The Inheritance of Pigmentation in Soybean (*Glycine max* (L.) Merril)

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Abstract

All colors for flower, pubesence, pod wall, seedcoat, and cotyledon of soybean F_2 generation segregated as expected except in one cross for pubescence color and one cross for pod color. No segregation for seedcoat and cotyledon colors was found when the female parent had green seedcoat and cotyledon. Seedcoat color had an effect upon seed size and pod width, but had no effect on yield, seed number, plant height, flowering, maturity, fruiting period and pod length.

Introduction

Most qualitative characters, such as seed color, flower color, pod color and pubescence color, have little or no influence upon productivity or performance. Nevertheless, a knowledge of the mode of inheritance of these characters is of distinct aid to the breeder. From a practical standpoint, seedcoat colors are very improtant in the selection of pure line and in the detection of mixtures in commercial cultivars.

There are two distinct flower colors in soybeans, purple and white. It has been reported that a single gene pair controls these flower colors by a simple Medelian factor with purple dominant over white (Takahashi and Fukuyama, 1919; Nagai, 1926; Woodworth, 1923; Piper and Morse, 1923). Woodworth (1923) assigned the gene symbols W for purple flower and ww for white flower.

Purple pigmentation shows considerable variation, with the color ranging from pink through lavender and purple to blue. Flower color in a dihybrid ratio of 9 purple :3 purple-bule : 4 white have been reported (Takahashi and Fukuyama, 1919; Nagai, 1926). Hartwig and Hinson (1962) classified the colors of flower into four different patterns of purple, dark purple, dilute-purple, purple and very dilute purple (or near white), and white.

Pubescence colors were classified as tawny (brown) and gray color groups (Palmer and Kilen, 1987). Pubescence colors were found to behave in inhertance as a simple alleleomorphic pair of characters, with tawny being dominant to gray (Piper and Morse, 1910; Woodworth 1921). The symbol T is desigated for tawny and t is for gray. Bernard (1975) described another major gene pair affecting pubescence color: Td controlled dark-tawny and td controlled light tawny in the presence of T.

The pods of soybean vary in color from gray, through various shades of brown, to black. Each cultivar has a typical pod color, used for description varieties and to differentiate between them (Woodworth 1923). The pod wall color is classified into black, brown and tan color for plant introductions and cultivars. Dark color (yellow or brown) was dominant to light color (yellow or tan), with a simple segregation of 3 to 1 (Woodworth, 1923; Piper and Morse, 1923; Nagai, 1926). The symbol, L, dark colored or black pods and l, light colored pods, was listed by Woodworth (1933).

Bernard (1967) classified the three major pod wall colors in soybeans as black, brown and tan in his study. He proposed the following gentypes for each phenotype:

pod color	genotype
black	L_1--
brown	$l_1l_1L_2$-
tan	$l_1l_1l_2l_2$

He found there was no evidence for any linkage or interaction effects between pubescence and pod color, with the color of the pubescence on the pod been inherited independently of pod wall color.

Soybeans exhibit a great variety of colors and patterns in the seed. Most seeds are yellow, green (presumably chlorophyll), black (intense anthocyanin (Owen, 1972)), and several shades of brown. Various patterns of black or brown may occur on yellow or green seeds. Most commercial cultivars are yellow-seeded, but a few have a light green seed coat. Terao (1918) first showed that green coat, G, was dominant to yellow, g, and was monogenic. The same results also were found by Piper and Morse (1923), Woodworth (1921) and Owen (1928).

Terao (1918) reported that green and yellow seed coats in soybean behave as a single allelomorphic pair when the female parent had yellow cotyledons. But when the cotyledon and seed coat of the female parent were green, there was no segregation. Certain green-seeded (seedcoat and cotyledon) types have also be had as maternally inherited greens (Williams, 1938; Johnson and Bernard, 1962).

Terao (1918) reported that the cotyledon color was maternally inherited, but Woodworth (1921) indicated that there were no maternal effects on his experiments. However, the work of Terao (1918), Woodworth (1921), Owen (1927), and Williams (1938) showed that two types of green cotyledons occur, one due to the complementary action of two recessive genes (d_1d_2) and one controlled by cytoplasmic factors.

When seedcoat and cotyledon colors are considered together, it is obvious that the two characters are not absolutely independent of each other in inheritance. No yellow seedcoats from green cotyledon plants were observed in F_2 segregating populations for green vs. yellow seedcoat and cotyledon color (Terao, 1918; Woodworth, 1921; Woodworth and Williams, 1938). Terao (1918) observed this fact, stating that "beans with green cotyledon have always green seed coats. "

The black and brown pigments are independent of the green and yellow plastid pigments in the soybean seedcoat. In self-browns, or mottled types, not all of the plastid color is concealed, so it is usually possible to detect the presence of green when it is present, but in self-black types, the plastid colors are entirely masked (Owen, 1928). When the black and brown pigments do not occur in part or all of the seed coat, its color will be light yellow or light green depending on the gene pair G or g (Johnson and Bernard, 1962)

Stewart (1930)and Bays (1973) found that a simple gene pair controlled seed coat color resulting in a 3:1 ratio from crosses of yellow x black seed coat with yellow dominant over black. Ting (1946) reported four seed color groups (green, yellow, black and brown) from segregating generations from a cross of a cultivar with yellow seed x a wild soybean with black seed.

The inheritance of seedcoat color is complex, relative to hilum, flower, and pubescence color. The reviews on this subject have been published by Woodworth (1921, 1923), Owen (1928), Steward (1930), Probst (1950), Williams (1938, 1952), Mahmud and Probst (1953) and Johmson and Bernard (1962). A list of genes affecting pigmentation in soybeans has been provided by Palmer and Kilen (1987).

Materials and Methods

Two highly productive commercial cultivars, Forrest and Tracy-M, and two unadapted germplasm accessions, PI 399077 and PI 416808, selected for differemces in colors of flower, pubescence, pod, seed, and seed size, (Hartwig and Edwards, 1986), were chosen for this study. The descriptive data of the four soybean parents are presented in Table 1. All experiments were conducted at the Delta Branch, Mississippi Agricultural and Forestry Experiment Station, Stoneville, Mississippi.

Table 1. Descriptive agronomic characters of the soybean parents.

Parents	Color					Weight
	Flower	Pubescence	Pod	Seed	Hilum	g/100 seed
Tracy-M	W	T	Tn	Y	Y	16.1
PI 416808	P	T	Br	Bl	Bl	27.6
Forrest	W	T	Tn	Y	Bl	13.8
PI 399007	P	G	Bl	Gn	Br	6.8

W = white, P = purple, T = tawny, G = gray, Tn = tan, Bl = black, Br = brown, Y = yellow, Gn = green, All crosses were made on field-grown plants. An attempt was made to obtain reciprocal crosses between both sets of commercial cultivar and germplasm accession. However, the PI 416808 X Tracy-Mcross was unsuccessful. For ease of discussion, the Tracy-M X PI 416808 cross will be identified as cross 1, Forrest X PI 399077 as cross 2, and PI 399007 X Forrest as cross 3. The F_1 plants were grown in a glasshouse during the winter of 1986-1987. Supplemental light was used to extend the photoperiod. Seed from the F_1 plants were planted in a field nursery with the parents on May 20, 1987. Plantings were made in rows 4m long with 10cm between seeds and rows 0.9 m apart. Four hundred eighty seeds of cross 1, 240 seeds of cross 2, and 240 seeds of cross 3 were planted.

The following qualitative traits were recorded on F_2 populations:

1. Flower color -- Flower color (purple or white) was recorded for all F_2 populations.
2. Pod wall color -- Pod wall color (black, brown or tan) was recorded at maturity for all F_2 populations.
3. Pubescence color -- Pubescence color (tawny or gray) was recorded at maturity for F_2 populations, except cross 1 (both parents have tawny pubescence).
4. Cotyledon color -- Cotyledon color (green or yellow) was determined by scratching the seedcoat of the seeds from reciprocal crosses Forrest X PI 399007.
5. Seedcoat color -- Seedcoat (black, green or yellow) was recorded at maturity for all F_2 populations.

The chi-square test (Steel and Torrie, 1980) was used to measure goodness of fit to the expected ratio of qualitative characters in all F_2 populations.

Results and Discussion

The inheritance of flower color was studied in the cross Tracy-M X PI 416808 and the reciprocal crosses between Forrest and PI 399007 (Table 2). In the cross Tracy-M X PI 416808, there were 287 plants with purple flowers and 108 plants with white flowers in the F_2 population. The X^2 test gave a value of 1.155 (P = 0.30 - 0.20) for a ratio of 3 purple : 1 white. There were 164 plants with purple flowers and 57 plants with white flowers in the F_2 population from the cross Forrest X PI 399007. The X^2 value was 0.007 ($P > 0.95$) for a ratio of 3:1. In the cross PI 399007 X Forrest, the ratio of plants with purple : white flowers was 169:57. This gave a X^2 value with 0.006 ($P > 0.95$) for a ratio of 3 : 1. The results are consistent with the hypothesis that flower color is controlled by a simple pair of genes with purple dominant to white (Woodworth, 1923; piper and Morse, 1923).

The literature indicates that pubescence color is controlled by one pair of genes with tawny dominant to gray (Piper and Morse, 1910; Woodworth, 1921). Segregation for pubescence color was observed in the reciprocal crosses of Forreset and PI 399007 (Table 3). The F_2 population had 179 plants with tawny pubescence and 47 plants with gray pubescence in the cross PI 399007 X Forrest. The X^2 value was 2.130 (P = 0.20 - 0.10) for an expected ratio of 3 tawny : 1gray. However, in the cross Forrest

Table 2. X^2 value and probabilities for segregation of flower color in the F_2 populations.

CROSS Tracy-M X PI 416808

Flower color	Observed	Expected (3 : 1)	X^2	P
Purple	287	296.25		
White	108	98.75		
Total	395	395	1.155	0.30 - 0.20

CROSS Forrest X PI 399007

Flower color	Observed	Expected (3 : 1)	X^2	P
Purple	164	165.75		
White	57	55.25		
Total	221	221	0.007	> 0.95

CROSS PI 399007 X Forrest

Flower color	Observed	Expected (3 : 1)	X^2	P
Purple	169	169.55		
White	57	56.55		
Total	226	226	0.006	> 0.95

X PI 399007, there were 193 F_2 plants with tawny pubsecence and only 28 with gray pubescence. The X^2 test gave a value of 17.92 ($P < 0.001$), showing it was not a good fit to the expected ratio of 3 tawny : 1 gray, The observed numbers also did not fit a ratio of 13 tawny : 3 gray (X^2 = 5.36, P = 0.50 - 0.01).

The inheritance of pod wall color was studied in all three crosses (Table 4). The results indicated that X^2 was 0.919 (P = 0.50 - 0.30) for an expected ratio of 3 : 1 for the cross Tracy-M X PI 416808 with a segregation of 288 brown pod wall and 107 tan pod wall. There were 169 plants with black pod wall and 52 with tan pod wall in the F_2 population from the cross Forrest X PI 399007. The X^2 value was 0.255 (P = 0.70 - 0.50) assuming a 3 black : 1 tan ratio. However, segregation for black and tan pod wall in the cross PI 399007 X Forrset did not fit this expected ratio but fit a ratio of 13 black : 3 tan, giving a X^2 value of 1.180 (P = 0.90 - 0.70). Dark (black or brown) pod wall dominant to light (yellow or tan) pod wall with a segregation ratio of 3 to 1 has been reported previously (Woodworth, 1923; Piper and Morse, 1923; Nagai, 1926).

It is unknown why the pubescence color of cross Forrest X PI 399007 and pod color of cross PI 399007 X Forrest failed to fit the established segregation pattern. Bays (1973) indicated that pod wall color of one cross failed to fit a hypothesis of 3 : 1, but fit a 1 : 1 ratio. He explained that weather and disease caused a failure to correctly identify pod wall color. It is difficult to identify pubescence color and pod color without experience, because of subtle differences in the intensity of pigmentation, although no interaction effects between pubecence and pod wall color should be expected (Bernard, 1967). However, the difference between reciprocal crosses, especialy for pubescence color, is so great that additional studies seem justified.

Seed color was more complex than other qualitative traits in this experiment (Tables 5 and 6). The seedcoat color was green for the F_1 plants from the cross of Tracy-M (yellow seeddcoat) X PI 416808 (black seedcoat). There were three groups of seedcoat colors (93 were black, 215 were green and 87 were yellow) segregating in the F_2 population from this cross. The X^2 value, assuming a ratio of 4 black : 9 green : 3 yellow, was 2.827 (P = 0.30 - 0.20).

Because Tracy-M has yellow seedcoat and PI 416808 has black seedcoat and both have black hila, the seed from F_1 plants has green seedcoat, and the seed from F_2 plants segregated into black, green and yellow seedcoat. Based on the known genes for seed

Table 3. X^2 value and probabilities for segregation of pubescence color in the F_2 populations.

CROSS Forrest X PI 399007

Pubescence color	Observed	Expected (3 : 1)	X^2	P
Tawny	193	165.75		
Gray	28	55.25		
Total	221	221	17.92	< 0.001

CROSS PI 399007 X Forrest

Pubescence color	Observed	Expected (3 : 1)	X^2	P
Tawny	179	169.5		
Gray	47	56.5		
Total	226	226	2.130	0.20 - 0.10

Table 4. X^2 value and probabilities for segregation of pod wall color in the F_2 populations.

CROSS Tracy-M X PI 416808

Pod wall color	Observed	Expected (3 : 1)	X^2	P
Brown	288	296.25		
Tan	107	98.75		
Total	395	395	0.919	0.50 - 0.30

CROSS Forrest X PI 399007

Pod wall color	Observed	Expected (3 : 1)	X^2	P
Black	169	165.75		
Tan	52	55.25		
Total	221	221	0.255	0.70 - 0.50

CROSS PI 399007 X Forrest

Pod wall color	Observed	Expected (3 : 1)	X^2	P
Black	190	165.75 (183.6)+		
Tan	36	56.25 (42.4)	9.917	< 0.01
Total	226	226	(1.180)	(0.70 - 0.90)

+. the value in parentheses tested for expected ratio of 13 : 3.

Table 5. X^2 value and probabilities for segregation of seed color in the F_2 populations.

CROSS Tracy-M X PI 416808

seedcoat color	Observed	Expected (4:9:3)	X^2	P
Black	93	98.75		
Green	215	222.19		
Yellow	87	74.06		
Total	395	395	2.827	0.30 - 0.20

CROSS Forrest X PI 399007

seedcoat color	Observed	Expected (13:3)	X^2	P
Green	184	179.56		
Yellow	37	41.44		
Total	221	221	0.585	0.50 - 0.30

CROSS PI 399007 X Forrest

Cotyledon	Observed	Expected (15:1)	X^2	P
Yellow	206	165.75		
Green	15	13.81		
Total	221	221	0.109	> 0.95

Table 6. X^2 value and probabilities for segregation of color of seedcoat and cotyledon in the F_2 populations of the cross Forrest X PI 399007.

Cotyledon color	Yellow		Green
Seedcoat color	Green	Yellow	Green
Observed	169	37	15
Expected (12 : 3 : 1)	165.75	41.44	13.81
X^2	0.641		
Probability	0.90 - 0.70		

pigmentation (Palmer and Kilen, 1987), the genotype of iiGG is considered to control the seed color for PI 416808; the genotype of Tracy-M is $i^i i^i$ gg. In this cross, the green seedcoat on F_1 plants was found and was consistent with the i^iiGg genotype. The results from the F2 segregating population also was consistent with the phenotype of 4 black : 9 green : 3 yellow, with the genotype of 4 ii -- : 9 i^i -G- : 3 i^i -gg.

There were two other types of seedcoat and cotyledon colors in the reciprocal crosses of Forrest and PI 399007. All seeds from F_1 plants had green seedcoats with a yellow cotyledon for the Forrest X PI 399007 cross, but had green seedcoats and green cotyledons in the reciprocal cross. In the F_2 population from the Forrest X PI 399007 cross, the segregation was 184 green : 37 yellow seedcoat, 206 yellow : 15 green cotyledon, but no segregation for seedcoat color was observed in the F_2 population of PI 399007 X Forrest. The results indicated that there is a maternal effect for green seedcoat and cotyledon. Similar results have been reported by Terao (1918).

In the F_2 population of the cross Forrest X PI 399007, the X^2 value for seedcoat did not indicate a good fit for the expected ratio of 3 green : 1 yellow. However, the X^2 value, assuming a ratio of 13 green : 3 yellow, was 0.585 (P = 0.50 - 0.30). The segregation of cotyledon color was a good fit to an expected ratio of 15 yellow : 1 green, giving a X^2 value of 0.109 (P $>$ 0.95). The seedcoat color and cotyledon color segregants were combined to test for independent assortment. The X^2 value indicated a good fit to an expected ratio of 12 : 3 : 1, with a value of 0.641 (P = 0.90 - 0.70) with 169 plants having green seedcoat and yellow cotyledon, 37 with yellow seedcoat and cotyledon, and 15 with green seedcoat and cotyledon.

Using the identified genes controlling cotyledon and seedcoat color (Palmer and Kilen, 1987), we give a genotype, $\underline{D_1D_1D_2D_2gg}$, for Forrest with yellow cotyledon and seedcoat, and a genotype, $\underline{d_1d_1d_2d_2GG}$, for PI 399007 with green cotyledon and seedcoat. The yellow cotyledon and green seedcoat of the F_1 plants was consistent with a genotype of $\underline{D_1d_1D_2d_2Gg}$. Accordingly, the segregation of 12 green seedcoat with yellow cotyledon (gentype is $\underline{D}$---$\underline{G}$-), 3 yellow seedcoat and cotyledon (genotype is $\underline{D}$---$\underline{gg}$) and 1 green seedcoat and cotyledon (genotype is $\underline{d_1d_1d_2d_2}$--) was expected in F_2 Plants.

Hartwig and Edwards (1970) found that no relationship of seed size, pubescence color and flower color on seed yield of soybean. In our studies we found that, in the F_2 populations, the means of seed size and pod width were larger from black seed than from green or yellow seed for cross Tracy-M X PI 416808, and the mean of seed size was larger from yellow seed than green seed for cross Forrest X PI 399007. The study provided no evidence that seedcoat color had effect on the yield, seed number, plant height, flowering, maturity, fruiting period and pod length (Table 7). The study emphasized the obstacles that confront a soybean breeder when a desirable trait (large seed) is associated with an undesirable trait (black seedcoat).

Table 7. Means of traits and tests of significance among different seed color groups for the F_2 populations of crosses Tracy-M X PI 416808 and Forrest X PI 399007.

Seedcoat color group	Seed size (g/100seed)	Yield (g/plant)	Seed number (na/plant)	Plant height (cm)	Flowering (days)	Maturity (days)	Fruiting (days)	Pod length (mm)	Pod width (mm)
Tracy-M x PI 416808									
Black	17.23[a]	39.20	232.2	68.1	53.0	129.4	76.3	45.2	11.3[a]
Green	15.95[b]	39.07	247.4	67.4	52.6	128.5	75.9	44.2	11.0[b]
Yellow	15.85[b]	35.03	221.4	66.3	52.3	127.5	75.2	44.0	10.9[b]
Forrest x PI 399007									
Green	9.37[a]	26.03	276.9	68.9	60.2	137.2	77.0	-	-
Yellow	10.17[b]	27.87	267.0	68.4	61.5	137.6	76.1	-	-

a. b. means with the same letter are not significantly different at 5% level by Student-Newman-Keuls' test. Mean not followed by letters are not significantly different from others for the same traits.

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大豆色素遺傳性

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大豆之花色、茸毛顏色、豆莢顏色及種子顏色是屬於質的性狀，這種特性通常被用作爲大豆品種特性之鑑定。尤其大豆種皮顏色常被用來檢定品系之純度，其色澤也影響大豆市場價格。本試驗目的在於瞭解大豆色素之遺傳特性，以便做爲育種上之參考。

大豆之色素遺傳性是以雜交後代 F_2 世代之各性狀遺傳分離比符合度卡方 (X^2)測驗來估算其信賴度。大豆之花色分爲紫色及白色兩種，而紫色對白色表現爲顯性，其分離比爲3：1。茸毛及豆莢顏色表現爲深色對淺色爲顯性，其分離比爲 3：1。雖然各有一組雜交組合之茸毛或豆莢顏色未符 3：1之分離比，綜合結果顯示大豆之花色、茸毛色及莢壁色爲一對單基因控制之孟德爾式的顯隱性遺傳特性。種子顏色具有複雜的遺傳特性，Tracy－M(黃色種皮)× PI 416808(黑色種皮)之雜交組合其 F_2 族群種皮顏色分離爲 4 黑色：9 綠色：3 黃色。其結果經檢定爲Tracy－M 之基因型爲$\underline{i}^1\ \underline{i}^1\ \underline{gg}$ 而 PI 416808之基因型爲$\underline{iiGG}$，其 F_2 族群則分離爲 4 $\underline{ii}$--：9 $\underline{i}^1$ -$\underline{G}$-：3 $\underline{i}^1$ -$\underline{gg}$。另一雜交組合 Forrest(種皮及子葉均黃色) × PI 399007(種皮及子葉均綠色)之F_2族群中子葉顏色分離比爲15黃色：1 綠色，顯然黃色具有複顯性上位作用。若種皮及子葉顏色合併考慮其獨立遺傳性其 F_2 族群分爲12綠色種皮具黃色子葉：3 種皮及子葉均黃色：1 種皮及子葉均綠色。其結果經檢定爲Forrest 之基因型爲$\underline{D}_1\ \underline{D}_1\ \underline{D}_2\ \underline{D}_2\ \underline{gg}$，而 PI 399007之基因型爲$\underline{d}_1\ \underline{d}_1\ \underline{d}_2\ \underline{d}_2\ \underline{GG}$。其$F_1$ 植株表現爲黃色子葉綠色種皮之基因型爲$\underline{D}_1\ \underline{d}_1\ \underline{D}_2\ \underline{d}_2\ \underline{Gg}$，而 F_2 族群則分離爲12 $\underline{D}$---$\underline{G}$-：3 $\underline{D}$----$\underline{gg}$：1 $\underline{d}_1\ \underline{d}_1\ \underline{d}_2\ \underline{d}_2$ --。由此顯示綠色子葉大豆之種皮亦爲綠色。另外反交組合 PI 399007 × Forrest 之F_2族群種皮及子葉顏色均無分離，其顏色均爲綠色。顯然綠色種皮及子葉具有母性遺傳效應。

此試驗中同時發現種皮顏色對種子大小及莢寬具有明顯效應。在Tracy-M × PI 416808之雜交組合 F_2 族群中，黑色種皮之種子百粒重及莢寬顯著大於綠色或黃色種皮者。在 Forrest × PI 399007 之雜交組合中，黃色種皮之種子百粒重則顯著的大於綠色種皮者。而種皮顏色對產量、單株種子粒數、株高、始花日數、成熟日數、子實充實日數及莢長則沒有影響。