

THE INHERITANCE OF SEEDCOAT COLOR  
IN PHASEOLUS VULGARIS

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## TABLE OF CONTENTS

	Page
LIST OF TABLES . . . . .	iv
INTRODUCTION . . . . .	1
LITERATURE REVIEW . . . . .	2
Basic Genes . . . . .	2
Color Genes . . . . .	3
Dominant Modifying Genes . . . . .	7
Recessive Modifying Gene . . . . .	8
Summary . . . . .	8
MATERIALS AND METHODS . . . . .	10
RESULTS AND DISCUSSION . . . . .	13
SUMMARY AND CONCLUSIONS . . . . .	46
LITERATURE CITED . . . . .	49
LITERATURE NOT CITED . . . . .	53

## LIST OF TABLES

Table		Page
1	Seedcoat color genotypes and phenotypes found in <u>Phaseolus vulgaris</u> . . . . .	5
2	Parental lines of <u>Phaseolus vulgaris</u> . . . . .	11
3	F <sub>2</sub> results for seedcoat color for cross 1: 455 (Dark brown) x 437 (Pale brown) . . . . .	14
4	F <sub>2</sub> results for seedcoat color for cross 2: 433 (Bluish brown) x 437 (Pale brown) . . . . .	16
5	F <sub>2</sub> results for seedcoat color for cross 3: 445 (Lilac red) x 437 (Pale brown) . . . . .	18
6	F <sub>2</sub> results for seedcoat color for cross 4: 433 (Bluish brown) x 445 (Lilac red) . . . . .	20
7	F <sub>2</sub> results for seedcoat color for cross 5: 455 (Dark brown) x 445 (Lilac red) . . . . .	22
8	F <sub>2</sub> results for seedcoat color for cross 6: 433 (Bluish brown) x 515 (Mottled orange red/buff) . . . . .	23
9	F <sub>2</sub> results for seedcoat color for cross 7: 445 (Lilac red) x 549 (Striped greenish brown/buff) . . . . .	26
10	F <sub>2</sub> results for seedcoat color for cross 8: 515 (Mottled orange red/buff) x 549 (Striped greenish brown/buff) . . . . .	27
11	F <sub>2</sub> results for seedcoat color for cross 9: 438 (Pale greenish yellow) x 445 (Lilac red) . . . . .	29
12	F <sub>2</sub> results for seedcoat color for cross 10: 436 (Whitish with brown hilumring) x 438 (Pale greenish yellow) . . . . .	31
13	F <sub>2</sub> results for seedcoat color for cross 11: 436 (Whitish with brown hilumring) x 549 (Striped greenish brown/buff) . . . . .	34
14	F <sub>2</sub> results for seedcoat color for cross 12: 188 (White) x 549 (Striped greenish brown/buff) . . . . .	36

## LIST OF TABLES (Contd.)

Table		Page
15	F <sub>2</sub> results for seedcoat color for cross 13: 188 (White) x 420 (Dotted reddish/buff) . . . . .	37
16	F <sub>2</sub> results for seedcoat color for cross 14: 529 (White) x 438 (Pale greenish yellow) . . . . .	40
17	F <sub>2</sub> results for seedcoat color for cross 15: 532 (Mottled reddish/pink) x 529 (White) . . . . .	42
18	F <sub>2</sub> results for seedcoat color for cross 16: 541 (Pale yellowish) x 549 (Striped greenish brown/buff) . . . . .	43
19	F <sub>2</sub> results for seedcoat color for cross 17: 549 (Striped greenish brown/buff) x 709 (Light yellowbrown) . . . . .	45
20	Summary of results for seedcoat color . . . . .	47

## INTRODUCTION

Seedcoats of Phaseolus vulgaris show great variation in color, exhibiting a wide range of solid colors from white through yellow, orange, red, brown and violet to black. There are also several types of patterned seedcoats including striped, mottled and dotted.

Seedcoat color is an important qualitative character often influencing marketability of dry bean varieties. People in different areas of the world prefer beans of certain colors. For example, in some parts of South or Central America only red and black beans are acceptable while in North America red and white beans are preferred (Moh, 1969). This is probably due to traditional food habits but these preferences are so difficult to change that it seriously affects commercial production of superior varieties of other colors. For instance, many black bean varieties are superior in disease resistance and yielding capacity to other-colored varieties (Yglesias, 1964). The cultivation of black beans is, however, limited in many areas because of their seedcoat color.

An understanding of the inheritance of seedcoat color is basic to breeding programs designed to change seedcoat color. Lamprecht (1932 and later) and Prakken (1934 and later) have been major workers on seedcoat color inheritance. Although these two workers agree on many points, they differ on others. The present study will attempt to elucidate the genetics of color inheritance.

## LITERATURE REVIEW

Seedcoat color in Phaseolus vulgaris depends upon the action of nine loci which can be grouped into three categories according to mode of action (Prakken, 1974): (1) basic genes of groundfactors, (2) color genes or chromogenous factors and (3) modifying genes or intensifying factors. Since Phaseolus vulgaris is highly self-pollinating most individuals are homozygous. Heterozygotes will not be discussed unless they fail to show complete dominance.

Basic Genes:

1. P, the groundfactor, which gives no color itself but is necessary for the plant to produce seedcoat color. Thus two types of white genotypes are possible: 'p' which lacks the groundfactor gene and 'P' which lacks all other color genes (Lamprecht, 1932 and later). Flower color is also white in the presence of 'p'. In 1907 Shull proposed the gene 'P' as necessary for color which he considered limited to brown or yellow pigments. In 1912 Tschermak designated 'A' for a similar effect. Kooiman (1931) also used 'A' to represent the presence of the primary color gene; however, because of priority, 'P' is now the generally accepted symbol for the groundfactor.

2. T, a gene necessary for a completely colored seedcoat. All 't' seeds are partly colored, i.e. they have a very small to a very large white part and a colored part. 'T' seeds are fully colored (self-colored). Emerson (1909) first studied the heredity of partial color in beans. Self-colored x eyed (partially colored) gave self-colored in the F<sub>1</sub> and segregation into 3 self-colored: 1 eyed in the F<sub>2</sub>. He assigned the symbol 'T' to this gene. Sax (1923) suggested that the

eye pattern was due to a double recessive condition for a 't' gene and an 'e' gene because white (pTE) x eyed (Pte) gave an F<sub>2</sub> which fitted the ratio of 45 colored: 3 eyed: 16 white, better than it did a 9:3:4 ratio (pT x Pt). In 1912 Tschermak proposed 'Z<sub>1</sub>' for 'T' and 'Z<sub>2</sub>' as a color extension factor. Although Prakken suggests only one gene, 'T', is responsible for partially colored seeds, Lamprecht (1934) reported five genes responsible in various combinations for twenty-two partial color patterns. His partially colored types varied from a single dot on either end of the hilum scar, to almost complete self color.

#### Color Genes:

3. J, a gene which causes a brown hilumring and shiny seedcoat. 'J' also causes an intense afterdarkening which continues over many years. 'j' seeds have a mat finish with no hilumring. Kooiman (1920) called this factor 'C', Lamprecht (1932) referred to it as 'J' and Prakken (1934) as 'Sh'. Prakken (1940) decided that his 'Sh' gene was analogous to Lamprecht's 'J' gene, which Lamprecht confirmed in 1960, and therefore adopted the symbol 'J', since 'C' already represented the mottling gene.

4. D, a gene causing a brown hilumring but with nominal influence on seedcoat color. Kooiman (1920) was the first to describe a hilumring factor. Lamprecht originally failed to recognize a specific hilumring gene but Prakken (1970) stated that the four symbols of Lamprecht, 'G', 'B', 'Can' and 'Ins', probably represent the action of the hilumring factor, 'D'. The effect of 'D' is only visible when 'J' is recessive.

5. C, referred to by Prakken (1974) as "the complex locus for ever-segregating and constant mottling", has two effects: 1) a color effect and 2) a pattern effect.

The color effect can be represented by three alleles: 'c', producing white to brown seedcoats (Table 1, rows 1,4,7,10), 'C', producing greenish yellow to black seedcoats (Table 1, rows 2,5,8,11) and 'C<sup>F</sup>', producing pale lilac to black seedcoats (Table 1, rows 3,6, 9,12).

Three types of patterned seedcoats have been distinguished from the beginning of the century (Tschermak, 1901, 1902, 1904; Emerson 1904, 1909; Shull, 1907, 1908). They are: a) solid colors, b) ever-segregating mottling and c) constant mottling. Solid colored seedcoats are produced by the alleles, 'c', 'C' and 'C<sup>F</sup>' discussed above. Ever-segregating mottling refers to the mottling in the heterozygotes of the 'c', 'C' and 'C<sup>F</sup>' alleles. A heterozygote is mottled in a darker and a paler color, with the actual colors determined by other genes present (see Table 1). For example, if CCddJJGGBBvv (row 8, column IV in Table 1) is dark brown and ccddJJGGBBvv (row 7, column IV in Table 1) is pale brown, then the heterozygote, CcddJJGGBBvv, will be mottled dark brown on pale brown. The background color in ever-segregating mottled seeds therefore is: in 'Cc' and 'C<sup>F</sup>c' heterozygotes, the same as the 'cc' homozygote, and in 'C<sup>F</sup>C' heterozygotes, the same as the 'CC' homozygotes. It is not always buff as in the constant mottled homozygotes. Mottling (or striping) will be indicated in the text and tables by a slant-line fraction with the darker color as the numerator and the lighter color as the denominator (i.e. from above, mottled dark brown/pale brown). A selfed ever-segregating mottled parent would produce offspring in the ratio: 1 self-colored in the darker color: 2 of an ever-segregating mottled type: 1 self-colored in the paler color.

Constant mottling is determined by two alleles according to Prakken

Table 1

Seedcoat Color Genotypes and Phenotypes found in Phaseolus vulgaris

				vv (or v <sup>lae</sup> .)				V.			
				bb		B.		bb		B.	
				gg	G.	gg	G.	gg	G.	gg	G.
				ggbbvv	G.bbvv	ggB.vv	G.B.vv	ggbbV.	G.bbV.	ggB.V.	G.B.V.
				I	II	III	IV	V	VI	VII	VIII
	cc	jjddcc	1	Seedcoat quite white				Seedcoat white or with light grey speckling			
dd	CC	jjddCC	2	Greenish yellow	Yellow	Greenish brown	Soft brown	Grey violet	Brown grey	Greenish black	Blackish
	C <sup>r</sup> C <sup>r</sup>	jjddC <sup>r</sup> C <sup>r</sup>	3	Pale lilac	Pale orange	Grey lilac	Dark brown	Grey purple	Grey brownish purple	Grey blackish	Grey blackish
jj	cc	jjD.cc	4	Seedcoat whitish with hilumring				Seedcoat whitish or with light grey speckling and with hilumring			
D.	CC	jjD.CC	5	Seedcoat colors slightly darker than row 2 and with hilumring							
	C <sup>r</sup> C <sup>r</sup>	jjD.C <sup>r</sup> C <sup>r</sup>	6	Seedcoat colors slightly darker than row 3 and with hilumring							
	cc	J.ddcc	7	Pale yellowish	Light yellow brown	Grey brown	Pale brown	Bluish violet	Ageratum blue	Bluish brown	Blackish
dd	CC	J.ddCC	8	Pale greenish yellow	Yellow brown	Grey greenish brown	Dark brown	Dark violet	Dark brown violet	Black	Black
	C <sup>r</sup> C <sup>r</sup>	J.ddC <sup>r</sup> C <sup>r</sup>	9	Lilac red	Orange red	Greenish brown	Blackish brown	Reddish purple	Brownish purple	Blackish	Blackish
J.	cc	J.D.cc	10	Seedcoat colors slightly darker than row 7							
D.	CC	J.D.CC	11	Seedcoat colors slightly darker than row 8							
	C <sup>r</sup> C <sup>r</sup>	J.D.C <sup>r</sup> C <sup>r</sup>	12	Seedcoat colors slightly darker than row 9							

(1970 and later): 'C<sup>m</sup>', constant mottled/buff and 'C<sup>st</sup>', constant striped/buff. The color range caused by these two pattern genes is the same as that for 'C<sup>r</sup>'. Selfing a homozygous constant mottled or striped parent produces all mottled or striped offspring. If one of the 'C<sup>m</sup>' alleles (or 'C<sup>st</sup>') is replaced by 'C', the 'C<sup>m</sup>C' (or 'C<sup>st</sup>C') heterozygotes are three colored, i.e. double mottled (or striped and mottled) as follows:

1. a buff background color not influenced by modifying genes.
2. mottling in a color determined by 'C'.
3. mottling (or striping) over it in a color determined by 'C<sup>m</sup>' (or 'C<sup>st</sup>').

If one of the 'C<sup>m</sup>' (or 'C<sup>st</sup>') alleles is replaced by 'c' the 'C<sup>m</sup>c' (or 'C<sup>st</sup>c') heterozygotes are two colored as follows:

1. a background color determined by 'c'.
2. mottling (or striping) over it in a color determined by 'C<sup>m</sup>' (or 'C<sup>st</sup>').

'C<sup>m</sup>C<sup>st</sup>' heterozygotes are two colored as follows:

1. a buff background color.
2. mottling and striping over it in a color determined by 'C<sup>m</sup>' and 'C<sup>st</sup>'.

Other alleles Prakken attributes to this locus are 'c<sup>u</sup>', unchangeable buff background, i.e. unchanged by modifying genes (Feenstra, 1960), and 'c<sup>cr</sup>', completely recessive, 'Cc<sup>cr</sup>' being one uniform color determined by 'C' (Nakayama, 1960-1965). 'M', corresponding to 'C', was first proposed by Shull (1908) as responsible for inconstant mottling independent of color genes. Emerson (1909) later used 'M' to represent a gene causing constant mottling. Emerson also introduced a gene 'R' for red seedcoat

colors, which is the same as the dark pattern color in constant mottled or striped types. Lamprecht (1947) proposed two rather closely linked loci, 'C' and 'R'; the locus 'C' responsible for ever-segregating mottling and the locus 'R' for red color and various types of constant pattern. He recognized seven alleles of 'R': 'R<sup>ma</sup>', marbled; 'R<sup>cir</sup>', marbled only around the hilum; 'R<sup>rho</sup>', rhomboid-shaped marbling; 'R<sup>res</sup>', sprinkled over (lighter dots of color); 'R<sup>st</sup>', striped; 'R', one-colored (reddish colors) and 'r', no color.

#### Dominant Modifying Genes:

These genes darken seedcoat colors; black or blackish being the darkest color.

6. G, the yellowbrown factor. When all other modifying genes are recessive and 'J' is dominant, 'G' changes yellow (c) or greenish yellow (C) colors into yellowbrown ones and generally increases the brown color in other genetic backgrounds. Many early workers were aware of a factor producing a yellowbrown color (Tschermak, 1901-1912; Emerson, 1902-1909). Lundberg and Akerman (1917) appear to be the first to give it the symbol 'G'. Lamprecht (1932 and later) also used 'G' for yellowbrown. According to Prakken (1970) Lamprecht wrongly ascribed a hilumring action to this gene in addition to the yellowbrown effect. Prakken believes that this gene has no influence on the presence or absence of a hilumring.

7. B, the greenish brown factor, changes, when all other modifying genes are recessive, the pale greenish yellow colors into greenish brown ones. 'G' and 'B' together produce a brown seedcoat. This factor was also recognized in the early literature (Tschermak, 1901-1912;

Lundberg and Akerman, 1917; Kooiman, 1920, 1931; Sirks, 1922).

Lamprecht (1932 and later) again ascribed a hilumring action to this gene which Prakken (1970) again denies.

8. V, the violet factor, changes yellow to brown seedcoats into violet to black ones. There are three alleles: 'v', which produces a white flower and yellow to brown seedcoats, 'v<sup>lae</sup>', which produces a lavender flower but the same yellow to brown seedcoats as 'v', and 'V' which produces a purple flower and violet to black seedcoats. 'V' also produces a light grey speckling ("tinged with glaucescens", Prakken, 1970) in the buff background color of 'C<sup>m</sup>' and 'C<sup>st</sup>' genotypes. This gene is discussed by Tschermak (1912) and Sirks (1920). In 1922 Sirks replaced 'V' with a factor 'Z' for black color. Both Lamprecht (1932-1940) and Prakken (1934-1977) refer to the violet-black gene as 'V'.

#### Recessive Modifying Gene:

9. rk, a gene causing red seedcoat color. The symbol was proposed by Smith (1939) from the variety Red Kidney which has red seeds. 'Rk' produces no color, 'rkrk' produces a red or testaceous tinge (such as Red Kidney) and a third allele, 'rk<sup>d</sup>rk<sup>d</sup>', produces a garnet brown tinge (a darker red) (Smith and Madsen, 1948). The effects of this locus can be seen in all genotypes except the darkest. The 'rk' series also determines the background color of 'C<sup>m</sup>' and 'C<sup>st</sup>' genotypes.

#### Summary:

P,p - ground factor or basic gene, necessary for color formation

T,t - factor for total color, necessary for a completely colored seedcoat as opposed to a partially colored one

J,j - shine factor, also producing a colored hilumring

D,d - hilumring factor

C,c,C<sup>r</sup>,C<sup>m</sup>,C<sup>st</sup> - factor for ever-segregating and constant mottling

G,g - yellowbrown factor

B,b - greenish brown factor

V,V<sup>lae</sup>,v - violet factor

rk,rk<sup>d</sup>,Rk - recessive red factor

## MATERIALS AND METHODS

Parental Lines:

For this study fourteen Phaseolus vulgaris lines were chosen on the basis of their different seedcoat colors (Table 2). All were plant introduction (PI) lines which were prolific, as well as uniform for seedcoat color when previously grown in Hawaii (Hartmann, unpublished data).

MethodsGreenhouse Cultural Conditions:

Three to five plants were grown in each 20 cm plastic pot in a mixture of 3 parts soil to 1 part vermiculite. Approximately 5 grams of Osmocote (14-14-14) were applied once a month from the time of germination. The temperature in the greenhouse varied from  $25 \pm 5^{\circ}\text{C}$  during the day to  $18 \pm 1^{\circ}\text{C}$  at night. The relative humidity was  $65 \pm 20\%$  during the day and  $90 \pm 10\%$  at night.

Crossing Methods:

Two plantings of the parental lines were made two and one half weeks apart in order to extend the length of time that flowers were available. All crosses were made in the greenhouse from 9 a.m. to 11:30 a.m. Buds due to open the next day were emasculated by removing the anthers with tweezers. Pollination was done by rubbing the stigma of the emasculated flower with the pollen-laden pistil of a flower from the male parent. After pollination, the pistil was re-covered by the wings and standard to prevent drying out.

Crosses between parental lines in as many combinations as possible

Table 2

Parental Lines of Phaseolus vulgaris

PI Number	Abbreviations used in Text	Origin	Flower Color	Seedcoat Color	Color Reference (D.C.)
310 455	455	U.S.S.R.	Lavender	Dark brown*	7E12
313 437	437	Mexico	White	Pale brown*	15H7
313 541	541	Mexico	White	Pale yellowish*	10F3
325 709	709	Mexico	White	Light yellowbrown*	10L7
339-529	529	Turkey	White	White	-----
353 532	532	U.S.S.R.	Lavender	Mottled reddish/pink*	7J3/3B10
358 188	188	Yugoslavia	White	White	-----
361 420	420	India	Lavender	Dotted reddish/buff*	7H6/9B2
361 433	433	India	Purple	Bluish brown*	32A3
361 436	436	India	Purple	Whitish*	-----
361 438	438	India	Lavender	Pale greenish yellow*	10L2
361 445	445	India	White	Lilac red*	7J9
361 515	515	India	Lavender	Mottled orange red/buff*	3K12/9B2
370 549	549	Yugoslavia	Lavender	Striped greenish brown/buff*	14I7/9B2

\*hilumring present

were attempted but due to incompatibility, poor flower production, or pod drop, all combinations were not obtained.

#### Field Cultural Conditions:

The hybrids obtained from 61 crosses were planted at the Poamoho Experimental Station, Oahu and allowed to self-pollinate. Seeds were planted in rows 120 cm apart. Within a row the seeds were spaced 30 cm apart.

Seeds from this population were also planted at the Poamoho Experimental Station to produce  $F_2$  progeny to permit study of seedcoat color. The seeds were again planted in rows 120 cm apart but spacing between plants within the row was 7 cm. Approximately 17,700 plants from seventeen  $F_1$  hybrids were grown. The other  $F_1$  hybrids were discarded due to insufficient seeds, lack of vigor or space limitations. One pod per plant was collected and one seed per pod used to calculate  $F_2$  ratios.

#### Statistical Methods:

The Chi-Square Goodness of Fit test (Snedecor and Cochran, 1967) was used to determine the probability that observed qualitative genetic ratios fit those expected.

#### Color Descriptions:

For color references, A. Maerz and M. Paul, A Dictionary of Color (1950), was used. References are listed as a D.C. number.

Seedcoat colors referred to in text or tables by a D.C. number represent the average for the range of colors found in each type.

## RESULTS AND DISCUSSION

Genetic analysis of the seventeen crosses made are presented below. Since no partially colored seeds were found, 'T' is assumed present in all parents and therefore, will not be mentioned again. The seedcoat colors indicated in this text are for fresh seeds. All seeds carrying the 'J' gene will darken with age; consequently, these descriptions may be inaccurate for older seeds. Mottled (or striped) seeds will be written as a fraction as explained in "Literature Review".

CROSS 1: 455 x 437

455 has dark brown seeds and lavender flowers while 437 has pale brown seeds and white flowers. The  $F_1$  seed color is mottled dark brown/pale brown. The  $F_2$  results (Table 3) show one gene segregating in a 1:2:1 ratio.

The presence of mottled seeds in the  $F_1$  and  $F_2$  when neither parent is mottled indicates that the parents differ at the 'C' locus. Pale brown seedcoats should be 'cc', dark brown seedcoats should be 'CC' and the mottled dark brown/pale brown seedcoats should be 'Cc'. Classification is sometimes difficult since dark brown and pale brown are similar and environmental variation may cause some overlap of colors. Mottling at times is also very faint and difficult to distinguish. 'J' is considered present in both parents because all seeds are shiny. When 'V' is absent the type of brown seeds encountered here are produced when both 'B' and 'G' are present, so it is assumed that these genes were present in both parents. No information could be obtained about 'D' because 'J' masked the 'D' locus. 455 should be 'V<sup>lae</sup>' and 437 'v'

Table 3

F<sub>2</sub> Results for Seedcoat Color for Cross 1:  
455 (Dark brown) x 437 (Pale brown)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Dark brown	206	191.5	1	CC
Mottled dark brown/pale brown	358	383.0	2	Cc
Pale brown	202	191.5	1	cc
Total: 766	$\chi^2=3.31$	0.250	$P>0.100$	

on the basis of flower color. Since no indication of red showed in the seeds, 'Rk' is also assumed present in both parents.

455 is therefore tentatively assumed to have the genotype PTC.JGBV<sup>lae</sup>Rk and 437 the genotype PTC.JGBvRk.

CROSS 2: 433 x 437

433 has bluish brown seeds and purple flowers while 437 has pale brown seeds, white flowers and a probable genotype of PTC.JGBvRk deduced from cross 1. F<sub>1</sub> from this cross is blackish. The F<sub>2</sub> results (Table 4) show two genes segregating in a 9:3:3:1 ratio.

There was some difficulty in separating the bluish brown seeds from the brown ones because the bluish color is just a tinge on the brown seeds and occasionally this bluish tinge does not develop completely (Prakken, 1934). Since no mottled seeds appeared in the F<sub>1</sub> or F<sub>2</sub>, 433 is assumed to be 'c' like 437. 'V' must be segregating because 433 had purple flowers (v) while 437 had white flowers (v). All seeds are shiny and there are no red ones so 'J' and 'Rk' are present in both parents. Again no information can be obtained about 'D' due to the hilumring action of 'J'. The second locus segregating must be either 'B' or 'G'. Since no yellowish (gbv) or yellowbrown (Gbv) seeds were found, but grey brown (gBv) and pale brown (GBv) seeds were found, it is concluded that the 'G' locus is segregating here.

The proposed genotype for 433 is PTC.JgBVRk.

CROSS 3: 445 x 437

445 has lilac red seeds and white flowers while 437 has pale brown seeds, white flowers and a probable genotype of PTC.JGBvRk deduced from crosses 1 and 2. The F<sub>1</sub> is mottled blackish brown/pale brown. F<sub>2</sub>

Table 4

F<sub>2</sub> Results for Seedcoat Color for Cross 2:  
433 (Bluish brown) x 437 (Pale brown)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Blackish	428	432.2	9	G. V.
Bluish brown	127	144.8	3	gg
Pale brown	165	144.8	3	G. vv
Grey brown	50	48.2	1	gg
Total:	770	$\chi^2=5.80$	0.250	$P>0.100$

results given in Table 5 show three genes segregating. Two genes show complete dominance and one shows no dominance.

Both parents must be 'v' because both have white flowers and 'J' because all seeds are shiny. No conclusions can be made about 'D' because it is masked by 'J'. Both parents must be 'Rk' because if 'rk' was producing the red seeds in 445 the background color of some of the mottled seeds would be reddish which it is not. The 'C' locus must be segregating because the F<sub>1</sub>, but not the parents, is mottled. The 'cc' seedcoat colors (see Table 1, row 7) are represented in the F<sub>2</sub> but the 'CC' colors (Table 1, row 8) are not therefore 445 must carry the 'C<sup>r</sup>' gene. The other two segregating loci seem to be 'G' and 'B' because all four 'cv' as well as 'C<sup>r</sup>v' seedcoat colors are present.

The genotype PTC<sup>r</sup>.JgbvRk is therefore proposed for 445.

CROSS 4: 433 x 445

433 has bluish brown seeds, purple flowers and a probable genotype of PTC.JgbvRk deduced from cross 2. 445 has lilac red seeds, white flowers and a probable genotype of PTC<sup>r</sup>.JgbvRk deduced from cross 3. The F<sub>1</sub> is mottled blackish/bluish brown (D.C.: blackish/32C6).

It was expected that three genes would be segregating in this cross, 'B', 'V' and 'C'. 'cc' genotypes should be expressed as colors from line 7 in Table 1, 'C<sup>r</sup>C<sup>r</sup>' seeds should exhibit colors from line 9 in Table 1, and 'C<sup>r</sup>c' seeds should be mottled with a reddish color/a non-reddish background. Segregation in 'B' would change yellows and bluish violets into grey browns and bluish browns in the presence of 'c' and reds and reddish dark purples into greyish violets and blacks in the presence of 'C<sup>r</sup>'. Segregation of 'V' would show yellow and reddish

Table 5

F<sub>2</sub> Results for Seedcoat Color for Cross 3:  
445 (Lilac red) x 437 (Pale brown)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Blackish brown	128	125.8	9	G.
Greenish brown	40	42.0	3	B. C <sup>r</sup> C <sup>r</sup> gg
Orangish red	45	42.0	3	G. bb
Lilac red	13	14.0	1	gg
Mottled blackish brown/pale brown	261	251.6	18	G. B.
Mottled greenish brown/grey brown	79	83.9	6	C <sup>r</sup> c gg
Mottled orangish red/pale yellowbrown	79	83.9	6	G. bb
Mottled lilac red/pale yellowish	30	28.0	2	gg
Pale brown	126	125.8	9	G. B.
Grey brown	41	42.0	3	gg cc
Light yellowbrown	39	42.0	3	G. bb
Pale yellowish	14	14.0	1	gg
Total: 895	X <sup>2</sup> =1.58	P>0.995		

colors along with bluish browns and blacks.

The  $F_2$  results given in Table 6 are consistent with these predictions so the genotypes proposed for 433 (PTc.JgBVRk) and 445 (PTC<sup>r</sup>.JgbvRk) are assumed correct.

CROSS 5: 455 x 445

455 has dark brown seeds, lavender flowers and a probable genotype of PTC.JGBV<sup>lae</sup>Rk deduced from cross 1 while 445 has lilac red seeds, white flowers and a probable genotype of PTC<sup>r</sup>.JgbvRk deduced from crosses 3 and 4. The  $F_1$  is mottled blackish brown/dark brown (D.C.: blackish brown/8H12).

It was expected that four genes would be segregating in this cross, 'G', 'B', 'C' and 'V'. However, the segregation of 'V<sup>lae</sup>-v' only affects the flower color. 'CC' genotypes should be expressed as colors from line 8 in Table 1, 'C<sup>r</sup>C<sup>r</sup>' seeds should exhibit colors from line 9 in Table 1, and 'C<sup>r</sup>C' seeds should be mottled with a reddish color/a non-reddish background. These color types were found in the  $F_2$  progeny but the fit to a 1:2:1 ratio was very poor ( $\chi^2=29.60$ ,  $P<0.005$ ). This is probably due to the fact that the mottling is very hard to see, so that many mottled seeds were probably misclassified as solid-colored ones. Segregation in 'G' would change yellows and greenish browns into yellow-browns and dark browns in the presence of 'C' and lilacs and greyish violets into oranges and blackish browns in the presence of 'C<sup>r</sup>'. Segregation of 'B' would show yellows and lilacs along with dark browns and blackish browns. One deviation from expected colors was the appearance of lilac yellowish in the  $F_2$ . The color was assumed to correspond to the lilac red color of 445 because, according to Prakken (1972),

Table 6

F<sub>2</sub> Results for Seedcoat Color for Cross 4:  
433 (Bluish brown) x 445 (Lilac red)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Blackish	246	248.8	9	B.
Reddish purple	75	82.9	3	V.
Greenish brown	80	82.9	3	C <sup>r</sup> C <sup>r</sup> bb
Lilac red	34	27.7	1	vv B.
Mottled blackish/bluish brown	493	497.5	18	bb
Mottled reddish purple/bluish violet	166	165.8	6	V.
Mottled greyish brown/grey brown	163	165.8	6	C <sup>r</sup> c B.
Mottled lilac red/pale yellowish	58	55.3	2	vv
Bluish brown	246	248.8	9	bb
Bluish violet	83	82.9	3	V.
Grey brown	90	82.9	3	cc B.
Pale yellowish	35	27.7	1	vv bb
Total: 1769	X <sup>2</sup> =5.24	0.950	P>0.900	

"the intensity of the 'red' etc. striping is variable and sometimes... it is hardly visible".

$F_2$  results given in Table 7 are consistent with these predictions and the genotypes proposed for 455 (PTC.JGBV<sup>lae</sup>Rk) and 445 (PTC<sup>r</sup>.JgbvRk) are therefore assumed correct.

CROSS 6: 433 x 515

433 has bluish brown seeds, purple flowers and a probable genotype of PTC.JGBVRk deduced from crosses 2 and 4 while 515 has mottled orange red/buff seeds and lavender flowers. The  $F_1$  is mottled black/blackish.  $F_2$  results (Table 8) show four genes segregating.

Since 515 is mottled, it is assumed to have the 'C<sup>m</sup>' gene. Phenotypes found in the  $F_2$  support the hypothesis that 'C<sup>m</sup>-c' is segregating but there is a bad fit to a 1:2:1 ratio ( $\chi^2=29.93$ ,  $P<0.005$ ). The 'C<sup>m</sup>C<sup>m</sup>' seeds are always mottled in a color from Table 1, row 9/buff background, 'cc' seeds are solid colors from Table 1, row 7, and 'C<sup>m</sup>c' seeds are mottled in row 9 colors/row 7 colors. Since all the colors in row 7 and 9 are present, the 'G', 'B' and 'V' loci all appear to be segregating. 515 therefore, is probably 'Gbv<sup>lae</sup>' (as opposed to 'Gbv' because 515 has lavender flowers). 'J' is assumed present in both parents because all seeds are shiny as is 'Rk' because of the lack of solid reddish colored seeds or a reddish background color on the 'C<sup>m</sup>C<sup>m</sup>' mottled seeds. 'D' is again masked by 'J'.

The proposed genotype for 515 is, therefore, considered to be PTC<sup>m</sup>.JGbv<sup>lae</sup>Rk.

CROSS 7: 445 x 549

445 has lilac red seeds, white flowers and a probable genotype of

Table 7

F<sub>2</sub> Results for Seedcoat Color for Cross 5:  
455 (Dark brown) x 445 (Lilac red)

Phenotypes	Observed No.	Expected No.	Ratio	Confirmed Genotypes
Blackish brown	255	246.5	9	G.
Greenish brown	92	82.2	3	B. C <sup>r</sup> C <sup>r</sup> gg
Orange red	85	82.2	3	G. bb
Lilac yellowish	36	27.4	1	gg
Mottled blackish brown/dark brown	450	493.0	18	G. B.
Mottled greenish brown/grey greenish brown	140	164.3	6	C <sup>r</sup> C gg
Mottled orange red/yellowbrown	135	164.3	6	G. bb
Mottled lilac yellowish/pale greenish yellow	43	54.8	2	gg
Dark brown	273	246.5	9	G. B.
Grey greenish brown	108	82.2	3	gg CC
Yellowbrown	96	82.2	3	G. bb
Pale greenish yellow	40	27.4	1	gg
Total: 1753	X <sup>2</sup> =38.42	P<0.005		

Table 8

F<sub>2</sub> Results for Seedcoat Color for Cross 6: 433 (Bluish brown) x 515 (Mottled orange red/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Mottled blackish/speckled	213	182.9	36	B. G. gg
Mottled brownish purple/speckled	57	45.7	9	V. G. bb
Mottled reddish purple/speckled	20	15.2	3	C <sup>m</sup> C <sup>m</sup> gg
Mottled blackish brown/buff	54	45.7	9	B. G.
Mottled greenish brown/buff	19	15.2	3	V <sup>lae</sup> V <sup>lae</sup> gg
Mottled orange red/buff	18	15.2	3	bb G.
Mottled lilac red/buff	8	5.1	1	gg
Mottled black/blackish	225	274.2	54	B. G.
Mottled blackish/bluish brown	83	91.4	18	V. gg
Mottled brownish purple/ageratum blue	72	91.4	18	bb G.
Mottled reddish purple/bluish violet	32	30.5	6	C <sup>m</sup> c gg
Mottled blackish brown/pale brown	68	91.4	18	B. G.
Mottled greenish brown/grey brown	30	30.5	6	V <sup>lae</sup> V <sup>lae</sup> gg

Table 8 (Contd.)

F<sub>2</sub> Results for Seedcoat Color for Cross 6: 433 (Bluish brown) x 515 (Mottled orange red/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Mottled orange red/light yellowbrown	33	30.5	6	G. bb
Mottled lilac red/pale yellowish	11	10.2	2	gg
Blackish	144	137.1	27	G. B.
Bluish brown	51	45.7	9	gg V.
Ageratum blue	46	45.7	9	G. bb
Bluish violet	20	15.2	3	gg cc
Pale brown	52	45.7	9	G. B.
Grey brown	19	15.2	3	gg v <sub>lae</sub> v <sub>lae</sub>
Light Yellowbrown	18	15.2	3	G. bb
Pale yellowish	7	5.1	1	gg
Total: 1300		$\chi^2=39.72$		0.025>P>0.010

PTC<sup>r</sup>.JgbvRk deduced from crosses 3, 4 and 5 while 549 has striped greenish brown/buff seeds and lavender flowers. The F<sub>1</sub> is striped greenish brown/brown (D.C.: 14F3/15H6). The F<sub>2</sub> results (Table 9) show two genes segregating, one with dominance and one without.

All seeds are shiny so 'J' is present in both parents. No information can therefore be obtained about 'D'. 'Rk' is present because no red was found in the background colors of the striped seeds. 'C<sup>st</sup>' is present because 549 is striped. The F<sub>2</sub> segregated into 1 self-colored: 2 striped/self-colored: 1 striped/buff which is as expected if 'C<sup>st</sup>' and 'C<sup>r</sup>' are segregating. The yellow and lilac yellow colors again probably correspond to the lilac red (gbv) color because, according to Prakken (1972), "the intensity of the 'red' etc. striping is variable". Since lilac yellowish (probably gbv) and greenish brown (gBv) seeds were found but orange (Gbv) and blackish brown (GBv) ones were not, it is concluded that the 'B' locus is segregating here. 549 is 'v<sup>lae</sup>' and not 'v' because it has lavender flowers.

The proposed genotype for 549 is PTC<sup>st</sup>.JgBV<sup>lae</sup>Rk.

#### CROSS 8: 515 x 549

515 has mottled orange red/buff seeds, lavender flowers and a probable genotype of PTC<sup>m</sup>.JgBV<sup>lae</sup>Rk deduced from cross 6 while 549 has striped greenish brown/buff seeds, lavender flowers and a probable genotype of PTC<sup>st</sup>.JgBV<sup>lae</sup>Rk deduced from cross 7. The F<sub>1</sub> is striped blackish/mottled blackish brown/buff (D.C.: blackish/16A6/9B2). The F<sub>2</sub> results are given in Table 10.

It was expected that three loci would be segregating in this cross, 'C', 'G' and 'B'. 'C<sup>m</sup>C<sup>m</sup>' seeds should be mottled in the colors in

Table 9

F<sub>2</sub> Results for Seedcoat Color for Cross 7:  
445 (Lilac red) x 549 (Striped greenish brown/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Greenish brown	235	224.1	3	B. C <sup>r</sup> C <sup>r</sup>
Lilac yellowish	69	74.7	1	bb
Striped greenish brown/brown	445	448.1	6	B. C <sup>st</sup> C <sup>r</sup>
Striped yellow/lilac yellowish	157	149.3	2	bb
Striped greenish brown/buff	223	224.1	3	B. C <sup>st</sup> C <sup>st</sup>
Striped yellow/buff	66	74.7	1	bb
Total: 1195		$\chi^2=2.39$		0.900 > P > 0.750

Table 10

F<sub>2</sub> Results for Seedcoat Color for Cross 8:  
515 (Mottled orange red/buff) x 549 (Striped greenish brown/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Confirmed Genotypes
Striped blackish/buff	160	176.6	9	G.
Striped brownish/buff	49	58.9	3	B. gg
Striped orangish/buff	47	58.9	3	C <sup>st</sup> C <sup>st</sup> bb gg
Striped pale red/buff	20	19.6	1	gg
Striped blackish/mottled blackish brown/buff	315	353.3	18	G. B.
Striped brownish/mottled greenish brown/buff	100	117.7	6	C <sup>m</sup> C <sup>st</sup> gg
Striped orange/mottled reddish/buff	110	117.7	6	G. bb
Striped pale red/mottled lilac red/buff	35	39.3	2	gg
Mottled blackish brown/buff	232	176.6	9	G. B.
Mottled greenish brown/buff	83	58.9	3	gg C <sup>m</sup> C <sup>m</sup>
Mottled orange red/buff	77	58.9	3	G. bb
Mottled lilac red/buff	28	19.6	1	gg
Total:	1256	X <sup>2</sup> =49.87	P<0.005	

Table 1, row 9/buff, 'C<sup>st</sup>C<sup>st</sup>' seeds should be striped in the same colors/buff and 'C<sup>st</sup>C<sup>m</sup>' should be mottled and striped in these same colors/buff. These patterns were found in the F<sub>2</sub> progeny but the fit to a 1:2:1 ratio was very poor ( $X^2=47.74$ ,  $P<0.005$ ); the mottled homozygote being represented in larger numbers than expected and the striped homozygote and the heterozygote is smaller numbers. According to Table 1, row 9 when 'G' and 'B' are segregating the colors should be lilac red, orange red, greenish brown and blackish brown. These colors were found in the mottled phenotypes but striped phenotypes were slightly different although generally comparable. The heterozygote showed mottling in one color and striping in another, which was also unexpected. According to Prakken (1972), 'C<sup>st</sup>', 'C<sup>m</sup>' and 'C<sup>rho</sup>' should always produce the same colors but this is not always the case. Generally when only one of these alleles was involved in a cross the colors produced were as expected (e.g. crosses 6,7) but when two are present as in this cross, differences between the two colors appear. It is impossible without further research to tell if this is due to genetic or environmental factors.

In general the information in Table 10 agrees with predicted results so that the genotypes proposed for 515 (PTC<sup>m</sup>.JGbv<sup>lae</sup>Rk) and 549 (PTC<sup>st</sup>.JgBV<sup>lae</sup>Rk) are assumed correct.

CROSS 9: 438 x 445

438 has pale greenish yellow seeds and lavender flowers while 445 has lilac red seeds, white flowers and a probable genotype of PTC<sup>r</sup>.JgBV<sup>r</sup>Rk deduced from crosses 3, 4, 5 and 7. The F<sub>1</sub> is mottled lilac red/pale greenish yellow (D.C.: 41F5/11G2). The F<sub>2</sub> results (Table 11)

Table 11

F<sub>2</sub> Results for Seedcoat Color for Cross 9:  
438 (Pale greenish yellow) x 445 (Lilac red)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Lilac red	239	231	1	C <sup>r</sup> C <sup>r</sup>
Mottled lilac red/pale greenish yellow	460	462	2	C <sup>r</sup> C
Pale greenish yellow	225	231	1	CC
Total: 924	$\chi^2=0.45$	0.900	$P>0.750$	

show segregation for one gene with no dominance.

Since mottling was found in the  $F_1$  and  $F_2$  when neither parent is mottled, it is concluded that the 'C' locus is segregating. 438 is assumed to be 'C' and not 'c' because of the presence of greenish yellow colors as opposed to yellowish ones. 438 is 'V<sup>lae</sup>', and not 'v' because it has lavender flowers. 'J' and 'Rk' are again present. 'G' and 'B' are both assumed recessive due to lilac red and pale greenish yellow seeds being found.

The proposed genotype for 438 is PTC.JgbV<sup>lae</sup>Rk.

CROSS 10: 436 x 438

436 is a hilumring type (Prakken, 1970) which has a brown hilumring with the rest of the seedcoat whitish. It also has purple flowers. 438 has pale greenish yellow seeds, lavender flowers and a probable genotype of PTC.JgbV<sup>lae</sup>Rk deduced from cross 9. The  $F_1$  is mottled black/bluish brown (D.C.: black/32A3). The  $F_2$ , with four genes segregating, shows 21 phenotypes (Table 12).

The presence of mottled seeds in the  $F_1$  and  $F_2$  when neither parent is mottled indicates that 'C' is segregating. Since 438 is 'C', 436 must be 'c'. Due to the presence of hilumring type seeds (cDj, Table 1, row 4) and the absence of totally white seeds (cdj, Table 1, row 1), it must be concluded that 'D' is present in both parents and at least one is 'j'. The appearance of both shiny seeds and mat seeds in the  $F_2$  confirms that 'J' is segregating. 'V' must be segregating because 438 is 'V<sup>lae</sup>' and 436 has purple flowers so must be 'V'. The fourth gene segregating must be 'B' or 'G'. It is concluded that the 'B' locus is the one because there are greenish brown (gB) seeds present, but no

Table 12

F<sub>2</sub> Results for Seedcoat Color for Cross 10:  
436 (Whitish with brown hilumring) x 438 (Pale greenish yellow)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Black	169	169.1	27	B.
Dark violet	58	56.4	9	V. bb
Grey greenish brown	67	56.4	9	J. B. vlaevlae
Pale greenish yellow	21	18.9	3	bb CC
Greenish black	53	56.4	9	B. V.
Dark grey violet	17	18.9	3	bb jj
Greenish brown	21	18.9	3	B. vlaevlae
Greenish yellow	6	6.4	1	bb
Mottled black/bluish brown	326	338.1	54	B. V.
Mottled dark violet/bluish violet	108	112.8	18	bb J.
Mottled grey greenish brown/grey brown	88	112.8	18	B. vlaevlae
Mottled pale greenish yellow/pale yellowish	29	37.7	6	bb Cc
Mottled greenish black/whitish	125	112.8	18	B. V.

Table 12 (Contd.)

F<sub>2</sub> Results for Seedcoat Color for Cross 10:  
 436 (Whitish with brown hilumring) x 438 (Pale greenish yellow)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Mottled dark grey violet/whitish	45	37.7	6	jj bb
Mottled greenish brown/whitish	43	37.7	6	jj B. vlaevlae
Mottled greenish yellow/whitish	14	12.7	3	bb
Bluish brown	167	169.1	27	B.
Bluish violet	52	56.4	9	V.
Grey brown	67	56.4	9	J.
Pale yellowish	14	18.9	3	B. vlaevlae
				cc bb
				B.
				V. bb
Whitish	115	100.5	16	jj B. vlaevlae bb
Total: 1605		$\chi^2=20.91$		0.500 > P > 0.250

yellowbrown (Gb) ones, and 438 is 'gb'. Both parents must be 'Rk' because no red seeds were found.

The proposed genotype for 436 is PTcDjgBVRk and since it is known that both have 'D' the genotype of 438 is PTCDJgbV<sup>lae</sup>Rk.

CROSS 11: 436 x 549

436 is whitish with a brown hilumring, has purple flowers and a probable genotype of PTcDjgBVRk deduced from cross 10 while 549 has striped greenish brown/buff seeds, lavender flowers and a probable genotype of PTC<sup>st</sup>.JgBV<sup>lae</sup>Rk deduced from cross 7. The F<sub>1</sub> is striped blackish/bluish brown (D.C.: blackish/32A3).

It was expected that three genes would be segregating in this cross, 'C', 'J' and 'V'. 'cc' seeds should be solid colored, 'C<sup>st</sup>C<sup>st</sup>' seeds should be striped/buff, and 'C<sup>st</sup>c' seeds should be striped/a background color corresponding to the 'c' solid colors. These types were all found (Table 13). 'V', as expected, increases the violet tinge of the genotypes in which it is present. 'j' seeds have a mat finish and are whitish when 'cc', while 'J' seeds are shiny and darker. Again, the presence of whitish seeds with a hilumring (cdj) and the absence of totally white seeds (cdj) would indicate that 'D' is also present in 549.

The F<sub>2</sub> results shown in Table 13 are consistent with these predictions and the genotypes proposed for 436 (PTcDjgBVRk) and 549 (PTC<sup>st</sup>DJgBV<sup>lae</sup>Rk) are assumed correct.

CROSS 12: 188 x 549

188 has white seeds and white flowers while 549 has striped greenish brown/buff seeds, lavender flowers and a probable genotype of

Table 13

F<sub>2</sub> Results for Seedcoat Color for Cross 11:  
 436 (Whitish with brown hilumring) x 549 (Striped greenish brown/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Confirmed Genotypes
Striped blackish/speckled	105	100.9	9	V.
Striped greenish brown/buff	37	33.6	3	J. V <sup>lae</sup> V <sup>lae</sup>
Striped grey blackish/speckled	28	33.6	3	C <sup>st</sup> C <sup>st</sup> V.
Striped grey lilac/buff	13	11.2	1	jj V <sup>lae</sup> V <sup>lae</sup>
Striped blackish/bluish brown	170	202.1	18	V.
Striped greenish brown/grey brown	86	67.4	6	J. V <sup>lae</sup> V <sup>lae</sup>
Striped grey blackish/whitish	75	67.4	6	C <sup>st</sup> c V.
Striped grey lilac/whitish	25	22.5	2	jj V <sup>lae</sup> V <sup>lae</sup>
Bluish brown	91	100.9	9	V.
Grey brown	30	33.6	3	J. V <sup>lae</sup> V <sup>lae</sup>
Whitish	58	44.8	4	cc V.
				jj V <sup>lae</sup> V <sup>lae</sup>
Total: 718	X <sup>2</sup> =18.36		0.050 > P > 0.025	

PTC<sup>st</sup>DJgBV<sup>lae</sup>Rk deduced from crosses 7 and 11. The F<sub>1</sub> is striped blackish/buff (with light grey speckling). The F<sub>2</sub> segregation is shown in Table 14. Three segregating genes were found in this cross; the white gene which is epistatic when recessive and two color genes which show dominance.

All 'p' seeds are white and easily distinguished from striped ones. Since all colored seeds are striped, 188 must also carry the 'C<sup>st</sup>' gene. All seeds are shiny and not red, so both parents must have 'J' and 'Rk'. Since greenish brown (gBv) and blackish (g or GBV) seeds were found 'V' must be segregating. 'V' also produced a light grey speckling on the otherwise buff background of the striped seeds. Therefore, 188 must be 'V' (the 'p' gene produces white flowers and is epistatic to 'V'). Due to the lack of lilac red (gbv) and orange red (Gbv) seeds 'B' must be present and not segregating. Both greenish brown (gBv) and blackish brown (GBV) seeds were found so 'G' must be segregating.

188 is tentatively assigned the genotype pTC<sup>st</sup>.JGBVRk.

#### CROSS 13: 188 x 420

188 has white seeds, white flowers and a probable genotype of pTC<sup>st</sup>.JGBVRk deduced from cross 12 while 420 is 'dotted' (rhomboid pattern, Lamprecht, 1947) reddish/buff with lavender flowers. The F<sub>1</sub> is striped blackish/dotted dark purple/buff (with light grey speckling) (D.C.: blackish/45G12/9B2). The F<sub>2</sub> results (Table 15) show four genes segregating producing 13 phenotypes.

All 'p' seeds are white and easily distinguished from 'P' colored seeds. 'C<sup>st</sup>C<sup>st</sup>' seeds are striped/buff, 'C<sup>rho</sup>C<sup>rho</sup>' have the rhomboid pattern/buff and the heterozygote 'C<sup>st</sup>C<sup>rho</sup>', has striping in one color/

Table 14

F<sub>2</sub> Results for Seedcoat Color for Cross 12:  
188 (White) x 549 (Striped greenish brown/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Striped blackish/speckled	643	662.0	36	G. V. gg
Striped blackish brown/buff	169	165.5	9	P. G. v <sup>lae</sup> v <sup>lae</sup>
Striped greenish brown/buff	47	55.2	3	gg
White	318	294.3	16	pp
Total: 1177	$\chi^2=7.87$	0.100>P>0.050		

Table 15

F<sub>2</sub> Results for Seedcoat Color for Cross 13: 188 (White) x 420 (Dotted reddish/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Dotted dark purple/speckled	46	43.7	27	B. V.
Dotted dark lavender/speckled	10	14.5	9	bb C <sup>rho</sup> C <sup>rho</sup>
Dotted brownish/buff	10	14.5	9	B. v <sup>lae</sup> v <sup>lae</sup>
Dotted reddish/buff	6	4.8	3	bb
Striped blackish/dotted dark purple/speckled	98	87.5	54	B. V.
Striped brownish purple/dotted dark lavender/speckled	14	29.1	18	bb P. C <sup>st</sup> C <sup>rho</sup>
Striped blackish brown/dotted brownish/buff	17	29.1	18	B. v <sup>lae</sup> v <sup>lae</sup>
Striped orange red/dotted reddish/buff	11	9.6	6	bb
Striped blackish/speckled	62	43.7	27	B. V.
Striped brownish purple/speckled	20	14.5	9	bb C <sup>st</sup> C <sup>st</sup>

Table 15 (Contd.)

F<sub>2</sub> Results for Seedcoat Color for Cross 13: 188 (White) x 420 (Dotted reddish/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Striped blackish brown/buff	16	14.5	9	$\frac{B}{v} \frac{v}{lae} \frac{v}{lae}$
Striped orange red/buff	2	4.8	3	bb
White	102	103.7	64	pp
Total: 414		$\chi^2=29.25$		P<0.005

the rhomboid pattern in another color/buff. Within each of these genotypes there are 3 with grey speckling to 1 with buff background, confirming the segregation of 'V-V<sup>lae</sup>'. The four colors found here in the 'C<sup>st</sup>' background are orange red, blackish brown, brownish purple, and blackish. Since 'V' is known to be segregating, it seems that the other gene segregating is 'B' (orange red (Gbv) is present, but greenish brown (gBv) is not (see Table 1, row 9)). The presence of a buff background color as opposed to red or pink indicates the presence of 'Rk' in both parents. All seeds are shiny, so both parents are also 'J'. The presence or absence of 'D' can not be determined here because of 'J'.

The proposed genotype for 420 is therefore PTC<sup>rho</sup>.JGbV<sup>lae</sup>Rk.

CROSS 14: 529 x 438

529 has white seeds and flowers while 438 has pale greenish yellow seeds, lavender flowers and a probable genotype of PTC.JgbV<sup>lae</sup>Rk deduced from crosses 9 and 10. The F<sub>1</sub> is dotted reddish/mottled yellowish/buff (D.C.: 47L6/9J1/9B2). The F<sub>2</sub> results are given in Table 16. Only two genes are segregating in this cross, 'P-p' and 'C<sup>rho</sup>-C'.

All 'p' seeds are white and all 'P' seeds colored. Segregation in the 'C' locus causes three patterns in the F<sub>2</sub>; self-colored, rhomboid dotted, and dotted and mottled. No segregation was observed for the modifying loci, so 529 must also be 'JgbV<sup>lae</sup>Rk' or possibly 'JgbvRk'.

The genotype proposed for 529 is therefore either pTC<sup>rho</sup>.JgbV<sup>lae</sup>Rk or pTC<sup>rho</sup>.JgbvRk.

CROSS 15: 532 x 529

532 has mottled reddish/pink seeds and lavender flowers while 529

Table 16

F<sub>2</sub> Results for Seedcoat Color for Cross 14:  
529 (White) x 438 (Pale greenish yellow)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Dotted lilac red/buff	176	153.2	3	C <sup>rho</sup> C <sup>rho</sup>
Dotted lilac red/mottled pale greenish yellow/buff	301	306.4	6	P. CC <sup>rho</sup>
Pale greenish yellow	153	153.2	3	CC
White	187	204.2	4	pp
Total: 817		$\chi^2=4.95$		0.250 > P > 0.100

has white seeds and flowers and a probable genotype of  $pTC^{rho}.JgbV^{lae}$  (or  $v$ )Rk deduced from cross 14. The  $F_1$  is dotted reddish/mottled slightly lighter reddish/buff (D.C.: 615/5H3/9B2). The  $F_2$  phenotypes are given in Table 17 with three genes segregating.

As expected, 'P-p' is segregating. Segregation of 'C' again produces three patterns; mottled, rhomboid dots or both corresponding to the ' $C^m C^m$ ', ' $C^{rho} C^{rho}$ ', or ' $C^m C^{rho}$ ', genotypes. In this cross the rhomboid pattern is only slightly darker in color than the mottled pattern so that identification of the heterozygotes is somewhat difficult, but still possible. The buff (Rk) or pink (rk) background colors result from segregation of the 'Rk' locus so 532 must be 'rk'. The 'J', 'G', 'B' and 'V' loci are not segregating here so 532 must be ' $JgbV^{lae}$ ' (lavender flowers).

The proposed genotype for 532 is therefore,  $PTC^m.JgbV^{lae}rk$ .

#### CROSS 16: 541 x 549

541 has pale yellowish seeds and white flowers while 549 has striped greenish brown/buff seeds, lavender flowers and a probable genotype of  $PTC^{st}.JgbV^{lae}Rk$  deduced from crosses 7, 11 and 12. The  $F_1$  has striped greenish brown/grey brown seeds (D.C.: 1417/13G7). The  $F_2$  results (Table 18) show two genes segregating.

Since 549 is striped and carries the ' $C^{st}$ ' gene and 541 is self-colored and therefore carries 'c' or 'C'; the  $F_2$  segregation into 1 self-colored: 2 striped/self-colored: 1 striped/buff shows that 541 must be 'c' ('C' would produce mottling and striping). In this cross as in cross 7, the yellowish and lilac yellowish stripes probably correspond to lilac red (gbv). The presence of pale yellowish (gbv) and grey brown

Table 17

F<sub>2</sub> Results for Seedcoat Color for Cross 15:  
532 (Mottled reddish/pink) x 429 (White)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Dotted reddish/buff	94	95.2	9	Rk. C <sup>rho</sup> C <sup>rho</sup>
Dotted reddish/pink	26	31.7	3	rkrk
Dotted reddish/mottled lighter reddish/buff	185	190.5	18	Rk. P. C <sup>m</sup> C <sup>rho</sup>
Dotted reddish/mottled lighter reddish/pink	58	63.4	6	rkrk
Mottled reddish/buff	97	95.2	9	Rk. C <sup>m</sup> C <sup>m</sup>
Mottled reddish/pink	28	31.7	3	rkrk
White	189	169.3	16	pp
<hr/>				
Total:	677	X <sup>2</sup> =4.47	0.750	P>0.500

Table 18

F<sub>2</sub> Results for Seedcoat Color for Cross 16:  
541 (Pale yellowish) x 549 (Striped greenish brown/buff)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Striped greenish brown/buff	185	192	3	B. C <sup>st</sup> C <sup>st</sup>
Striped yellowish/buff	57	64	1	bb
Striped greenish brown/grey brown	391	383	6	B. C <sup>st</sup> c
Striped lilac yellowish/pale yellowish	115	128	2	bb
Grey brown	208	192	3	B. cc
Pale yellowish	67	64	1	bb
Total: 1023	$\chi^2=3.94$	0.500	P>0.250	

(gBv) seeds shows that 'B' is segregating while 'G' and 'V' are both not segregating and recessive. 541 is 'v' and 549 'V<sup>lae</sup>' due to flower color. 'J' and 'Rk' are again present.

The proposed genotype for 541 is PTC.JgbvRk.

CROSS 17: 549 x 709

549 has striped greenish brown/buff seeds, lavender flowers and a probable genotype of PTC<sup>st</sup>.JgBV<sup>lae</sup>Rk deduced from crosses 7, 11, 12 and 16 while 709 has light yellowbrown seeds and white flowers. The F<sub>1</sub> is striped blackish brown/pale brown. The F<sub>2</sub> distribution (Table 19) shows 12 phenotypes from the segregation of three genes.

There are four self-colored phenotypes, four striped phenotypes with buff background, and four striped phenotypes with background colors the same as the self-colors. The striped phenotypes with buff background are 'C<sup>st</sup>C<sup>st</sup>', the striped phenotypes with colored backgrounds are 'C<sup>st</sup>c', and the self-colored ones are 'cc' because the heterozygotes are two-colored ('C<sup>st</sup>C' would produce three-colored seeds). Since 549 is 'V<sup>lae</sup>' and 709 has white flowers and thus is 'v', this locus is not segregating for seed color. Segregation at the 'G' and 'B' loci produce the four colors found in the self-colored seeds because these colors are the same as in Table 1, row 7, columns I-IV; since 549 is 'gB', 709 must then be 'Gb'. 'Rk' and 'J' are not segregating here.

The proposed genotype for 709 is, therefore, PTC.JGbvRk.

Table 19

F<sub>2</sub> Results for Seedcoat Color for Cross 17:  
549 (Striped greenish brown/buff) x 709 (Light yellowbrown)

Phenotypes	Observed No.	Expected No.	Ratio	Proposed Genotypes
Striped blackish brown/buff	84	89.3	9	G.
Striped greenish brown/buff	26	29.8	3	B. C <sup>st</sup> C <sup>st</sup> gg
Striped orange red/buff	27	29.8	3	G. bb
Striped yellow/buff	7	9.9	1	gg
Striped blackish brown/pale brown	186	178.6	18	G. B.
Striped greenish brown/grey brown	64	59.5	6	C <sup>st</sup> c gg
Striped orange red/light yellowbrown	45	59.5	6	G. bb
Striped yellow/pale yellowish	17	19.8	2	gg
Pale brown	79	89.3	9	G. B.
Grey brown	30	29.8	3	gg cc
Light yellowbrown	43	29.8	3	G. bb
Pale yellowish	27	9.9	1	gg
Total: 635	X <sup>2</sup> =46.87	P<0.005		

## SUMMARY AND CONCLUSIONS

Seventeen crosses between fourteen parents were analysed for the inheritance of seedcoat color. The genotypes calculated for these parents are listed in Table 20. Nine loci, seven of them segregating, were identified in the progenies grown:

1. the groundfactor, alleles P and p
2. the factor for total color, only allele T
3. the factor for ever-segregating and constant mottling, alleles C, c, C<sup>r</sup>, C<sup>st</sup>, C<sup>m</sup> and C<sup>rho</sup>
4. the hilumring factor, only allele D
5. the shine factor, alleles J and j
6. the yellowbrown factor, alleles G and g
7. the greenish brown factor, alleles B and b
8. the violet factor, alleles V, V<sup>lae</sup> and v
9. the factor for recessive red, alleles Rk and rk

Generally the results obtained in this study agree with those of Prakken (1970, 1972, 1974). One possible exception is in regard to the locus 'C'. It is difficult to determine if the present results confirm Prakken's position regarding 'C' as he does not list the alleles at this locus (Prakken, 1970, p. 4; 1972, p. 5; 1974, p. 4). In the present study it was found necessary to include at least one of Lamprecht's (1947) alleles at the 'R' locus (R<sup>rho</sup>) at Prakken's 'C' locus in order to explain some of the results obtained in F<sub>1</sub> and F<sub>2</sub> progenies (crosses 13, 14, 15). Aside from 'R<sup>st</sup>' (striped), 'R<sup>ma</sup>' (marbled) and 'R' (red) none of the other alleles described by Lamprecht were found in the material used. It appears from this work that possibly there is only

Table 20

## Summary of Results for Seedcoat Color

CROSS	PARENT 1		PARENT 2		SEGREGATING LOCI
	PHENOTYPE	GENOTYPE	PHENOTYPE	GENOTYPE	
1 455x437	Dark brown*	PTC.JGBV <sup>lae</sup> Rk	Pale brown*	PTc.JGBvRk	C-c, V <sup>lae</sup> -v
2 433x437	Bluish brown*	PTc.JgBVRk	Pale brown*	PTc.JGBvRk	G-g, V-v
3 445x437	Lilac red*	PTC <sup>r</sup> .JgbvRk	Pale brown*	PTc.JGBvRk	C <sup>r</sup> -c, G-g, B-b
4 433x445	Bluish brown*	PTc.JgBVRk	Lilac red*	PTC <sup>r</sup> .JgbvRk	C <sup>r</sup> -c, B-b, V-v
5 455x445	Dark brown*	PTC.JGBV <sup>lae</sup> Rk	Lilac red*	PTC <sup>r</sup> .JgbvRk	C <sup>r</sup> -c, G-g, B-b, V <sup>lae</sup> -v
6 433x515	Bluish brown*	PTc.JgBVRk	Mottled orange red/buff*	PTC <sup>m</sup> .JgbV <sup>lae</sup> Rk	C <sup>m</sup> -c, G-g, B-b, V <sup>lae</sup> -v
7 445x549	Lilac red*	PTC <sup>r</sup> .JgbvRk	Striped greenish brown/buff*	PTC <sup>st</sup> DJgBV <sup>lae</sup> Rk	C <sup>st</sup> -C <sup>r</sup> , B-b, V <sup>lae</sup> -v
8 515x549	Mottled orange red/buff*	PTC <sup>m</sup> .JgbV <sup>lae</sup> Rk	Striped greenish brown/buff*	PTC <sup>st</sup> DJgBV <sup>lae</sup> Rk	C <sup>st</sup> -C <sup>m</sup> , G-g, B-b
9 438x445	Pale greenish yellow*	PTCDJgbV <sup>lae</sup> Rk	Lilac red*	PTC <sup>r</sup> .JgbvRk	C <sup>r</sup> -c, V <sup>lae</sup> -v
10 436x438	Whitish*	PTcdJgBVRk	Pale greenish yellow*	PTCDJgbV <sup>lae</sup> Rk	C-c, J-j, B-b, V <sup>lae</sup> -v
11 436x549	Whitish*	PTcdJgBVRk	Striped greenish brown/buff*	PTC <sup>st</sup> DJgBV <sup>lae</sup> Rk	C <sup>st</sup> -c, J-j, V <sup>lae</sup> -v
12 188x549	White	pTC <sup>st</sup> .JGBVRk	Striped greenish brown/buff*	PTC <sup>st</sup> DJgBV <sup>lae</sup> Rk	P-p, G-g, V <sup>lae</sup> -v
13 188x420	White	pTC <sup>st</sup> .JGBVRk	Dotted reddish/buff*	PTC <sup>rho</sup> .JgbV <sup>lae</sup> Rk	P-p, C <sup>st</sup> -C <sup>rho</sup> , B-b, V <sup>lae</sup> -v
14 529x438	White	pTC <sup>rho</sup> .Jgb(v or V <sup>lae</sup> )Rk	Pale greenish yellow*	PTCDJgbV <sup>lae</sup> Rk	P-p, C <sup>rho</sup> -c
15 532x529	Mottled reddish/pink*	PTC <sup>m</sup> .JgbV <sup>lae</sup> Rk	White	pTC <sup>rho</sup> .Jgb(v or V <sup>lae</sup> )Rk	P-p, C <sup>m</sup> -C <sup>rho</sup> , Rk-rk
16 541x549	Pale yellowish*	PTc.JgbvRk	Striped greenish brown/buff*	PTC <sup>st</sup> DJgBV <sup>lae</sup> Rk	C <sup>st</sup> -c, B-b, V <sup>lae</sup> -v
17 549x709	Striped greenish brown/buff*	PTC <sup>st</sup> DJgBV <sup>lae</sup> Rk	Light yellowbrown*	PTc.JGBvRk	C <sup>st</sup> -c, G-g, B-b, V <sup>lae</sup> -v

\*with hilum ring

one locus, 'C', since no evidence was found to support the hypothesis of two closely linked loci, 'C' and 'R', as proposed by Lamprecht. 'C', 'c', 'C<sup>st</sup>', 'C<sup>m</sup>', 'C<sup>rho</sup>', and 'C<sup>r</sup>' appear to be alleles of the same locus.

Results which cannot be explained by the proposals of either Prakken or Lamprecht were encountered when two "constant mottled" alleles (for ex: 'C<sup>st</sup>', 'C<sup>m</sup>', 'C<sup>rho</sup>') are present. The same color relationship between the "constant mottled" alleles does not always exist. For example, in cross 15 the heterozygote, 'C<sup>m</sup>C<sup>rho</sup>', showed two types of patterns, mottling and dotting, and both were essentially in the same color with the dotting being very slightly darker. In crosses 8 and 13, each allele produced a color that was slightly different but still similar (e.g. from cross 8: striped pale red/mottled lilac red/buff or striped brownish/mottled greenish brown/buff). This is possibly not a significant color difference but probably insures that both patterns are seen.

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