A Complex C Region Genotype [? R] that with GB vlae Produces Dark Seal-brown Seedcoat Color in Common Bean

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Abstract. Common bean (Phaseolus vulgaris L.) plant introduction 527829 (formerly Lamprecht M0048) has dark seal-brown (DSB) seedcoats and pink flowers. An investigation was conducted to determine the genotype of DSB seedcoat color. M0048 was crossed with Florida breeding line 5-593, which has genotype P[Cr] DJ GB V Rk. A series of crosses involving M0048, 5-593, and three genetic tester stocks (v BC, 5-593, c BC, 5-593, and b v BC, 5-593) led to determination of the genotype. Data analysis indicated that M0048 has the genotype [? R] J G B vlae, where DSB color is produced by the interaction of R with B. Crosses between [? R] and testers with [Cr] always produced seedcoat mottling in F2, except where V masks the effect. The cross [? R] B v (DSB) x c BC, 5-593 (cartridge buff seedcoat) produced marbled seedcoats (black/cartridge buff) with genotype [? R] c B V. No way was found to determine whether the mottled or marbled seedcoat patterns were controlled at C or R; hence, the allelic ambiguity is indicated with a question mark. Illustrations are provided showing the difference between seedcoat mottling (a highly variable low-contrast patterning) and seedcoat marbling (a less variable high-contrast patterning, usually with cartridge buff as the background color). The development of a new genetic tester stock, [? R] b v BC, 5-593, was described, where [? R] b v gives unpatterned dominant red seedcoat color.

In 1989 I initiated a study of the seed collection of common beans (Phaseolus vulgaris) left by Herbert Lamprecht, which is now available under the plant introduction (PI) accession numbers 527711 through 527878 (168 accessions). One of the accessions, PI 527829 (formerly Lamprecht line M0048), had pink flowers due to vlae, but the seedcoat color was described by Lamprecht as dark seal brown, a color that appears nearly black upon casual inspection. All the known rules of genetic interaction affecting seedcoat colors were described in two treatises (Prakken, 1970, 1972). In an accession with pink flowers one would expect mineral brown seedcoat color or some paler hue, unless the dominant gene R for red seedcoat was present. The R G B v interaction would produce dark (blackish) brown (Prakken, 1972). Because R usually is accompanied by a seedcoat pattern and M0048 does not have a seedcoat color pattern, it appeared probable that some unusual genotype is responsible for the dark seal-brown (DSB) color. It is well established that vlae has pleiotropic effects and changes the flower color from bishops violet (Vv) to pink (vlae/v-), and the seedcoat color from the blue to black color series (Vv ->) to mineral brown or some paler hue (vlae/v-), depending on the background genotype (Prakken, 1970). Also, vlae has the pleiotropic effect of producing a dark (black to purple) corona about the hilum ring (Bassett, 1995a). This investigation was conducted to determine the inheritance of the DSB color of M0048 and to test the hypothesis that there may be a new allele at V that contributes to DSB seedcoat color.

Materials and Methods

PI 527829 was designated by Lamprecht as M0048, where the letter M signifies multigaris, i.e., the line was derived from an interspecific cross between P. vulgaris x P. coccineus (formerly multiflorus). Most of the accessions in the Lamprecht collection have no original notes (transcribed by S. Blixt) on the genotype of the seedcoat color, and line M0048 is no exception.

Line 5-593 is a Florida dry bean breeding line with genotype P[Cr] DJ GB V Rk (Bassett, 1994a; Prakken, 1970). Line 5-593 was the recurrent parent in the construction of three genetic tester stocks developed by backcrossing a single recessive allele or a double recessive combination (b v) into the 5-593 genetic background: v BC, 5-593, c BC, 5-593, and b v BC, 5-593. Details of the construction of those genetic stocks are given elsewhere (Bassett, 1994b, 1995a, 1995b). A description of the genetic materials used in the study and their genotypes are given in Table 1. M0048 is designated as P1, 5-593 as P2, and the three genetic tester stocks as P3, P4, and P5 (Table 1).

It is well established that genetic composition of the complex C region includes a C locus that controls heterozygous C/c seedcoat mottling, an R locus controlling dominant red seedcoat colors, an M locus for seedcoat marbling that is independent of R and probably independent of C, and other loci controlling color in plant parts (e.g., flowers and pods) other than the seed (Bassett, 1994b; Prakken, 1970, 1972, 1974). The genes C and R are very tightly linked, which is indicated by the use of brackets, but the map distance between the genes is unknown (Bassett, 1991; Prakken, 1972). No crossovers were observed in the experiments described below. Whenever the allelic genotype of only one of the genes (C and R) is known, the uncertainty of the other allelic designation is indicated by an italicized question mark, e.g., [? R], which is the conclusion made from the results presented below.

The cross M0048 x 5-593 was made and the F1 progeny were grown in the field in the spring of 1991. Data were taken on flower and seedcoat color in the F1, and F2 progeny. An F1 selection was made that had pink flowers (confirmed to be vlae/vlae) and DSB.
seeds and was progeny tested in the greenhouse (16 F₂ progeny). The F₁ progeny were true breeding for the F₁ parental phenotype, and an F₂ selection (F₁ [? R] v) was crossed to P₁ (v BC₂ 5-593). The F₂ progenies were grown in the field in the spring of 1992 and data were taken on flower and seedcoat color in the F₁ and F₂.

From the cross F₁ [? R] v x P₁, an F₂ plant selection was made in 1992 that had DSB seeds and white flowers. The F₂ progeny (16 plants) were true breeding for the F₂ phenotype, and an F₃ selection (F₂ [? R] v) was crossed with P₃ (c² BC₂ 5-593). Thus, an allelism test was performed at the C locus. The F₂ progeny were grown in the field in the spring of 1993. Data were taken as above on F₁ and F₂ plants.

The selection, F₂ [? R] v, was also crossed with P₁ and the F₂ was grown in the field in the spring of 1993. Selection was made for an F₂ plant with seed of DSB color. An F₃ progeny test (15 plants) grown in the field in the spring of 1993. Data were taken as above on F₁ and F₂ plants. The F₂ progenies were grown in the field in the spring of 1992 and an F₃ selection (F₃ [? R] v) was progeny tested in the greenhouse (16 F₃ progeny). Selection was made for an F₃ plant with unpatterned red color. An F₄ progeny test (16 plants) showed that it was true breeding. One of the F₃ plants, designated [? R] b v BC₂ 5-593, was crossed with P₅ ([C r] b v BC₂ 5-593). The F₂ from the cross [? R] b v BC₂ 5-593 x P₅ was grown in the field in the spring of 1995. Data were taken on seed colors of the F₁ and F₂ plants.

The dry bean variety ‘Prim’ ([c r] d j g b v) Rk; Bassett, unpublished data) was crossed to P₃ (v BC₂ 5-593) and the F₁ progeny were grown in the greenhouse. The F₁ seeds ([C r] x [c r] v in seedcoat tissue) were used for illustration purposes in this paper.

**Results and Discussion**

The F₁ plants from the cross P₁ x P₂ had cobalt violet flowers produced by V/lae and unpatterned, pure black seedcoats (Bassett et al., 1990) (Table 2). The segregation in the F₂ at the V locus was

### Table 1. The phenotype and genotype of M0048 and several genetic tester stocks used in the investigation of M0048.

| Parental no. | Cultivar or line | Flower Phenotype | Seed Phenotype | Genotype⁴ |
|--------------|------------------|------------------|----------------|-----------|
| P₁           | M0048, PI 527829| Pink             | Dark seal brown | [? R] J G B V lae |
| P₂           | 5-593            | Purple           | Black          | [C r] J G B V |
| P₃           | v BC₂ 5-593      | White            | Mineral brown  | [C r] J G B V |
| P₄           | c² BC₂ 5-593     | Purple           | Cartridge buff | [c² ?] J G B V |
| P₅           | b v BC₂ 5-593    | White            | Yellow brown   | [C r] J G b v |

⁴The genotype given for M0048 was established by the investigation reported in this paper. The other genotypes were determined by previously reported work.

### Table 2. Segregation for flower and seedcoat color in the F₂ from the cross P₁ x P₂, where the F₁ progeny produced unpatterned black seeds with genotype [C r]/[? R] J G B V/lae.

| Flower color | Seedcoat color | Genetic hypothesis | Number observed⁴ |
|--------------|----------------|--------------------|------------------|
| Bishops violet or cobalt violet⁵ | Unpatterned | [C r] /– V/– and [? R]/[? R] V/– | 202 |
| Pink         | Dark seal brown | [? R] v lae | 14 |
| Pink         | Mottled, dark seal brown/mineral brown⁶ | [C r]/[? R] v lae | 17 |
| Pink         | Mineral brown  | [C r] v lae | 10 |

⁵The X² (12:1:2:1) = 9.894, P = 0.02. Combining the three classes with pink flowers the X² (3:1) = 8.561, P = 0.003; testing the three pink flower classes only, the X² (1:2:1) = 1.976, P = 0.37.

⁶The V/V genotype gives bishops violet flowers and V/v gives cobalt violet.

The seedcoat mottling probably is produced by interaction of the C locus in [C r] v with an c allele in [? R], but because other genetic models are possible, the c hypothesis has been replaced by a question mark.

### Table 3. Segregation for flower and seedcoat color in the F₂ from the cross F₂ [? R] v lae (dark seal brown) x P₅ ([C r] v, mineral brown), where the F₁ progeny produced mottled seeds (dark seal brown/mineral brown) with genotype [C r]/[? R] J G B v lae/v.

| Flower color | Seedcoat color | Genetic hypothesis | Number observed⁴ |
|--------------|----------------|--------------------|------------------|
| Pink         | Mineral brown  | [C r] v lae/–     | 92               |
| Pink         | Mottled, dark seal brown/mineral brown | [C r]/[? R] v lae/– | 173 |
| Pink         | Dark seal brown | [C r] v lae/–     | 101              |
| White        | Mineral brown  | [C r] v/v         | 56               |
| White        | Mottled, dark seal brown/mineral brown | [C r]/[? R] v/v | 106 |
| White        | Dark seal brown | [? R] v/v        | 50               |

⁴The X² (3:6:3:1:2:1) = 43.84, P < 0.001. If the seedcoat color classes with [C r] v are combined within each flower color class to create an F₂, with four genotypic classes, orthogonal contrasts can be calculated (Mather, 1957); X² V = 42.04, P < 0.001; X² C = 0.389, P = 0.53; X² v = 1.053, P = 0.31. For the data 92, 173, 101, the X² (1:2:1) = 1.536, P = 0.46; for the data 56, 106, 50, the X² (1:2:1) = 0.3396, P = 0.84.
known genotype of P2 it is clear that M0048 has the same genotype
of the allele at C in doubt (indicated with a question mark).

The F1 plants from the cross F1 [? R] v*/v from F2 seed with
mottled seedcoats, DSB/MB, and pale pink flowers (v*/v) (Table
3). The appearance of the mottled seeds is illustrated (Fig. 1). The
F1 progeny showed a highly significant segregation disturbance at
the V locus, but the segregation at C was not disturbed (Table
3). Within the two flower color classes there was a good fit to a 1:2:1
ratio for DSB, mottled (DSB/MB), and MB seedcoat colors,
respectively (Table 3). Those results conclusively demonstrate
that control of the DSB color is independent of the V locus, and
the original hypothesis about a new allele of the v locus type that controls
seedcoat color is falsified.

The cross F1 [? R] v (DSB) × P4 (I[c] ? V, cartridge buff) provided
an allellism test for the hypothesis that the heterozygous mottling
is controlled at the C locus. The F1 plants produced seed with
marbled seedcoats, black/cartridge buff (Table 4). The marbled
pattern is different from the mottle produced by [C r]/[? R] and is
illustrated (Fig. 2). The same marbled pattern in the F1 was
observed in all F2 segregants with marbled seeds (Table 4). All the
F2 segregants with marbled seeds had the cartridge buff color
substituted for MB in the light color pattern area (a comparison
with the [C r]/[? R] mottle). Thus, it is conclusively demonstrated
that the locus in M0048 producing the heterozygous mottling is the
color complex C locus.

Table 4. Segregation for flower and seedcoat color in the F2 from the cross F3 [? R] v (dark seal brown) × P5 (I[c] ? V, cartridge
buff), where the F1 progeny produced marbled seeds (black/cartridge buff) with genotype [? R]/[c?] J G B v/v.

| Flower color | Seedcoat color | Genetic hypothesis | Number observed |
|--------------|----------------|-------------------|-----------------|
| Purple       | Black          | [? R] V/–         | 67              |
| Purple       | Marbled, black/cartridge buff | [? R]/[c?] V/–   | 124             |
| Purple       | Cartridge buff | [c?] V/–         | 66              |
| White        | Dark seal brown| [? R] v/v        | 31              |
| White        | Marbled, dark seal brown/cartridge buff | [? R]/[c?] v/v | 42              |
| White        | Cartridge buff | [c?] V/v        | 27              |

*The χ² (3:6:3:1:2:1) = 5.263, P = 0.39.

The cross [? R] B v BC2 5-593 (DSB) × P4 (I[C r] b v, yellow
brown) segregated in F1 at the B locus, but the segregation was
significantly disturbed (Table 5). Nevertheless, the observed seed
color classes fit the expectations of the genetic hypothesis. Of
particular interest was the segregation for mottled red/yellow
brown and unpattered red (Table 5). The appearance of those
classes demonstrated that the DSB color is the result of an interac-
tion between the R gene for dominant red color and the B allele.

The cross [? R] B v BC2 5-593 (red seed) × P5 (I[C r] b v, yellow
brown) segregated in F1 for the three expected color classes in a
1:2:1 ratio for red, mottled (red/yellow brown), and yellow brown,
respectively (Table 6). Thus, it is conclusively demonstrated that
M0048 carries the [? R] allele that produces heterozygous mottling
and the expression of heterozygous mottling by C/c is a long
established fact of seedcoat genetics in common bean (Leakey,
1988; Prakken, 1970), but heterozygosity at R also can produce a
patterned seedcoat, which will be discussed in detail below (Lam-
precht, 1934; Nakayama, 1961, 1964; Smith, 1939). It is assumed
that in the presence of V/– the mottling effects of heterozygosity at
C are masked by the intense anthocyanin pigmentation. Hence,
plants with purple flowers (bishops violet and cobalt violet
combined) never express seedcoat mottling (Table 2). [Seedcoats that
are segregating for the dominant patterns at the C locus (marbled,
striped, pinto, and other patterns) are not usually masked by V
locus color effects.] From the segregation data in Table 2 and
the known genotype of P2, it is clear that M0048 has the same genotype
as 5-593 except for gene substitutions at C and V. Thus, the
genotype of M0048 must be P ? J G B v*, with only the identity
highly disturbed (Table 2). Aberrant ratios are commonplace in
segregating materials derived from crosses involving P. vulgaris × P. coccineus (Smartt, 1970), and M0048 was derived from that
interspecific cross as noted above. Among the F2 plants segregat-
ing for pink flowers the data fit a 1:2:1 ratio for the seedcoat colors
with the DSB, mottled (DSB/mineral brown (MB)), and MB, respectively (Table 2). The appearance of mottled colored associated with
heterozygosity is consistent with the hypothesis that DSB is con-
trolled by a recessive allele at C, which is given the tentative symbol [? R] (rather than [c R]) because alternative hypotheses are
possible (Table 2).

The term mottled is used as a term of art in this paper to denote
only the low-contrast C/c seedcoat patterning. The term low-
contrast means that the darker pattern color is only slightly darker
than the lighter pattern color, such that it is often difficult to detect
the patterning in detail without the use of a loupe for magnification.
Other authorities, e.g., Leakey (1988) use the term mottled as a
generic word for all types of patterning at the C locus. The
differences between mottled and marbled seedcoats are illustrated
below.

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as 5-593 except for gene substitutions at C and V. Thus, the
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![Image](image-url)
with \([C\, r]\) and produces red color with \(b\, v\) or DSB with \(B\, v\).

Considering all the evidence above, the full genotype for seedcoat color of M0048 has been demonstrated to be \(P\, [\, \? \, R] \, J \, G \, B\, v^{\text{lae}}\).

Selection was made for plants with unpatterned red seedcoats, which is the minimum number of crossing all b v substitutions into the \(S\, 597\) background needed to permit dominant red seedcoat color expression.

Lamprecht (1934) reported inheritance data for the common bean ‘Canadian Express’, which is the only unpatterned dominant red seedcoat genotype investigated in his published work. The cross ‘Canadian Express’ (\(P\, C\, R\, J\, g\, b\, v\)) x ‘de la Chine’ (\(P\, C\, r\, j\, g\, b\, v\)) produced seedcoat marbling in the \(F_1\) progeny, which Lamprecht attributed to the heterozygote \(R\, r\). Smith (1939) reported crosses of ‘Red Kidney’ (\(P\, r\, r\, k\, b\, l\)) and probably \(P\, c\, e\, r\, v\, r\, k\, r\) in Prakken’s (1970) symbols with two varieties with unpatterned dominant red seedcoats, viz., ‘China Red’ (\(P\, R\, R\, k\, b\, l\)) and ‘Dark Red Kidney’ (\(P\, R\, R\, k\, b\, l\)). The \(F_1\) progeny of both crosses had mottled seedcoats, possibly due to the same genotype \(\{\, ? \, R\}\, [\, c\, e\, \? \, ? \}\).

The typical pattern of \(C\, c\) marbling is illustrated using \(F_2\) seed from the cross ‘Prim’ x BC, 5-593 (Fig. 3). There is very great variability (from seed to seed) in the ratio of dark pattern color to light pattern color. The mottled pattern is MB cartridge buff for the cross with ‘Akasando’ and red/chinook for the cross with ‘Bene-Kintoki’. Unfortunately, Nakayama (1961, 1964) did not test his genetic hypothesis of \([C\, R]\) in ‘Akasando’ and ‘Bene-Kintoki’ by crossing them to varieties with \([C\, r]\) although Nakayama (1961) had determined that ‘Masterpiece’ and ‘Premier’ carried \([C\, r]\).

The data in Tables 2 through 6 show no evidence of crossing over between \(C\) and \(R\). When the linkage map of common bean was revised and updated (Bassett, 1991), I discussed the disagreement between Lamprecht (1961) and Prakken (1970) over the 8 linkage map units reported by Lamprecht (1961) between \(C\) and \(R\). On the basis of the data presented in this paper and other data (Bassett, unpublished data) it is now clear that all the seedcoat patterns controlled at the \(C\) locus are independent of the dominant red color controlled at \(R\). Thus, my results agree with those of Prakken (1970) and those of Feenstra and Nakayama (as reviewed by Prakken, 1970).

Table 5. Segregation for seedcoat color in the \(F_2\) from the cross \([\, ? \, R\] \, B\, v\, BC, 5-593\) (dark seal brown) \(x\, P_2\, ([C\, r]\, b\, v\), yellow brown), where the \(F_1\) progeny produced mottled seeds (dark seal brown/mineral brown) with genotype \([C\, r]\, /[\, ? \, R\] \, J \, G \, B\, v\).

| Seedcoat color          | Genetic hypothesis | Number observed |
|-------------------------|--------------------|-----------------|
| Mineral brown           | \([C\, r]\, B\, v\) | 23              |
| Yellow brown            | \([C\, r]\, b\, b\) | 8               |
| Mottled, dark seal brown/mineral brown | \([C\, r]\, /[\, ? \, R\] \, B\, v\) | 50 |
| Mottled, red/yellow brown | \([C\, r]\, /[\, ? \, R\] \, B\, v\) | 4              |
| Dark seal brown         | \([\, ? \, R]\, B\, v\) | 19             |
| Red                     | \([\, ? \, R]\, b\, b\) | 4               |

\(^2\)The \(\chi^2\) (3:1:6:2:3:1) = 10.716, \(P = 0.06\). Combining the two \(B\) locus classes within each of the three \(C\) locus classes gives 31, 54, 23, for which the \(\chi^2\) (1:2:1) = 1.185, \(P = 0.55\). Combining the three \(C\) locus classes over the two \(B\) locus classes gives 92 (\(B\, v\, \) ) and 16 (\(b\, b\)), for which the \(\chi^2\) (3:1) = 5.975, \(P = 0.02\).

Table 6. Segregation for seedcoat color in the \(F_2\) from the cross \([\, ? \, R\] \, b\, v\, BC, 5-593\) (red seed) \(x\, P_2\, ([C\, r]\, b\, v\), yellow brown), where the \(F_1\) progeny produced mottled seeds (red/yellow brown) with genotype \([C\, r]\, /[\, ? \, R\] \, J \, G \, B\, v\).

| Seedcoat color          | Genetic hypothesis | Number observed |
|-------------------------|--------------------|-----------------|
| Red                     | \([\, ? \, R]\, b\, v\) | 3               |
| Mottled, red/yellow brown | \([\, ? \, R]\, [C\, r]\, b\, v\) | 119 |
| Yellow brown            | \([C\, r]\, b\, v\) | 61              |

\(^2\)The \(\chi^2\) (1:2:1) = 3.915, \(P = 0.14\).
color shows a distribution different from that of typical $C/c$ mottling, it is nonetheless much more variable than the ratio found in seed with typical marbling pattern. Although most mottled patterns (as defined above) are low-contrast patterns, the mottled patterns with $[? R]/[C r]$ are much higher contrast because of the $R$ gene effects, but the high pattern variability (from seed to seed) remains.

The marbled pattern produced by $[? R] v/[c" ?] V$ heterozygosity (Fig. 2) more closely resembles a typical marbled pattern (Fig. 4) than it does the typical $C/c$ mottle (Fig. 3). The marbled pattern is known to be controlled by the $C$ locus and usually has the gene symbol $C_{ma}$, or in older literature $M$ (Prakken, 1970). The marbled allele is dominant to the unpatterned $C$ allele (Prakken, 1970).

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