A Test Cross Protocol for Determining the Genotype of Dark Red Seedcoat Colors in Common Bean

Mark J. Bassett¹

Horticultural Sciences Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 32611

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ABSTRACT. The red common bean (*Phaseolus vulgaris* L.) seedcoat colors produced by the dominant gene *R* and the dark red kidney gene *rk^d* are very similar, making it difficult for breeders of red bean varieties to know which genotype is in their materials. A protocol employing test crosses with genetic stocks having known genotypes for seedcoat colors was developed to identify genotypes with either of two very similar dark red seedcoat colors: garnet brown controlled by *rk^d* and oxblood controlled by *R*. Twenty bean varieties and breeding lines were test crossed with genetic tester stocks *c^u* BC₃ 5-593 and *b v* BC₃ 5-593, and four of the varieties were test crossed with [*? R*] *b v* BC₃ 5-593. Analysis of the seedcoat colors and patterns in the F₁ progenies from the test crosses demonstrated that unambiguous identification of the genotypes of the two dark red colors could be achieved using the *c^u* BC₃ 5-593 and *b v* BC₃ 5-593 testers. The dark red color (garnet brown) of the Small Red market class materials was demonstrated to be produced by *rk^d*, and the dark red color (oxblood) of 'Jacobs Cattle' was demonstrated to be produced by *R*. A Light Red Kidney market class stock was derived from 'Redkloud' and used in two crosses: *c^u b v rk* BC₁ 5-593 × *b v* BC₃ 5-593 and *c^u b v rk* BC₁ 5-593 × *c^u* BC₃ 5-593. Classification of the F₂ progenies demonstrated that the *c^u* gene does not entirely prevent *rk* red color from being modified by *V*. The interactions of *rk*, *rk^d*, and *R* with *C*, *c^u*, *G*, *B*, and *V* are discussed, and previous literature concerning those interactions is critically reviewed.

The genetics of seedcoat color in common bean (*Phaseolus vulgaris* L.) has been extensively investigated, and Prakken (1970, 1972) reconciled the different gene symbols used for the same loci by various authors and combined the results in summary tables. The Light Red Kidney market class has a red seedcoat color called testaceous by Smith (1939), which is controlled by the *rk* allele at the *Rk* locus. The Dark Red Kidney market class has a dark red seedcoat color called garnet brown by Smith and Madsen (1948). Garnet brown is a recessive red color controlled by the gene *rk^d*, which is the dark red allele at the red kidney (*Rk*) locus. The Small Red market class also has dark red seedcoats, but the inheritance of the seedcoat color of the Small Red class has not been investigated. The *rk* and *rk^d* alleles require that *J/-* (Joker locus) be present for expression of red color, whereas *j/j* prevents red color expression at *Rk* (Lamprecht, 1961; Smith, 1961). The *R* locus produces a dominant dark red color called oxblood by Smith (1939, 1961). Thus, there are two dark red seedcoat colors, garnet brown and oxblood, that are very similar in hue (easily mistaken for each other), but have different genotypes.

The fact that two similar dark red seedcoat colors are controlled fundamentally at two different genes for red color, viz., *rk^d* and *R*, has practical implications for bean breeders, especially those working with the Small Red market class. The two genes have different interactions with other genes for seedcoat color (Prakken, 1972), which will be discussed below. A simple test to determine which dark red color gene is present in any stock in question would be useful to bean breeders. This paper presents a protocol for a genetic identity test, in which test crosses with specific genetic tester stocks were applied to 12 Small Red bean lines (of unknown genotype) and eight other varieties (seven checks and one of unknown genotype).

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¹Professor.

Materials and Methods

The protocol uses three genetic tester stocks: *c^u* BC₃ 5-593, *b v* BC₃ 5-593, and [*? R*] *b v* BC₃ 5-593. The question mark in the [*? R*] symbol indicates that the genetic constitution at *C* is undefined, and the brackets indicate very tight linkage between *C* and *R* (Bassett, 1996a; Nakayama, 1961). Each of the testers carries recessive alleles only for the seedcoat color genes indicated, with the exception of *r*, which is always present unless otherwise stated. Those recessive alleles are in backcross three (BC₃) to the recurrent parent 5-593, a Florida dry bean breeding line with the seedcoat color genotype *P* [*C r*] *D J G B VRk* (Bassett, 1994a, 1996b). The backcross procedure for constructing a genetic tester was described in detail by Bassett (1994b). The *c^u* allele in *c^u* BC₃ 5-593 was derived from Prakken's all recessive tester, and the dominant red gene [*? R*] in [*? R*] *b v* BC₃ 5-593 was derived from Plant Introduction (PI) accession 527829 (Bassett, 1996a). The sources of the *b* and *v* alleles in the *b v* BC₃ 5-593 tester are as follows: *b* was derived from PI 527774, and *v* was derived from either PI 527774 or PI 527830 (origins confounded by the development program).

The basic approach used in this protocol was first proposed by Bassett (1992). The general form of the procedure is as follows. Cross a stock of unknown seedcoat genotype with a series of genetic tester stocks and evaluate the seedcoat colors of the seed produced by the F₁ progeny. The genetic testers allow the efficient and (usually) unambiguous performance of an allelism test for the recessive genes they carry. The special utility of the genetic tester stocks is that they block (mask) the expression of other recessive genes in the stock to be tested. Because of the extraordinary complexity of the *C* locus (high number of alleles or very closely linked gene combinations), it is necessary to test that locus with a tester having only one recessive gene, viz., *c^u* BC₃ 5-593, in the tester stock. This simplifies the set of possible interpretations in case the test cross F₁ has some unusual result. The ideal tester for the three color modifying genes *G*, *B*, and *V* would be the triple recessive tester *g b v* BC₃ 5-593, but that stock was not available. The tester *b v* BC₃ 5-593 was used instead. Direct allelism tests for the presence of *R* were performed with the tester [*? R*] *b v* BC₃ 5-593.

Table 1. Source and seedcoat color phenotypes of common bean varieties used in the development of the protocol to identify genotypes at the *R* and *Rk* loci.

Name	Source	Seedcoat description ²
NW63	G. Hosfield ^y	Garnet brown
Garnet	G. Hosfield ^y	Garnet brown
Rufus	G. Hosfield ^y	Garnet brown
UI-37	G. Hosfield ^y	Garnet brown
Hidasta	G. Hosfield ^y	Garnet brown
ARS-R93007	G. Hosfield ^y	Garnet brown
ARS-R93008	G. Hosfield ^y	Garnet brown
Coulee	G. Hosfield ^y	Garnet brown
PI 173763	G. Hosfield ^y	Garnet brown
Huetar	G. Hosfield ^y	Garnet brown
PI 165948	G. Hosfield ^y	Oxblood
212694-3	J. Myers ^x	Oxblood
Jacobs Cattle	D. Wallace	Partly colored, Oxblood/white
Commodore	National Seed Lab, Ft. Collins	Oxblood
Akasando	Sakata Seed Co.	Oxblood
Beni-Kintoki	Sakata Seed Co.	Oxblood
Sutter Pink	P. Gepts ^z	Pink
Redkloud	D. Wallace ^w	Testaceous
PI 527771	R. Hannan ^u	Testaceous
Montcalm	G. Hosfield ^y	Garnet brown

²Color names taken from Smith (1939, 1961).

^yGeorge Hosfield, Crop and Soil Science Dept., Michigan State University, East Lansing, Mich.

^xJames Myers, formerly Univ. of Idaho, now Dept. of Horticulture, Oregon State Univ., Corvallis, Ore.

^wDonald Wallace, Plant Breeding Dept., Cornell Univ., Ithaca, N.Y.

^zPaul Gepts, Dept. of Agronomy and Range Sci., Univ. of California, Davis.

^uRichard Hannan, Plant Introduction, USDA, Pullman, Wash.

The 20 stocks tested are listed in Table 1. George Hosfield provided 10 varieties and breeding lines with dark red seedcoats from his breeding program for development of dry bean varieties of the Small Red market class (Table 1). James Myers sent me a dark red seeded breeding line, 212694-3, from his Small Red dry bean breeding program to determine its seedcoat color genotype (Table 1). 'Jacobs Cattle' is a partly colored variety that was included because the genotype of its dark red color (oxblood) is not reported in the literature (Table 1). Seven other genotypes were included as checks with known seedcoat genotypes, at least with respect to the principal genes controlling the red seedcoat color (Table 1). 'Commodore', 'Akasando', and 'Beni-Kintoki' are known to have dominant red color controlled by the *R* locus (Table 2). 'Sutter Pink', an industry standard for the Pink market class, and 'Redkloud', an industry standard for the Light Red Kidney market class, are known to have recessive red color controlled by the *rk* gene (Table 2). PI 527771 is Line V0687 of Lamprecht (1961) and is one of the most thoroughly studied genotypes for recessive red (*rk*) seedcoat color in the literature. 'Montcalm', an industry standard for the Dark Red Kidney market class, is known to carry *rk*^d, i.e., it is not different from the 'Michigan Dark Red Kidney' studied by Smith and Madsen (1948).

Tester stocks *c*^u BC₃ 5-593 and *b v* BC₃ 5-593 were crossed to all the materials (Table 3); but [*? R*] *b v* BC₃ 5-593 was crossed only with 'Commodore', 'Jacobs Cattle', 'Beni-Kintoki', and 'Akasando', but to save space no separate column was used in the table for this work (Table 3). Test crosses were performed in the

greenhouse during the winter (January–March 1996) and the F₁ progeny were grown either in the field in Spring 1996 or in the greenhouse in Fall 1996. Data were taken on the flower color and seedcoat color and pattern of the F₁ progeny plants.

A breeding program to create a light red kidney genetic tester line on the 5-593 genetic background was started in Winter 1994 with the cross 'Redkloud' × *b v* BC₂ 5-593. The first backcross, F₁ ('Redkloud' × *b v* BC₂ 5-593) × *b v* BC₃ 5-593, was made in Fall 1994. In Spring 1995 the BC₁-F₂ was grown in the field and selection was made for a plant with red kidney seedcoat genotype *c*^u *b v rk*. Two crosses were made with progeny of this single plant selection, viz., *c*^u *b v rk* BC₁-F₃ × *b v* BC₃ 5-593 and *c*^u *b v rk* BC₁-F₃ × *c*^u BC₃ 5-593. The F₂ progenies of the two crosses were grown in the field in Spring 1996, and data were taken on flower color and seedcoat color in F₁ and F₂.

Results and Discussion

Test cross results and interpretation. The Hosfield materials, with the exception of 'Montcalm', all produced unpatterned black seedcoats in the F₁ progenies of the test crosses with *c*^u BC₃ 5-593 (Table 3). This is a nonallelic response, indicating that the tested stocks carry the dominant allele at *C*. The test cross between 'Montcalm' and *c*^u BC₃ 5-593 produced cartridge buff seedcoats in the F₁ progeny, which is an allelic response (Table 3). The *c*^u symbol stands for unchangeable cartridge buff, which means that the buff color is not modified by the dominant genes *G*, *B*, and *V*. The cross between the *c*^u BC₃ 5-593 tester and PI 165948 produced a marbling pattern with grayish purple/cartridge buff (Table 3). This is a heterozygous marbling response typical of the *R* locus. Lamprecht (1934) was the first to report that such heterozygosity always resulted in a patterned seedcoat color. The heterozygous mottling produced by *R/r* was confirmed by Smith (1939), Nakayama (1961), and Bassett (1996a).

Most of the Hosfield materials produced yellow brown seedcoats in the F₁ progenies of the test cross with *b v* BC₃ 5-593 (Table 3). This an allelic response, indicating that the stocks tested carry *b* and *v*. The failure of red color to appear in those test cross progenies also indicates that the dark red color of the stocks being tested is recessive. The presumption is that the dark red color must be controlled by *rk*^d rather than *R*. The test cross between 'Montcalm'

Table 2. Documentation of seedcoat color inheritance of common bean varieties used as check genotypes.

Name	Genotype ^z	Authors
Commodore	<i>R Rk V</i>	Smith and Madsen, 1948
Akasando	<i>P [C R] Rk v^{lae}</i>	Nakayama, 1961
Beni-Kintoki	<i>P [C R] rk v^{lae}</i>	Nakayama, 1961
Sutter Pink	<i>P c^u D J b rk</i>	Smith, 1961 ^y
Redkloud	<i>rk</i>	Wallace, personal communication ^x
PI 527771	<i>P c^u J g b v^{lae} rk</i>	Lamprecht, 1961 ^w
Montcalm	<i>rk^d</i>	Hosfield, personal communication ^x

^zGene symbols according to Prakken's system (Prakken, 1970).

^yThe work of Smith (1961) only gives *m* at the complex *C* locus, but Bassett (unpublished data) has determined that the *m* of Smith (1961) is a synonym for *c*^u.

^x'Redkloud' is an industry standard for the Light Red Kidney class and 'Montcalm' for the Dark Red Kidney class. The alleles at *Rk* for the two classes were determined by Smith (1939) and Smith and Madsen (1948).

^wThe work of Lamprecht (1961) only gives *c* and *v*, but Bassett (unpublished data) has determined that PI 527771 carries *c*^u (by means of an allelism test using *c*^u BC₃ 5-593) and *v^{lae}* (by means of an allelism test with *b v* BC₃ 5-593).

Table 3. Test crosses between common bean varieties of unknown genotype at [*C R*], *B*, *V* and *Rk* (and some check varieties with known genotypes) and genetic tester stocks with known genotypes at those loci.

Stocks tested	Testcross F ₁ phenotypes using two genetic tester stocks ^z		Genotypes of stocks tested
	<i>c</i> ^u BC ₃ 5-593	<i>b v</i> BC ₃ 5-593	
NW63	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
Garnet	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
Rufus	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
UI-37	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
Hidasta	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
ARS-R93007	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
ARS-R93008	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
Coulee	Unpatterned black	Yellow brown	[<i>C r</i>] <i>b v rk</i> ^d
PI 173763	Unpatterned black	Mineral brown	[<i>C r</i>] <i>B v rk</i> ^d
Huetar	Unpatterned black	YB with red haze, scarlet pods	[<i>C Prp</i>] <i>b v rk</i> ^d
PI165948	Marbled grayish purple/CB	Mottled red or (more frequently) reddish haze on YB/YB	[?] <i>R</i>] <i>b v</i>
212694-3	Marbled black/purple buff	Mottled red/YB	[?] <i>R</i>] <i>b v</i>
Commodore ^y	Marbled dark/purple/bluish CB	YB with red haze	[?] <i>R</i>] <i>b v</i>
Jacobs Cattle ^y	Marbled dark purple/CB	Mottled yellowish red/YB	[?] <i>R</i>] <i>b v</i>
Akasando ^y	Marbled dark purple/CB with violet tint	Mottled YB with pale violet haze/YB	[?] <i>R</i>] <i>b v</i>
Beni-Kintoki ^y	Marbled navy blue/CB with violet tint	Mottled red/CB or pale reddish brown/YB	[?] <i>R</i>] <i>b v</i>
Sutter Pink	CB with veins	Yellow brown	<i>c</i> ^u <i>b v rk</i>
Redcloud	CB with pinkish haze	Mineral brown or grayish brown	<i>c</i> ^u <i>B v rk</i>
PI 527771	CB with pinkish haze	YB with purple corona	<i>c</i> ^u <i>b v</i> ^{lac} <i>rk</i>
Montcalm	CB with pinkish haze	Mineral brown or grayish brown	<i>c</i> ^u <i>B v rk</i> ^d

^zYB = yellow brown; CB = cartridge buff.

^yThese varieties were test crossed with [?] *R*] *b v* BC₃ 5-593, and the F₁ progeny showed an allelic response, i.e., they were identical to the genetic tester in color and lack of pattern on the seedcoat.

and *b v* BC₃ 5-593 produced mineral brown or grayish brown seedcoats in the F₁ progeny, indicating that 'Montcalm' carries *B v* (the genotype for mineral brown) (Table 3). 'Montcalm' is known to carry the *rk*^d allele (Smith and Madsen, 1948) and has seedcoat color identical to that of the Small Red materials of Hosfield, excepting PI 165948. The seedcoat color of the test cross F₁ from PI 165948 x *b v* BC₃ 5-593 is unique, in my experience (Table 3). The obvious mottling favors the [?] *R*] hypothesis although the red color in often more of a haze than a solid color, which is atypical for the standard [?] *R*] allele.

Besides 'Montcalm', 'Sutter Pink' and 'Redcloud' are also known to have red seedcoat color controlled at the *Rk* locus and were included as check varieties for the recessive red hypothesis. Both varieties produced an allelic response in the F₁ of the test cross with *c*^u BC₃ 5-593, indicating that both carry *c*^u (Table 3). 'Sutter Pink' produced yellow brown seedcoats in the F₁ with the *b v* BC₃ 5-593 tester, an allelic response indicating that 'Sutter Pink' carries *b* and *v* (Table 3). 'Redcloud' produced mineral brown or grayish brown F₁ progeny seedcoats, an allelic response with *v*, but not with *b* (Table 3). The mineral brown color is produced by the *B* allele carried by 'Redcloud'.

Three check varieties for the dominant red hypothesis were included. The color name Granada (Nakayama, 1961) denotes the same hue as the oxblood color of Smith (1939). Similarly, the cornhusk color name (Nakayama, 1961) denotes the same hue as the buff of Smith (1939) and the cartridge buff of this paper. The partly colored variety 'Jacobs Cattle' was also included because it has the oxblood red color in its colored zone. The test crosses of [?] *R*] *b v* BC₃ 5-593 with 'Commodore', 'Jacobs Cattle', 'Beni-Kintoki', and 'Akasando' produced F₁ progenies with an allelic response (Table 3, see footnote). When the four varieties were crossed with *c*^u BC₃ 5-593, the F₁ progenies were marbled either dark purple or navy blue/cartridge buff or tinted cartridge buff (Table 3). The test cross progenies of these four varieties with the

b v BC₃ 5-593 tester produced a range of responses (Table 3). Typically there is mottling, except for 'Commodore', which may have had mottling so faint that a red haze is all that could be seen (Table 3). Although the test cross of 'Commodore' with [?] *R*] *b v* BC₃ 5-593 is inconclusive, the test cross with *c*^u BC₃ 5-593 was still conclusive for the presence of *R* in 'Commodore' (Table 3).

The use of the genetic testers *c*^u BC₃ 5-593 and *b v* BC₃ 5-593 was sufficient to distinguish dominant red (oxblood) materials from recessive dark red (garnet brown) without ambiguity in the lines tested. The *c*^u tester always produced marbled patterns with dominant red materials (Table 3). Marbling and mottling are terms of art as used here. Marbling has a high contrast between the dark pattern and light pattern colors, and the ratio of the area of dark pattern color with light pattern color is relatively constant (compared to mottled seeds). Mottled seeds have low contrast between the dark pattern color and light pattern color (often requiring strong light and magnification for detection), and the ratio of dark pattern color with light pattern color is highly variable, including many seeds that are nearly all one or the other. The *b v* tester is useful, but the results are sometimes ambiguous as with 'Huetar' and 'Commodore' (Table 3). It is necessary to include the *b v* BC₃ 5-593 tester to eliminate materials with reddish seedcoat colors produced by *g b v* and other genes (Prakken, 1970). True recessive red (*Rk*) colors will disappear in the F₁ progeny from the test cross with *b v* BC₃ 5-593.

The protocol is limited to answering the following question. Does the parent carry *R*, or does it carry only *rk* or *rk*^d? The protocol cannot detect whether the parent carries both *R* and a recessive allele at *Rk*.

Gene Interactions and practical implications

The Pink and Red Kidney checks all carry *c*^u *J* (Table 3). Interestingly, the gene *c*^u was first described by Feenstra (1960), who said that the gene "originated from the variety Red Kidney." The seedcoat color names given to *P c*^u *J Rk* by various authors are

Table 4. Segregation for seedcoat color in the F₂ from the cross *c^u b v rk* BC₁-F₃ 5-593 × *b v* BC₃ 5-593 (*C Rk*).

<i>C/- b v</i>		<i>c^u/c^u b v</i>		χ^2	<i>P</i>
<i>Rk/-</i>	<i>rk/rk</i>	<i>Rk/-</i>	<i>rk/rk</i>		
Yellow	Yellow brown	Cartridge	Light red	9:3:3:1	0.53
brown	with red haze	buff	kidney ²		
183	53	51	16	2.232	0.53

²Same color as the testaceous of Smith (1939, 1961).

Table 5. Segregation for flower color and seedcoat color in the F₂ from the cross *c^u b v rk* BC₁-F₃ × *c^u* BC₃ 5-593 (*B V Rk*).

All with <i>c^u/c^u</i>					
<i>V/-</i> , Purple flowers		<i>v/v</i> , White flowers		χ^2	<i>P</i>
<i>Rk/-</i>	<i>rk/rk</i>	<i>Rk/-</i>	<i>rk/rk</i>		
Cartridge	Light red	Cartridge	Light red	9:3:3:1	0.17
buff	kidney ²	buff	kidney		
129	33	49	9	4.970	0.17

²Not the true light red kidney color of the 'Redkloud' source of the *rk* gene. This color is more violet, i.e., a bluish tinge comes through from *V* even in the presence of *c^u*.

creamish (Feenstra, 1960), cartridge buff (Nakayama, 1960) or cornhusk (Nakayama, 1961), cartridge buff (Lamprecht, 1947) or rohseiden (raw silk) (Lamprecht, 1961), and buff (Smith, 1939; 1961) and (Smith and Madsen, 1948). What role does the *c^u* gene play in producing a reliable Red Kidney class seedcoat color? In the work of Smith (1939) the gene *m* is identical to the *c^u* gene. Thus, when Smith says that the phenotype of segregants with *Rk/-* is buff, a more complete statement is that in the absence of color modification by *rk* the phenotype of *Rk/-* in a *c^u J* background is buff. When *CJ* is present, there are complex interactions for all possible gene combinations at *G*, *B*, *V*, and *Rk* (Prakken, 1972). When *c^u J* is present, the recessive alleles at *Rk* modify the buff color of *c^u* to their respective red colors without interference by *G*, *B*, and *V* according to Prakken (1972).

Prakken (1972) reported seedcoat color genetic work with only one variety ('Soldaat K') carrying a recessive red color gene, which he designated *rk^d*. In the present work, the seedcoat color genotype [*C r*] *b v rk^d* produces garnet brown, the typical color of the Small Red market class (Tables 1 and 3). That result is not consistent with the results of Prakken (1972, p. 44–50) with the cross 'Yellowbrown J' × 'Soldaat K'. In the F₂ from the latter cross, the genotype *C G b v rk^d* produced "reddish colour over yellowbrown" (Prakken, 1972, Table 11). In the experience of the present author in work developing a *c^u b v rk* BC₃ 5-593 genetic tester, the "reddish colour over yellowbrown" color is a good description of the color given by genotype *C G b v rk* (M.J. Bassett, unpublished data). Thus, my hypothesis, i.e., interpretation of the data of Prakken (1972), is that 'Soldaat K' carries *rk*, not *rk^d*, and the summary tables of Prakken (1972, p. 73-78) need to be revised accordingly.

If *c^u* protects *rk* from modification by *G*, *B*, and *V*, the question remains, is the color produced by *C J g b v rk* the same as *c^u J g b v rk*? Lamprecht (1961) called the color of the former ockerrot and the color of the latter weinrosa. Hence, it makes a difference in the color of the seedcoat whether a breeder of Red Kidney chooses to go with *CJ* or with *c^u J*. If my Red Kidney materials (Tables 1 and 3, last four entries) are representative of most varieties used by the industry, then the industry standard for color must be based on selection (probably unconscious) for *c^u J*, especially for Pink and

Light Red Kidney market classes. Thus, the simplest strategy for a Red Kidney breeder to use to maintain true market class color with the minimum concern with other modifier genes is to maintain *c^u* in all his breeding materials.

According to the above findings, and the literature, a good Light Red Kidney stock could be developed with the least effort by pursuing the genotype *P c^u J G B V rk*. Only two recessive gene substitutions are needed with respect to my "all dominant" 5-593 genetic background stock. This thesis was surprising because all the Red Kidney varieties and breeding materials that I have seen have recessive alleles at *V*. If either *v* or *v^{lae}* are not necessary, why have breeders persisted in using them?

My efforts to develop a genetic tester for recessive red kidney stocks confirmed some aspects of the summary tables of Prakken (1972). For the cross *c^u b v rk* BC₁-F₃ × *b v* BC₃ 5-593 the F₂ segregated for the four expected classes and fit the 9:3:3:1 ratio (Table 4). Note that the *C/- b v rk* (with *JG* understood) class had a seedcoat color that is not the desired Light Red Kidney market class color. Thus, with *C* the presence of *G* throws the color out of grade. With *c^u* the color effect of the presence of *G* is nullified (Table 4). Using the same female parent plant as above, the cross *c^u b v rk* BC₃ 5-593 × *c^u* BC₃ 5-593 segregated for the four expected classes and fit a 9:3:3:1 ratio (Table 5). According to Prakken (1972), there should have been no difference in the seedcoat color of the genotypes *c^u V/- rk* and *c^u v rk*, but the former genotype had a more violet color that would not be acceptable to the Light Red Kidney market. Lamprecht, Nakayama, and Prakken never published any reports of *V* gene interactions with recessive alleles at *Rk*. Smith and Madsen (1948) did work with this interaction and Prakken (1972) may have relied on their data. In various tables (Smith and Madsen, 1948) the genotypes *r/r rk/rk Bl* or *bl* produce testaceous seedcoat color and *r/r rk^d/rk^d Bl* or *bl* produces the garnet brown seedcoat color. What is not obvious from the presentation of Smith and Madsen (1948) is that their *r* allele is not some random recessive allele at the complex *C* locus, but the *c^u* allele that alone can protect the recessive red alleles at *Rk* from color modification by *G*, *B*, and *V*. My findings (Table 5) differ from those of Smith and Madsen (1948) and Prakken's (1972) summary table in that *c^u* does not fully protect *rk* from color modification by *V*.

Prakken (1972) also gives summary tables for the interactions of *R* (his *Cst* is really *Cst R*) with *G*, *B*, *V*, and *Rk*. The tables of Prakken (1972, p. 73-78) give only *Rk* or *rk^d*, and not *rk*, but as I have discussed above, I believe that the data really describe the effects of *rk* and not *rk^d*. The colors of Prakken (1972, section IIIa., p. 75) describe typical *rk* effects, not *rk^d* effects, in my experience. The contrast in colors between Prakken (1972, section IIIa) and Prakken (1972, section IIIc) are typical of the need for *rk* to be protected by *c^u* and atypical of the independence of *rk^d* in *C* (versus *c^u*) backgrounds. Similarly, the colors of Prakken (1972, section IV) probably describe [*Cst R*] *rk* interactions and not [*Cst R*] *rk^d* interactions.

Literature Cited

- Bassett, M.J. 1992. Development of a protocol for determining the genotype of seed coat color and color pattern in common bean. Annu. Rpt. Bean Improv. Coop. 35:191–192.
 Bassett, M.J. 1994a. The genotype for seedcoat color of breeding line 5-593. Annu. Rpt. Bean Improv. Coop. 37:244–245.
 Bassett, M.J. 1994b. The *griseoalbus* (gray-white) seedcoat color is controlled by an allele (*pst*) at the *P* locus in common bean. HortScience 29:1178–1179.
 Bassett, M.J. 1996a. A complex *C* region genotype [*? R*] that with *GB v^{lae}* produces dark seal brown seedcoat color in common bean. J. Amer. Soc. Hort. Sci. 121:594–598.

- Bassett, M.J. 1996b. The margo (*mar*) seedcoat color gene is a synonym for the Joker (*j*) locus in common bean. J. Amer. Soc. Hort. Sci. 121:1028–1031.
- Feenstra, W.J. 1960. Biochemical aspects of seedcoat colour inheritance in *Phaseolus vulgaris* L. Meded. Landbouwhogeschool, Wageningen 60–2:1–53.
- Lamprecht, H. 1934. Zur Genetik von *Phaseolus vulgaris*, IX. Über den Einfluss des Genpaares *R-r* auf die Testafarbe. Hereditas 20:32–46.
- Lamprecht, H. 1947. The seven alleles of the gene *R* of *Phaseolus*. Agr. Hort. Genet. 5:46–64.
- Lamprecht, H. 1961. Die Vererbung der rezessiv roten Testafarbe von *Phaseolus*. Sowie Bemerkungen zur Manifestation und Symbolik von Testafarbgenen. Agr. Hort. Genet. 19:344–359.
- Nakayama, R. 1960. Genetical studies on kidney beans (*Phaseolus vulgaris*). V. On the inheritance of seed-coat color 1. Bul. Fac. Agr. Hirosaki Univ. 6:21–36.
- Nakayama, R. 1961. Genetical studies on kidney beans (*Phaseolus vulgaris*). VI. Genetical behavior of plant color, with special reference to seed-coat color in the hybrids between white kidney and other varieties. Bul. Fac. Agr. Hirosaki Univ. 7:37–65.
- Prakken, R. 1970. Inheritance of colour in *Phaseolus vulgaris* L. II. A critical review. Meded. Landbouwhogeschool, Wageningen 70–23:1–38.
- Prakken, R. 1972. Inheritance of colours in *Phaseolus vulgaris* L. III. On genes for red seedcoat colour and a general synthesis. Meded. Landbouwhogeschool, Wageningen 72–29:1–82.
- Smith, F.L. 1939. A genetic analysis of red seed-coat color in *Phaseolus vulgaris*. Hilgardia 12:553–621.
- Smith, F.L. 1961. Seed-coat color genes in six commercial varieties of beans. Hilgardia 31:1–14.
- Smith, F.L. and C.B. Madsen. 1948. Seed-color inheritance in beans. J. Hered. 39:191–194.