A Complex *C* Region Genotype [*? R*] that with *G B v^{lae}* 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 [C r] D J G B V Rk*. A series of crosses involving M0048, 5-593, and three genetic tester stocks (*v BC₂* 5-593, *c^u BC₂* 5-593, and *b v BC₂* 5-593) led to determination of the genotype. Data analysis indicated that M0048 has the genotype *P [*? R*] J G B v^{lae}*, where DSB color is produced by the interaction of *R* with *B*. Crosses between [*? R*] and testers with [*C r*] always produced seedcoat mottling in *F₁*, except where *V* masks the effect. The cross [*? R*] *B v* (DSB) × *c^u BC₂* 5-593 (cartridge buff seedcoat) produced marbled seedcoats (black/cartridge buff) with genotype [*? R*]/[*c^u ?*] *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 BC₂* 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 *v^{lae}*, 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 were 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 *v^{lae}* has pleiotropic effects and changes the flower color from bishops violet (*V*/–) to pink (*v^{lae}/–*) and the seedcoat color from the blue to black color series (*V*/–) to mineral brown or some paler hue (*v^{lae}/–*), depending on the background genotype (Prakken, 1970). Also, *v^{lae}* 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* × *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 [C r] D J G B 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 BC₂* 5-593, *c^u BC₂* 5-593, and *b v BC₂* 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*], where it is not known beyond all possible doubt whether a dominant or recessive allele exists at *C*. To make the paper easier to follow I will describe the genotype of M0048 at the complex *C* locus (throughout the paper) as being [*? R*], which is the conclusion made from the results presented below.

The cross M0048 × 5-593 was made and the *F₂* 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 *F₂* selection was made that had pink flowers (confirmed to be *v^{lae}/v^{lae}*) and DSB

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seeds and was progeny tested in the greenhouse (16 F₃ progeny). The F₃ progeny were true breeding for the F₂ parental phenotype, and an F₃ selection (F₃ [*? R*] *v*^{lae}) was crossed to P₃ (*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 F₃ [*? R*] *v*^{lae} × P₃ an F₂ plant selection was made in 1992 that had DSB seeds and white flowers. The F₃ progeny (16 plants) were true breeding for the F₂ phenotype, and an F₃ selection (F₃ [*? R*] *v*) was crossed with P₄ (*c*^u 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, F₃ [*? R*] *v*, was also crossed with P₃ 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) showed the F₂ selection to be 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) to test the hypothesis that DSB color is the result of an interaction between *B* and *R*. The F₂ was grown in the field in the

spring of 1994, and data were taken on seedcoat color in F₁ and F₂ plants.

From the cross [*? R*] *B v* BC₂ 5-593 × P₅ an F₂ selection was made for a plant with unpatterned red color. An F₃ 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 × 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*^{lae} *Rk*; Bassett, unpublished data) was crossed to P₃ (*v* BC₂ 5-593) and the F₁ progeny were grown in the greenhouse. The F₂ seeds ([*C r*]/[*c r*] in seedcoat tissue) were used for illustration purposes in this paper.

Results and Discussion

The F₁ plants from the cross P₁ × P₂ had cobalt violet flowers produced by *V/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		Phenotype		
no.	Cultivar or line	Flower	Seed ^y	Genotype ^z
P ₁	M0048, PI 527829	Pink	Dark seal brown	[<i>? R</i>] <i>J G B v</i> ^{lae}
P ₂	5-593	Purple	Black	[<i>C r</i>] <i>J G B V</i>
P ₃	<i>v</i> BC ₂ 5-593	White	Mineral brown	[<i>C r</i>] <i>J G B v</i>
P ₄	<i>c</i> ^u BC ₂ 5-593	Purple	Cartridge buff	[<i>c</i> ^u <i>?</i>] <i>J G B V</i>
P ₅	<i>b v</i> BC ₂ 5-593	White	Yellow brown	[<i>C r</i>] <i>J G b v</i>

^zThe 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 × P₂, where the F₁ progeny produced unpatterned black seeds with genotype [*C r*]/[*? R*] *J G B V/v*^{lae}.

Flower color	Seedcoat color	Genetic hypothesis	Number observed ^z
Bishops violet or cobalt violet ^y	Unpatterned	[<i>C r</i>]/– <i>V</i> /– and [<i>? R</i>]/[<i>? R</i>] <i>V</i> /–	202
Pink	Dark seal brown	[<i>? R</i>] <i>v</i> ^{lae}	14
Pink	Mottled, dark seal brown/mineral brown ^x	[<i>C r</i>]/[<i>? R</i>] <i>v</i> ^{lae}	17
Pink	Mineral brown	[<i>C r</i>] <i>v</i> ^{lae}	10

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

^yThe *V/V* genotype gives bishops violet flowers and *V/v* gives cobalt violet.

^xThe seedcoat mottling probably is produced by interaction of the *C* locus in [*C r*] with a *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 F₃ [*? R*] *v*^{lae} (dark seal brown) × P₃ ([*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 observed ^z
Pink	Mineral brown	[<i>C r</i>] <i>v</i> ^{lae} /–	92
Pink	Mottled, dark seal brown/mineral brown	[<i>C r</i>]/[<i>? R</i>] <i>v</i> ^{lae} /–	173
Pink	Dark seal brown	[<i>? R</i>] <i>v</i> ^{lae} /–	101
White	Mineral brown	[<i>C r</i>] <i>v</i> / <i>v</i>	56
White	Mottled, dark seal brown/mineral brown	[<i>C r</i>]/[<i>? R</i>] <i>v</i> / <i>v</i>	106
White	Dark seal brown	[<i>? R</i>] <i>v</i> / <i>v</i>	50

^zThe χ^2 (3:6:3:1:2:1) = 43.84, *P* < 0.001. If the seedcoat color classes with [*C r*]/– are combined within each flower color class to create an F₂ with four genotypic classes, orthogonal contrasts can be calculated (Mather, 1957); χ^2_v = 42.04, *P* < 0.001; χ^2_c = 0.389, *P* = 0.53; χ^2_L = 1.053, *P* = 0.31. For the data 92, 173, 101, the χ^2 (1:2:1) = 1.536, *P* = 0.46; for the data 56, 106, 50, the χ^2 (1:2:1) = 0.3396, *P* = 0.84.

Fig. 1. Seedcoat patterns produced by the genotype $[C r]/[? R] G B v^{lac}/v$ from F_2 seed of the cross $F_3 [? R] v^{lac}$ (dark seal brown) $\times P_3 ([C r] v)$, which is a heterozygous mottling at the C locus that is not typical of those in the published literature. Left seed has mottling (dark seal brown/mineral brown), which is not always this striped; right seed has the "reverse" mottling pattern.

highly disturbed (Table 2). Aberrant ratios are commonplace in segregating materials derived from crosses involving *P. vulgaris* $\times$ *P. coccineus* (Smartt, 1970), and M0048 was derived from that interspecific cross as noted above. Among the F_2 plants segregating for pink flowers the data fit a 1:2:1 ratio for the seedcoat colors DSB, mottled (DSB/mineral brown (MB)), and MB, respectively (Table 2). The appearance of mottled color associated with heterozygosity is consistent with the hypothesis that DSB is controlled by a recessive allele at C , which is given the tentative symbol $[? R]$ (rather than $[c R]$) because alternative hypotheses are possible (Table 2).

of the allele at C in doubt (indicated with a question mark).

The F_1 plants from the cross $F_3 [? R] v^{lac} \times P_3$ produced seed with mottled seedcoats, DSB/MB, and pale pink flowers (v^{lac}/v) (Table 3). The appearance of the mottled seeds is illustrated (Fig. 1). The F_2 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^{lac} type that controls seedcoat color is falsified.

The cross $F_3 [? R] v$ (DSB) $\times P_4 ([c^u ?] V, \text{cartridge buff})$ provided an allelism test for the hypothesis that the heterozygous mottling is controlled at the C locus. The F_1 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 F_1 was observed in all F_2 segregants with marbled seeds (Table 4). All the F_2 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 complex C locus.

Table 4. Segregation for flower and seedcoat color in the F_2 from the cross $F_3 [? R] v$ (dark seal brown) $\times P_4 ([c^u ?] V, \text{cartridge buff})$, where the F_1 progeny produced marbled seeds (black/cartridge buff) with genotype $[? R]/[c^u ?] J G B V/v$.

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

^aThe χ^2 (3:6:3:1:2:1) = 5.263, P = 0.39.

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.

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 (Lamprecht, 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 P_2 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 $P ? J G B v^{lac}$, with only the identity

The cross $[? R] B v BC_2 5-593$ (DSB) $\times P_5 ([C r] b v, \text{yellow brown})$ segregated in F_2 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 unpatterned red (Table 5). The appearance of those classes demonstrated that the DSB color is the result of an interaction between the R gene for dominant red color and the B allele.

The cross $[? R] b v BC_2 5-593$ (red seed) $\times P_5 ([C r] b v, \text{yellow brown})$ segregated in F_2 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

Fig. 2. Seedcoat patterns produced by the genotype $[? R]/[c^u ?] G B V/v$ from F_2 seed of the cross $F_3 [? R] v$ (dark seal brown) $\times P_4 ([c^u ?] V)$. Left seed is marbled (black/cartridge buff); right seed has the "reverse" marbling pattern.

Table 5. Segregation for seedcoat color in the F_2 from the cross $[? R] B \nu BC_2 5-593$ (dark seal brown) $\times P_5 ([C r] b \nu$, yellow brown), where the F_1 progeny produced mottled seeds (dark seal brown/mineral brown) with genotype $[C r]/[? R] J G B/b \nu$.

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

^zThe χ^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 χ^2 (1:2:1) = 1.185, $P = 0.55$. Combining the three C locus classes over the two B locus classes gives 92 ($B/-$) and 16 (b/b), for which the χ^2 (3:1) = 5.975, $P = 0.02$.

Table 6. Segregation for seedcoat color in the F_2 from the cross $[? R] b \nu BC_2 5-593$ (red seed) $\times P_5 ([C r] b \nu$, yellow brown), where the F_1 progeny produced mottled seeds (red/yellow brown) with genotype $[C r]/[? R] J G b \nu$.

Seedcoat color	Genetic hypothesis	Number observed ^z
Red	$[? R] b \nu$	3
Mottled, red/yellow brown	$[? R]/[C r] b \nu$	119
Yellow brown	$[C r] b \nu$	61

^zThe χ^2 (1:2:1) = 3.915, $P = 0.14$.

with $[C r]$ and produces red color with $b \nu$ or DSB with $B \nu$. Considering all the evidence above, the full genotype for seedcoat color of M0048 has been demonstrated to be $P [? R] J G B \nu^{lac}$. Selection was made for plants with unpatterned red seedcoats, having the genotype $[? R] b \nu BC_2 5-593$ (Table 6). Thus, a genetic tester stock for the R gene (with unpatterned dominant red) has been created on a $b \nu$ background, which is the minimum number

cartridge buff for the cross with 'Akasando' and red/chinook for the cross with 'Beni-Kintoki'. Unfortunately, Nakayama (1961, 1964) did not test his genetic hypothesis of $[C R]$ in 'Akasando' and 'Beni-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).

The typical pattern of C/c mottling is illustrated using F_2 seed from the cross 'Prim' $\times \nu BC_2 5-593$ (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 dark pattern/paler brown light pattern color (a low contrast patterning). It is obvious that the mottled pattern produced by the $[C r]/[? R]$ heterozygosity (Fig. 1) is different from that in Fig. 3. The $[C r]/[? R]$ pattern is more striped and is usually either mostly MB pattern (with limited DSB striping) or mostly DSB pattern color (with only a few MB flecks), i.e., rarely do seeds have roughly equal amounts of the two colors. Although the variability (from seed to seed) in the ratio of dark pattern color to light pattern

Fig. 3. Three examples of the range of C/c mottling patterns observed in the F_2 seed from the cross 'Prim' $\times \nu BC_2 5-593$ with genotype $C/c G B/b \nu^{lac}/\nu$. Left seed has minimal dark pattern (mineral brown) on the light pattern area (pale grayish brown); middle seed has a nearly equal area of dark pattern on light pattern; right seed has the maximum dark pattern area on the remaining light pattern area. The variation of ratios of dark to light pattern in the mottling is continuous among the F_2 seeds.

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' ($P C R J g b \nu$) $\times$ 'de la Chine' ($P C r j g b \nu$) produced seedcoat marbling in the F_1 progeny, which Lamprecht attributed to the heterozygote R/r . Smith (1939) reported crosses of 'Red Kidney' ($P r r k bl$; probably $P c^u r V r k$ in Prakken's (1970) symbols) with two varieties with unpatterned dominant red seedcoats, viz., 'China Red' ($P R R k bl$) and 'Dark Red Kidney' ($P R R k Bl$). The F_1 progenies of both crosses had marbled seedcoats, probably due to the same genotype $[? R]/[c^u ?]$ that is presented in my investigation. Nakayama (1961, 1964) made crosses of 'White Kidney' ($p c^u r g B \nu^{lac} R k$) with two varieties that had unpatterned dominant red seedcoats, viz., 'Akasando' ($P C R J g b \nu^{lac} R k$) and Beni-Kintoki ($P C R \nu^{lac} r k$). The F_1 progenies of both crosses had marbled seedcoats, viz., red/

Fig. 4. The marbled (red/cartridge buff) seedcoat pattern of 'Calima' with genotype $[C^{ma} R] g b \nu$.

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^u ?*] *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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