilum is black.

LITERATURE CITED

Bateson, W., and Punnett, R. C., 1911 On gametic series involving reduplication of certain terms. Jour. Genetics **1**: 293–302. *Pl. 40.*

Bridges, C. B., and Morgan, T. H., 1919 The second-chromosome group of mutant characters. Carnegie Institution of Washington Publication No. 278, pp. 123–304.

Burtt-Davy, J., 1914 Maize, its history, cultivation, handling, and uses, xl + 831 pp. *Figs. 1–245.* London: Longmans, Green & Co.

Castle, W. E., 1916 Tables of linkage intensities. Amer. Nat. **50**: 575, 576.

Collins, J. L., 1919 Chimeras in corn hybrids. Jour. Heredity **10**: 3–10.

Darbishire, A. D., 1911 Breeding and the Mendelian discovery. vi+282 pp., *34 figs. 6 pls.* New York: Cassell & Co.

EAST, E. M., 1910 A Mendelian interpretation of variation that is apparently continuous. Amer. Nat. **44**: 65–82.
EAST, E. M., and HAYES, H. K., 1911 Inheritance in maize. Connecticut Agric. Exp. Sta. Bull. No. 167, pp. 1–141, *Pls. 1–25*.
EMERSON, R. A., 1911 Genetic correlation and spurious allelomorphism in maize. 24th Ann. Rept. Nebraska Agric. Exp. Sta., pp. 1–58.
1916 The calculation of linkage intensities. Amer. Nat. **50**: 411–420.
HARRIS, J. A., 1912 A simple test of the goodness of fit of Mendelian ratios. Amer. Nat. **41**: 741–745.
IKENO, S., 1917 Variegation in Plantago. Genetics **2**: 390–416.
LINDSTROM, E. W., 1917 Linkage in maize; aleurone and chlorophyll factors. Amer. Nat. **46**: 225–237.
NILSSON-EHLE, H., 1908 Einige Ergebnisse von Kreuzungen bei Hafer und Weizen. Bot. Notiser **1908**: 257–294.
1909 Kreuzungsuntersuchungen an Hafer und Weizen. Lunds Univ. Årsskr. N. F. Afd. 2, Bd. 5, Nr. 2, pp. 1–122.
PEARSON, KARL, 1914 Tables for statisticians and biometricians. Pp. lxxxiii + 143. London: Cambridge University Press.
PIPER, C. V., and MORSE, W. J., 1910 The soy-bean: history, varieties, and field studies. U. S. Dept. Agric., Bur. Plant Industry Bull. No. 197, pp. 1–84. *Pls. 1–8*.
SHULL, G. H., 1914 Duplicate genes for capsule-form in *Bursa bursa-pastoris*. Zeitschr. f. ind. Abstamm. u. Vererb. **12**: 97–149.
1918 The duplication of a leaf-lobe factor in the shepherd's purse. Brooklyn Bot. Gard. Mem. **1**: 427–445.
1920 A third duplication of genetic factors in shepherd's purse. Science **51**: 596.
TERAO, H., 1918 Maternal inheritance in the soy-bean. Amer. Nat. **52**: 51–56.
WHITE, O. E., 1916 Inheritance studies in Pisum. I. Inheritance of cotyledon color. Amer. Nat. **50**: 530–547.

APPENDIX

TABLE 11

Cotyledon color in F_3 generation. Plants produced from seeds with green cotyledons.

PARENT	PLANT NUMBER	NUMBER SEEDS OBSERVED WITH	
		Yellow cotyledon	Green cotyledon
(339)	(470)– 73	0	39
(471)–80	(801)–110	3	375
(471)–80	–112	0	311
(471)–80	–118	3	285
(471)–80	–122	3	426
(471)–80	–132	5	264
(471)–81	(803)–248	2	209
(471)–81	–252	0	468
(471)–81	–254	2	377
Totals		18	2754

TABLE 12

Cotyledon color in F_3 generation. Plants produced from seeds with yellow cotyledons. Progeny of (471)–80.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev. / P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(801)– 4	458	0				
– 14	322	0				
– 18	501	0				
– 22	95	0				
– 24	320	0				
– 26	266	0				
– 30	298	0				
– 32	505	0				
– 36	403	0				
– 40	281	0				
– 50	318	0				
– 54	486	0				
– 62	332	0				
– 66	601	0				
– 70	422	0				
– 74	302	0				
– 84	350	0				
– 90	451	0				
– 92	434	0				
– 94	325	0				
– 96	415	0				
– 98	534	0				
–114	294	0				
–260	553	0				
–264	504	0				
–276	353	0				
–284	433	0				
–292	406	0				
–294	423	0				
–296	184	0				
–298	213	0				
–300	365	0				
Sub-total	12,579	0				
– 2	293	19	.5	2.88	.174	15.4:1
– 10	284	16	3.0	2.83	1.06	17.7:1
– 42	493	38	5.0	3.76	1.33	12.9:1
– 46	570	64	24.0	4.11	5.84	8.9:1
– 52	315	17	4.0	2.97	1.347	18.5:1
– 58	243	12	4.0	2.61	1.533	20.2:1
– 64	235	20	4.0	2.61	1.533	11.7:1
– 76	520	41	6.0	3.867	1.552	12.6:1

TABLE 12 (continued)

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	$\frac{\text{Dev.}}{\text{P. E.}}$	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(801)– 78	160	12	1.0	2.14	.468	13.3:1
– 82	408	25	2.0	3.397	.589	16.3:1
– 86	412	19	8.0	3.39	2.057	21.7:1
–282	271	13	5.0	2.75	1.819	20.8:1
–286	344	24	1.0	3.13	.318	14.3:1
Sub-total	4548	320	16.0	11.39	1.405	14.2:1
– 16	209	64	4.0	4.83	.829	3.26:1
– 20	242	63	13.0	5.10	2.548	3.84:1
– 34	229	87	8.0	5.19	1.542	2.63:1
– 60	354	115	2.0	6.33	0.316	3.07:1
– 68	294	81	14.0	5.66	2.474	3.63:1
– 80	282	110	12.0	5.78	2.077	2.56:1
– 88	262	102	11.0	5.57	1.975	2.56:1
–100	203	76	6.0	4.88	1.228	2.67:1
–104	291	107	7.5	5.83	1.287	2.71:1
–266	357	117	1.5	6.36	0.236	3.05:1
–268	395	118	10.0	6.62	1.511	3.35:1
–272	247	91	6.5	5.37	1.211	2.70:1
–278	208	69	0.0	4.86	0.000	3.01:1
–280	226	70	4.0	5.03	0.795	3.22:1
–290	402	121	10.0	6.68	1.498	3.32:1
Sub-total	4201	1391	7.0	21.84	.321	3.02:1

TABLE 13

Cotyledon color in F_3 generation. Plants produced from seeds with yellow cotyledons. Progeny of (471)–81.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P.E.)	$\frac{\text{Dev.}}{\text{P. E.}}$	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(803)– 2	303	0				
– 4	130	0				
– 10	211	2				
– 26	430	0				
– 30	346	0				
– 32	374	0				
– 34	333	0				
– 42	426	0				
– 44	199	0				
– 50	227	0				
– 52	506	0				
– 54	319	0				
– 60	586	0				
– 64	213	0				
– 66	390	0				
– 72	359	0				
– 76	185	0				
– 80	328	0				
– 82	513	1				
– 86	122	0				
– 88	332	0				
– 90	417	0				
– 94	451	0				
– 98	412	0				
–270	309	0				
–274	415	0				
–276	340	0				
–282	376	0				
–284	294	0				
–286	486	0				
–290	541	0				
–292	337	0				
–300	350	0				
Sub-total	11,560	3				
– 14	276	23	4.0	2.82	1.419	12.0:1
– 18	385	34	8.0	3.34	2.395	11.3:1
– 28	277	19	0.5	2.81	0.178	14.6:1
– 62	336	22	0.0	3.09	0.000	15.3:1
– 68	474	39	7.0	3.70	1.892	12.2:1
– 78	394	27	1.0	3.35	0.299	14.6:1
– 84	309	25	4.0	2.98	1.342	12.4:1

TABLE 13 (continued)

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P.E.)	Dev./P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(803)– 96	311	17	3.5	2.96	1.183	18.3:1
–100	426	31	2.0	3.49	0.573	13.7:1
–278	270	15	3.0	2.756	1.089	18.0:1
–288	201	14	2.0	2.756	0.837	13.3:1
–296	412	27	0.0	3.42	0.000	15.2:1
Sub-total	4071	293	20.0	10.79	1.860	13.9:1
– 6	290	107	8.0	5.82	1.374	2.71:1
– 8	58	25	5.0	2.66	1.880	2.32:1
– 16	332	120	7.0	6.21	1.127	2.77:1
– 36	242	87	5.0	5.30	0.943	2.78:1
– 40	222	66	6.0	4.96	1.209	3.36:1
– 48	468	141	11.0	7.21	1.526	3.32:1
– 56	223	69	4.0	4.99	0.802	3.23:1
– 74	313	96	6.0	5.91	1.015	3.26:1
– 92	151	54	3.0	4.18	0.718	2.80:1
–272	264	87	1.0	5.47	0.183	3.03:1
–294	141	61	10.5	4.15	2.530	2.31:1
Sub-total	2704	913	9.0	17.56	0.513	2.96:1

TABLE 14

Cotyledon color in F_3 generation. Plants produced from yellow-cotyledon seeds of F_1 plants. Variety 8 (yellow) ♀ × variety 9 (green) ♂.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(470)–59	94	0				
–61	51	0				
–62	97	0				
–66	73	0				
–67	100	0				
–68	73	0				
–69	59	0				
–76	64	0				
–78	53	3 (?)				
–79	58	0				
Sub-total	722	3 (?)				
–60	72	3	2	1.410	1.419	24.0:1
–70	63	5	1	1.346	0.743	12.6:1
–71	21	4	2	0.816	2.451	5.3:1
–75	42	4	1	1.110	0.901	10.5:1
–77	24† (18)*	6† (12)*	4	0.894	4.475	4.0:1
Sub-total	242	22	7	2.550	2.750	10.1:1
–63	54	15	2	2.430	0.823	3.60:1
–65	26† (20)*	15† (22)*	5	1.870	2.674	1.73:1
–72	27	8	1	1.730	0.578	3.38:1
Sub-total	107	38	2	3.520	0.570	2.82:1

* Original figures.
† Corrected figures. See text.

TABLE 15

Cotyledon color in F_3 generation. Data from a natural cross. Progeny of plant B82a.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(1233)–1	109	0				
(1233)–4	146	0				
Sub-total	255	0				
(1233)–2	175	10	2	2.221	0.9005	17.5:1
(1233)–3	186	9	3	2.280	1.3160	20.7:1
Sub-total	361	19	5	3.183	1.5710	19.0:1

TABLE 16

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–60.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(906)–24	339	0				
–26	508	0				
–32	284	0				
–34	246	0				
–42	178	0				
–58	559	0				
–60	397	0				
Sub-total	2511	0				
–30	439	27	2.0	3.52	0.570	16.30:1
–36	428	25	3.0	3.475	0.864	17.10:1
–40	359	29	5.0	3.220	1.550	12.40:1
–56	214	17	3.0	2.480	1.210	12.60:1
Sub-total	1440	98	2.0	6.400	0.313	14.70:1
–44	195	62	2.0	4.680	0.430	3.15:1
–46	474	180	16.0	7.470	2.140	2.63:1
–50	285	93	1.5	5.680	0.260	3.06:1
–52	330	126	12.0	6.240	1.920	2.62:1
–54	592	203	4.0	8.240	0.486	2.92:1
–62	164	67	9.0	4.440	2.030	2.45:1
Sub-total	2040	731	38.0	15.370	2.470	2.79:1

TABLE 17

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–77.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	$\frac{\text{Dev.}}{\text{P. E.}}$	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(907)–80	210	0				
–82	231	0				
–88	437	0				
–90	284	0				
–92	271	2 (?)				
–94	328	0				
Sub-total....	1761	2 (?)				
–76	283	21	2.0	2.850	0.702	13.50:1
–84	7	1	0.5	0.462	1.083	7.00:1
–86	332	26	4.0	3.090	1.295	12.80:1
Sub-total....	622	48	6.0	4.230	1.420	13.00:1
–74	282	93	1.0	5.660	0.177	3.03:1
–78	294	111	10.0	5.880	1.710	2.65:1
Sub-total....	576	204	9.0	8.160	1.103	2.82:1

TABLE 18

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–75.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P.E.)	$\frac{\text{Dev.}}{\text{P.E.}}$	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(912)–278	256	0				
–284	498	0				
–288	474	0				
–296	152	0				
Sub-total	1380	0				
–262	435	26	3	3.51	0.855	16.70:1
–266	382	24	1	3.29	0.304	15.90:1
–276	442	31	1	3.55	0.282	14.30:1
–292	416	30	2	3.45	0.580	13.90:1
–294	395	24	2	3.34	0.599	16.50:1
–298	405	33	6	3.42	1.755	12.30:1
Sub-total	2070	168	28	7.72	3.267	12.30:1
–260	359	124	3	6.42	0.468	2.90:1
–268	454	158	5	7.23	0.692	2.87:1
–270	334	102	7	6.10	1.150	3.28:1
–272	291	121	18	5.93	3.036	2.41:1
–274	250	79	3	5.30	0.567	3.17:1
–280	453	137	10.5	7.09	1.481	3.30:1
–286	275	85	5	5.54	0.903	3.20:1
Sub-total	2416	806	0.5	16.58	0.030	3.00:1

TABLE 19

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–70.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(920)–20	157	0				
–22	381	0				
–26	308	0				
–30	408	0				
–32	433	0				
–38	407	0				
–40	295	0				
–44	270	0				
–46	590	0				
–50	200	0				
–52	517	0				
Sub-total	3946	0				
–34	497	28	5	3.74	1.337	17.70:1
–36	375	17	7.5	3.23	2.322	22.10:1
–48	349	20	3	3.14	0.956	17.50:1
Sub-total	1221	65	15	5.85	2.565	18.80:1
–24	291	101	3	5.78	0.519	2.88:1
–28	147	45	3	4.05	0.741	3.27:1
–42	335	98	10	6.08	1.645	3.42:1
–54	388	95	26	6.42	4.050	4.08:1
–56	413	125	9.5	6.77	1.403	3.30:1
Sub-total	1574	464	45.5	13.19	3.450	3.39:1

TABLE 20

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–71.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P.E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(903)–190	247	0				
–194	571	1 (?)				
–196	399	0				
–198	515	0				
–202	459	0				
–204	335	0				
–210	418	0				
–212	605	0				
–216	512	0				
Sub-total	4061	1 (?)				
–188	274	18	0	2.79	0.0	15.2:1
–192	412	20	7	3.39	2.065	20.6:1
Sub-total	686	38	7	4.39	1.595	18.0:1
–208	385	119	7	6.56	1.068	3.2:1

TABLE 21

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–72.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P.E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(913)–18	484	0				
–28	517	0				
–38	388	0				
–44	482	0				
–48	502	0				
–54	486	0				
Sub-total	2859	0				
–22	267	104	11.0	5.62	1.960	2.57:1
–24	322	117	7.0	6.12	1.144	2.75:1
–26	295	104	4.0	5.83	0.687	2.82:1
–30	258	80	4.5	5.37	0.838	3.23:1
–32	273	92	1.0	5.58	0.179	2.97:1
–34	382	132	3.5	6.62	0.529	2.89:1
–40	381	128	1.0	6.59	0.152	2.98:1
–46	408	135	1.0	6.81	0.147	3.02:1
–50	178	72	9.5	4.62	2.057	2.47:1
–52	265	91	2.0	5.51	0.363	2.91:1
–56	403	125	7.0	6.71	1.044	3.20:1
Sub-total	3432	1180	27.0	19.83	1.362	2.91:1

TABLE 22

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–65.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	$\frac{\text{Dev.}}{\text{P. E.}}$	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(909)–164	364	5				
–166	349	1 (?)				
–170	117	2				
Sub-total	830	7+(1?)				
–150	282	80	10.5	5.56	1.89	3.53:1
–160	272	91	0.0	5.57	0.00	3.00:1
–162	124	43	1.0	3.77	0.266	2.88:1
–168	242	97	12.0	5.38	0.230	2.49:1
–172	391	127	2.5	6.65	0.376	3.08:1
Sub-total	1311	438	1.0	12.21	0.082	3.00:1

TABLE 23

Cotyledon color in F_4 generation. Plants produced from seeds with yellow cotyledons. Progeny of (470)–63.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	$\frac{\text{Dev.}}{\text{P. E}}$	ACTUAL RATIO
	Yellow cotyletons	Green cotyledons				
(915)–102	424	0				
–104	493	1				
–114	188	0				
–116	235	0				
–120	104	0				
–134	419	0				
Sub-total	1863	1				
– 98	110	27	7.0	3.42	2.047	4.08:1
–106	265	82	5.0	5.44	0.919	3.23:1
–108	299	101	1.0	5.84	0.171	2.96:1
–112	233	74	3.0	5.12	0.586	3.15:1
–118	252	78	4.5	5.31	0.847	3.23:1
–122	206	59	7.0	4.75	1.474	3.49:1
–124	216	67	4.0	4.91	0.815	3.22:1
–128	284	96	1.0	5.69	0.176	2.96:1
Sub-total	1865	584	28.0	14.45	1.938	3.19:1

TABLE 24

Cotyledon color in F_4 generation. Progeny of plant (470)–59.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(911)–220	485	0
–222	487	0
–224	409	0
–228	192	0
–232	320	0
–234	329	0
–236	406	2 (?)
–238	437	0
–240	310	0
–242	648	2 (?)
–248	401	0
–252	394	0
–258	423	0
Total....................	5241	4 (?)

TABLE 25

Cotyledon color in F_4 generation. Progeny of plant (470)–61.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(905)– 2	366	0
– 4	450	0
– 6	216	0
– 8	239	0
– 10	290	0
– 12	261	0
– 14	180	0
– 16	270	0
–270	309	0
–272	390	0
–274	379	0
–276	270	0
–294	411	0
–278	312	0
–280	385	0
–282	307	0
–284	342	0
–288	305	9
–290	406	0
–298	252	0
Total....................	6340	0

TABLE 26

Cotyledon color in F_4 generation. Progeny of plant (470)–62.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER OF SEEDS WITH GREEN COTYLEDONS
(918)–238	284	0
–240	467	1
–242	348	0
–244	328	0
–246	395	5
–248	317	0
–250	280	0
–252	201	0
–254	437	3
–260	628	0
–262	472	0
–264	257	0
–266	511	0
–270	396	1
–272	250	2
–274	343	1
–276	350	0
Total....................	6264	13

TABLE 27

Cotyledon color in F_4 generation. Progeny of plant (470)–66.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(914)–58	423	0
–60	348	0
–64	241	0
–66	380	0
–68	413	0
–70	365	0
–72	274	0
–74	208	0
–76	68	0
–78	246	0
–80	406	0
–82	298	0
–84	417	0
–86	323	0
–88	594	0
–90	320	0
–92	387	0
Total....................	5711	0

TABLE 28

Cotyledon color in F_4 generation. Progeny of plant (470)–67.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(916)–162	539	0
–164	350	0
–166	473	0
–168	481	0
–170	185	0
–174	475	0
–176	473	0
–178	575	0
–180	506	0
–182	484	0
–184	490	0
–186	436	0
–188	469	0
–192	415	0
–194	437	0
–196	372	0
Total....................	7160	0

TABLE 29

Cotyledon color in F_4 generation. Progeny of plant (470)–68.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(904)–218	362	0
–220	340	0
–230	485	0
–234	578	0
–236	244	0
–238	321	0
–242	486	0
–244	452	0
–246	386	0
–248	236	0
–250	390	0
–252	427	0
–254	396	3 (?)
–256	412	2 (?)
–258	230	0
–260	203	0
–262	388	0
–264	427	0
–266	561	5
Total....................	7324	5+ (5?)

TABLE 30

Cotyledon color in F_4 generation. Progeny of plant (470)–69.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(908)– 96	416	1
– 98	398	0
–100	699	0
–102	159	0
–104	391	0
–106	538	0
–108	229	0
–110	429	0
–112	446	3
–118	201	1
–122	666	0
–124	348	1 (?)
–126	466	0
–128	342	0
–132	472	0
–134	176	0
Total....................	6376	5+ (1?)

TABLE 31

Cotyledon color in F_4 generation. Progeny of plant (470)–76.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(921)– 70	193	0
– 72	373	0
– 80	482	0
– 82	222	0
– 84	477	0
– 86	340	0
– 88	459	0
– 90	431	0
– 92	448	0
–96	557	0
– 98	706	0
–100	420	0
–104	456	0
Total.....................	5564	0

TABLE 32

Cotyledon color in F_4 generation. Progeny of plant (470)–78.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(917)–198	362	0
–200	94	0
–202	650	0
–204	79	0
–206	382	0
–208	593	0
–210	228	0
–212	102	0
–214	172	0
–216	350	0
–218	400	0
–220	312	0
–222	237	0
–228	355	0
–230	210	0
–232	350	0
–234	292	0
–236	267	0
Total....................	5435	0

TABLE 33

Cotyledon color in F_4 generation. Progeny of plant (470)–79.

PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(910)–180	364	0
–182	394	1 (?)
–184	204	0
–186	197	0
–188	292	0
–190	289	0
–192	476	0
–196	300	0
–200	303	0
–202	319	0
–204	501	0
–208	361	0
–212	520	0
–218	353	0
Total....................	4873	1 (?)

TABLE 34

Cotyledon color in F_4 generation. Plants produced from seeds with green cotyledons.

PARENT	PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(470)–60	(906)– 18	0	306
	– 20	0	427
	– 22	0	412
	Sub-total..........	0	1145
(470)–63	(915)–138	2	448
	–140	2	265
	–142	10	366
	–144	1	427
	–146	0	389
	–148	0	56
	–150	1	236
	–152	1	262
	–156	4	392
	Sub-total..........	21	2841
(470)–65	(909)–136	0	270
	–138	0	260
	–140	1	437
	–142	0	265
	–148	0	214
	–152	2	494
	–154	0	276
	Sub-total..........	3	2216
(470)–70	(920)– 58	0	300
	– 60	0	319
	– 62	0	420
	– 64	0	389
	Sub-total..........	0	1428
(470z)–71	(903)–184	2	475
	–186	2	456
	Sub-total..........	4	931
(470)–72	(913)– 2	0	305
	– 10	0	459
	– 12	2	386
	– 14	0	478
	– 16	0	325
	Sub-total..........	2	1953
(470)–77	(907)– 72	3	215

TABLE 34 (continued)

PARENT	PLANT NUMBER	NUMBER SEEDS WITH YELLOW COTYLEDONS	NUMBER SEEDS WITH GREEN COTYLEDONS
(470)–73	(919)– 2	3	269
	– 4	0	316
	– 6	0	455
	– 12	1	445
	–278	0	471
	–282	0	448
	–284	0	352
	–286	1	424
	–288	0	543
	–294	0	462
	–296	0	283
	–298	0	230
	–300	1	448
	Sub-total	9	5416

TABLE 35

Inheritance of cotyledon color in Auburn variety. Progeny of beans with green cotyledons.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH	
	Yellow cotyledons	Green cotyledons
(210)–292	9	446
–298	14	542
–300	14	977
–304	20	986
–306	12	738
–308	27	508
–310	3	590
–312	8	604
–314	6	656
–316	6	324
–318	4	907
–320	13	770
–322	7	753
–324	19	575
–326	8	1028
–328	8	502
–330	14	987
Total.....................	192	11,893

TABLE 36

Inheritance of cotyledon color in the Auburn variety. Progeny of beans with yellow cotyledons.

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev. / P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(211)–334	713	1				
–340	1027	1				
–342	965	0				
–360	872	0				
–372	786	0				
–394	1008	0				
–396	859	0				
–408	740	0				
–410	905	0				
–418	750	2				
–424	491	0				
–430	744	0				
Sub-total	9860	4				
(211)–332	614	214	7.0	8.40	0.83	2.869:1
–336	539	176	3.0	7.81	.38	3.063:1
–338	646	239	18.0	8.69	2.07	2.701:1
–344	614	217	9.0	8.42	1.07	2.830:1
–346	554	165	15.0	7.83	1.92	3.358:1
–348	597	178	16.0	8.13	1.97	3.354:1
–350	582	197	2.0	8.15	2.45	2.950:1
–352	679	214	9.0	8.73	1.03	3.173:1
–354	516	158	10.5	7.58	1.39	3.266:1
–356	786	248	10.5	9.39	1.12	3.169:1
–358	765	207	36.0	9.11	3.95	3.696:1
–364	367	106	12.0	6.35	1.89	3.460:1
–368	781	254	5.0	9.39	.53	3.075:1
–370	827	292	12.0	9.77	1.23	2.830:1
–374	528	175	1.0	7.74	.13	3.017:1
–376	480	137	16.0	7.25	2.21	3.504:1
–378	491	138	19.0	7.32	2.60	3.558:1
–380	827	259	4.5	9.62	.47	3.190:1
–382	759	276	17.0	9.39	1.81	2.750:1
–386	787	276	10.0	9.52	1.05	2.850:1
–388	449	143	5.0	7.11	.70	3.140:1
–390	452	127	18.0	7.01	2.57	3.560:1
–392	613	216	9.0	8.41	1.07	2.840:1
–400	1055	318	25.0	10.82	2.31	3.318:1
–402	629	197	9.5	8.39	1.07	3.190:1
–404	732	221	17.0	9.02	1.88	3.310:1
–406	820	251	17.0	9.56	1.78	3.267:1
–412	730	224	14.5	9.02	1.61	3.259:1
–414	236	72	5.0	5.13	.97	3.278:1
–416	750	237	10.0	9.18	1.09	3.165:1

TABLE 36 (continued)

PLANT NUMBER	NUMBER SEEDS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Yellow cotyledons	Green cotyledons				
(211)–420	903	283	13.5	10.06	1.34	3.190:1
–426	1077	335	18.0	10.97	1.64	3.215:1
–428	622	181	20.0	8.28	2.42	3.440:1
–432	311	106	2.0	5.96	.34	2.930:1
–434	712	205	24.0	8.84	2.72	3.470:1
–436	784	227	26.0	9.29	2.80	3.450:1
–440	843	284	2.0	9.81	2.04	2.970:1
–442	754	235	12.0	9.18	1.31	3.210:1
Sub-total....	25,211	7988	312.0	53.22	5.86	3.156:1

TABLE 37

Segregation in cotyledon color shown by plants grown from yellow-cotyledon seeds of plant (210)-330.

PLANT NUMBER	SEED COAT	NUMBER SEEDS WITH		Dev.*	P. E.	Dev./P. E.	ACTUAL RATIO
		Yellow cotyledons	Green cotyledons				
469–50	Mottled	183	19	6.0	2.320	2.586	9.60:1
–51	Mottled	182	10	2.0	2.260	0.885	18.20:1
–52	Mottled	23† (?)	0 (?)	0.0	0.000	0.000	
–53	Self-black	172	25	13.0	2.290	5.677	6.88:1
–54	Mottled	157	11	0.5	2.116	0.236	14.30:1
–56	Mottled	286	15	4.0	2.833	1.412	19.00:1
–57	Mottled	228	15	0.0	2.545	0.000	15.20:1
Total...............		1208	95	13.5	5.893	2.291	12.70:1

* Calculated on basis of 15:1 ratio.
† Not included in total. See text.

TABLE 38

Seed-coat color in the F_2 generation.

PROGENY NUMBER	NUMBER PLANTS WITH		Dev.	P. E.	Dev./P. E.	ACTUAL RATIO
	Green coat	Yellow coat				
470	16	3	2.0	1.273	1.571	5.34:1
801	47	17	1.0	2.337	0.428	2.76:1
803	40	17	3.0	2.205	1.361	2.35:1
Total........	103	37	2.0	3.456	0.579	2.78:1

TABLE 39

Seed-coat color in F_3 generation. Progeny of F_2 plants with green seed coats.

PROGENY NUMBER	NUMBER PLANTS WITH		Dev.	P. E.	$\frac{\text{Dev.}}{\text{P.E.}}$	ACTUAL RATIO
	Green coat	Yellow coat				
908	16					
909	15					
913	24					
914	19					
919	13					
Sub-total....	87					
903	7	7	3.5	1.093	3.203	1.00:1
904	15	4	1.0	1.273	0.786	3.75:1
906	15	5	0.0	1.306	0.000	3.00:1
907	8	4	1.0	1.012	0.988	2.00:1
910	9	5	1.5	1.093	1.372	1.80:1
911	9	4	1.0	1.053	0.949	2.25:1
912	14	3	1.0	1.204	0.831	4.67:1
916	14	2	2.0	1.168	1.712	7.00:1
917	13	5	0.5	1.239	0.404	2.60:1
918	13	4	0.0	1.204	0.000	3.25:1
920	16	7	1.0	1.401	0.714	2.29:1
Sub-total....	133	50	4.0	3.951	1.012	2.66:1

TABLE 40

Individual progenies in F_2 and F_3 showing distribution with respect to both cotyledon and seed-coat colors.

COTYLEDON COLOR	SEED-COAT COLOR	PROGENY NUMBERS								
		(470)	(801)	(803)	(903)	(906)	(907)	(912)	(920)	Totals
All yellow....................	Green	8	18	15	4	2	3	2	5	57
All yellow....................	Yellow	2	15	17	5	5	3	2	6	55
15 yellow : 1 green...........	Green	5	12	12	1	4	2	6	3	45
15 yellow : 1 green...........	Yellow	0	1	0	1	0	1	0	0	3
3 yellow : 1 green...........	Green	2	14	11	0	6	2	6	4	45
3 yellow : 1 green...........	Yellow	1	1	0	1	0	0	1	1	5
All green....................	Green	1	4	3	2	3	1	0	4	18
All green....................	Yellow	0	0	0	0	0	0	0	0	0
Totals		19	65	58	14	20	12	17	23	228

TABLE 41

Linkage of cotyledon and seed-coat colors. Comparison of actual with expected numbers calculated on the given gametic ratios.

	OBSERVED NUMBERS	DEVIATIONS OF ACTUAL FROM EXPECTED NUMBERS BASED ON GAMETIC RATIO OF										
		1:2	1:3	1:4	1:5	1:6	2:13	1:7	1:8	1:9	1:10	1:11
All yellow cotyledons												
Green seed coat	57	8.0	3.0	0.5	2.0	4.0	5.0	5.0	6.0	7.0	8.0	8.0
Yellow seed coat	55	22.0	17.0	14.5	12.0	10.0	9.0	9.0	8.0	7.0	6.0	6.0
15 yellow: 1 green cotyledon						4.0						
Green seed coat	45	1.0	0.5	1.5	3.0	4.0	5.0	5.0	5.5	6.0	6.0	7.0
Yellow seed coat	3	9.0	7.5	6.0	5.0	4.0	3.0	3.0	2.5	2.0	2.0	1.0
3 yellow: 1 green cotyledon												
Green seed coat	45	2.0	4.0	7.0	6.0	7.0	7.0	7.5	8.0	8.0	8.0	9.0
Yellow seed coat	5	4.0	2.0	0.5	0.0	1.0	1.0	1.5	2.0	2.0	2.0	3.0
Percentage of crossing over		33.33	25.0	20.0	16.66	14.28	13.33	12.5	11.11	10.0	9.11	8.33
χ^2		24.288	14.015	10.2312	7.441	6.3291	5.434	5.9558	6.343	6.048	6.088	9.233
P		0.000195	0.01553	0.069720	0.1923	0.278055	0.368287	0.31107	0.27685	0.302111	0.298688	0.101182

TABLE 42

F_2 generation with respect to hilum color.

PROGENY NUMBER	NUMBER PLANTS OBSERVED WITH		Dev.	P. E.	Dev./P. E.
	Black hilum	Brown hilum			
470	10	9	1	1.46	0.680
801	40	26	3	2.72	1.100
803	35	24	2	2.57	0.780
Total.........	85	59	4	4.02	0.995
Expected 9:7	81	63			

TABLE 43

F_3 generation in hilum color. Progenies of F_2 plants bearing seeds with black hilum.

PROGENY NUMBER	NUMBER PLANTS WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Black hilum	Brown hilum				
904	19					
910	14					
Sub-total	33					
908	8	8	4*	1.17	3.42	1.000:1
911	7	6	3	1.05	2.86	1.167:1
916	11	5	1	1.17	0.94	2.200:1
1158	28	11	1	1.82	0.55	2.550:1
1160	31	4	5	1.73	2.89	7.750:1
1161	28	9	0	1.78	0.00	3.100:1
1162	20	9	2	1.57	1.27	2.220:1
Sub-total	133	52	6	3.97	1.51	2.560:1
905	12	8	1†	1.50	0.67	
907	7	5	0	1.16	0.00	
912	7	10	3	1.38	2.17	
914	8	11	3	1.46	2.05	
917	14	4	4	1.42	2.82	
1152	22	15	1	2.04	0.49	
1154	32	17	4	2.34	1.28	
1159	19	15	0	1.95	0.00	
Sub-total	121	85	6	4.80	1.25	

* Calculated on basis of 3:1 ratio.

† Calculated on basis of 9:7 ratio.

TABLE 44

F_4 generation in hilum color. Progenies of F_3 plants bearing seeds with black hilum.

PROGENY NUMBER	NUMBER PLANTS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	$\frac{Dev.}{P. E.}$	ACTUAL RATIO
	Black hilum	Brown hilum				
1244	23	0				
1247	24	0				
1248	20	0				
1251	22	0				
Sub-total	89	0				
1246	18	4	1.5*	1.37	1.09	4.50:1
1249	17	5	0.5	1.37	3.65	3.40:1
1252	13	6	1.0	1.27	0.79	2.17:1
Sub-total	48	15	1.0	2.32	0.43	3.20:1
1242	9	12	3.0†	1.53	1.96	
1243	13	6	2.0	1.46	1.37	
1245	10	9	1.0	1.46	0.68	
1250	16	6	4.0	1.57	2.55	
Sub-total	48	33	2.0	3.01	0.66	

* Calculated on basis of 3:1 ratio.
† Calculated on basis of 9:7 ratio.

TABLE 45

Pubescence color in the F_2 generation.

PROGENY NUMBER	NUMBER PLANTS OBSERVED WITH		Dev.	P. E.	$\frac{Dev.}{P. E.}$	ACTUAL RATIO
	Tawny pubescence	Gray pubescence				
470	12	7	2.0	1.27	1.58	1.710:1
801	50	16	0.5	2.37	0.21	3.130:1
803	42	17	2.0	2.24	0.89	2.470:1
Sub-total	104	40	4.0	3.50	1.14	2.600:1
Expected 3:1	108	36				

TABLE 46

F_3 generation in pubescence color. Progenies of F_2 plants with tawny pubescence.

PROGENY NUMBER	NUMBER PLANTS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	$\frac{Dev.}{P.E.}$	ACTUAL RATIO
	Tawny pubescence	Gray pubescence				
904	19					
910	14					
911	13					
916	16					
920	23					
1153	43					
1160	35					
1162	29					
Sub-total	192					
905	14	6	1.0	1.31	0.76	2.33:1
907	11	1	2.0	1.01	1.98	11.00:1
908	8	8	4.0	1.17	3.42	1.00:1
912	12	5	1.0	1.20	0.83	2.40:1
914	12	7	2.0	1.27	1.57	1.72:1
917	17	1	3.5	1.24	2.82	17.00:1
921	11	4	0.0	1.13	0.00	2.75:1
1152	30	7	2.0	1.78	1.12	4.29:1
1154	44	5	7.0	2.05	3.42	8.80:1
1158	28	11	1.0	1.82	0.55	2.55:1
1159	30	4	4.5	1.70	2.65	7.50:1
1161	29	8	1.0	1.78	0.56	3.63:1
Sub-total	246	67	11.0	5.17	2.13	3.67:1
Expected 3:1	236	78				

TABLE 47

F_4 generation in pubescence color. Progenies of tawny plants of (917).

PROGENY NUMBER	NUMBER PLANTS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	$\frac{Dev.}{P.E.}$	ACTUAL RATIO
	Tawny	Gray				
1244	23	0				
1247	24	0				
1248	20	0				
1249	22	0				
1251	22	0				
1252	19	0				
Sub-total	130	0				

TABLE 47 (Continued)

PROGENY NUMBER	NUMBER PLANTS OBSERVED WITH		DEVIATION (Dev.)	PROBABLE ERROR (P. E.)	Dev./P. E.	ACTUAL RATIO
	Tawny	Gray				
1242	16	5	0.0	1.34	0.00	3.20:1
1243	15	4	1.0	1.27	0.79	3.75:1
1245	12	7	2.0	1.27	1.58	1.71:1
1246	18	4	1.5	1.37	1.09	4.50:1
1250	19	3	2.5	1.37	1.82	6.30:1
Sub-total	80	23	3.0	2.96	1.01	3.48:1

TABLE 48

F_3 generation of cross black tawny × brown gray. Progenies of F_2 black tawny plants.

PROGENY NUMBER	NUMBER PLANTS OBSERVED			
	Black tawny	Black gray	Brown tawny	Brown gray
904	19	0	0	0
910	14	0	0	0
Sub-total	33			
911	7	0	6	0
916	11	0	5	0
1160	31	0	4	0
1162	20	0	9	0
Sub-total	69	0	24	0
Expected 3:1	70	0	23	0
908	8	0	0	8
1158	28	0	0	11
1161	29	0	0	8
Sub-total	65	0	0	27
Expected 3:1	69	0	0	23
905	12	0	2	6
907	7	0	4	1
912	7	0	5	5
914	8	0	4	7
917	14	0	3	1
1152	22	0	8	7
1154	32	0	12	5
1159	19	0	11	4
Sub-total	121	0	49	36
Expected 9:3:4	116	0	39	51

TABLE 49

F_4 generation of cross black tawny × brown gray. Progenies of F_3 black tawny plants.

PROGENY NUMBER	NUMBER PLANTS OBSERVED			
	Black tawny	Black gray	Brown tawny	Brown gray
1244	23	0	0	0
1247	24	0	0	0
1248	20	0	0	0
1251	22	0	0	0
Sub-total	89	0	0	0
1249	17	0	5	0
1252	13	0	6	0
Sub-total	30	0	11	0
1246	18	0	0	4
1242	9	0	7	5
1243	13	0	2	4
1245	10	0	2	7
1250	16	0	3	3
Sub-total	48	0	14	19

TABLE 50

Showing the independence of cotyledon and pubescence colors in inheritance.

COTYLEDON COLOR	PUBESCENCE COLOR	PROGENY NUMBERS					TOTAL	EXPECTED ON BASIS 21:7:12:4:12:4
		(470)	(801)	(803)	(907)	(912)		
Bred true for yellow	Tawny	9	25	22	5	4	65	56
	Gray	1	8	10	1	0	20	20
Segregated in 15:1 ratio	Tawny	3	10	9	3	3	28	32
	Gray	2	3	3	0	3	11	11
Segregated in 3:1 ratio	Tawny	0	12	7	2	5	26	32
	Gray	3	3	4	0	2	12	11
Totals		18	61	55	11	17	162	162

$\chi^2 = 3.162$. P = .675594.

TABLE 51

Showing the independence of cotyledon and hilum colors in inheritance.

COTYLEDON COLOR	HILUM COLOR	PROGENY NUMBERS					TOTAL	EXPECTED ON BASIS 63:49:36:28:36:28
		(470)	(801)	(803)	(907)	(912)		
Bred true for yellow	Black	8	18	20	4	3	53	43
	Brown	2	15	12	2	1	32	33
Segregated in 15:1 ratio	Black	2	10	7	1	1	21	24
	Brown	3	3	5	2	5	18	19
Segregated in 3:1 ratio	Black	0	10	6	2	3	21	24
	Brown	3	5	5	0	4	17	19
Totals		18	61	55	11	17	162	162

$\chi^2 = 3.370$. P = .759944.

TABLE 52

Showing the independence of seed-coat and hilum colors in inheritance.

SEED-COAT COLOR	HILUM COLOR	PROGENY NUMBERS								TOTAL	EXPECTED 27:21:9:7
		(470)	(801)	(803)	(907)	(911)	(912)	(916)	(917)		
Green	Black	9	28	23	5	6	5	9	11	96	91
Green	Brown	7	19	17	3	3	9	5	2	65	71
Yellow	Black	1	10	12	2	1	2	2	2	32	30
Yellow	Brown	2	7	5	2	3	1	0	3	23	24
Totals		19	64	57	12	13	17	16	18	216	216

$\chi^2 = .957$ P = .809799.

TABLE 53

Showing the independence of seed-coat and pubescence colors in inheritance.

SEED-COAT COLOR	PUBESCENCE COLOR	PROGENY NUMBERS						TOTAL	EXPECTED 9:3:3:1
		(470)	(801)	(803)	(907)	(912)	(917)		
Green	Tawny	10	34	28	7	9	13	101	105
Green	Gray	6	13	12	1	5	0	37	35
Yellow	Tawny	2	14	13	4	3	4	40	35
Yellow	Gray	1	3	4	0	0	1	9	12
Totals		19	64	57	12	17	18	187	187

$\chi^2 = 1.730$ P = .634195