

A Test Cross Protocol for Determining the Seedcoat Genotype at the *C* Locus in Common Bean

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Abstract. Studying the genetics of seedcoat color in common bean (*Phaseolus vulgaris* L.) in F_2 progenies is very difficult because of complex epistatic interactions, and the analysis is complicated further by multiple allelism, especially at the *C* locus. An alternative approach is to study seedcoat genetics by analyzing the F_1 progeny of test crosses between a variety with unknown seedcoat genotype and genetic tester stocks with known genotypes. Twenty varieties, 18 with known genotype at *C*, were test crossed with the genetic tester stock c^u BC₃ 5-593, where 5-593 is a recurrent parent with seedcoat genotype $P [C r] D J G B V Rk$. The resulting F_1 progenies were classified into seven phenotypic classes and discussed. The crosses $g B v$ BC₃ 5-593 \times c^u BC₃ 5-593 and c^u BC₃ 5-593 \times v BC₃ 5-593 were made and the F_2 progeny classified for flower color and seedcoat color and pattern. No tiny cartridge buff flecks were observed in the segregants with $C/c^u v/v$, whereas $C/c^u V/-$ always showed such flecks. The contrasting seedcoat color expression at *C* in different environmental conditions is discussed.

Seedcoat color in common bean is controlled primarily by a system of eight genes, viz., *P*, *C*, *D*, *J*, *G*, *B*, *V*, and *Rk*, and the effect of each of the genes has been described by Prakken (1970, 1972). Leakey (1988) gave a highly speculative hypothesis about the role each of those genes may play in the metabolic pathways in the synthesis of flavonoid pigments in the seedcoats of common bean.

The knowledge about the genetics of seedcoat color was developed typically by analyzing F_2 and F_3 populations derived from a cross of two inbred parents with different seedcoat colors. An easier method for determining seedcoat genotype is needed to enable nonspecialists to obtain reliable results without prior mastery of the very complicated system of interactions among the seedcoat color genes. A method of determining seedcoat genotype using test crosses between an inbred line to be studied and a series of genetic testers stocks was proposed by Bassett (1992). The seedcoat color of the F_1 progeny of the test crosses is used to determine the seedcoat genotype of the inbred tested.

The *C* locus has been, by far, the most difficult object of study for bean seedcoat geneticists. This locus can be viewed either as having a multiple allelic series (Nakayama, 1964) or as a complex locus (Prakken, 1970, 1974). The term 'complex *C* locus' of Prakken (1970, 1974) refers to a series of tightly linked genes that control color expression not only in

the seedcoat, but also in the stems, leaves, flowers, and pods (Bassett, 1994a). This locus can produce a great number of seedcoat patterns that are inherited either as homozygous genotypes for various patterns (Prakken, 1970, 1974) or as mottled patterns inherited only as heterozygous genotypes (Leakey, 1988; Prakken, 1970). Also, the 'complex *C* locus' includes the dominant *R* gene for red seedcoat color (Prakken, 1970). A bracket convention, viz., [*C R*], was introduced by Bassett (1991) to indicate very tight linkage (virtually unbreakable) between genes within this region.

A standard recessive allele at the *C* locus produces mottling with *C/c* and slightly paler colors with *c/c*, given any background seedcoat genotype except *V/-* (Lamprecht, 1932). Feenstra (1960) discovered a second recessive allele, c^u , that produces "unchangeable" cartridge buff, i.e., the color (nonpatterned) is not affected by gene substitutions at *G*, *B*, and *V*. In materials used by Feenstra (1960) and Nakayama (1964) the heterozygous genotype C/c^u produced a patterned seedcoat called "mottled" by Feenstra (1960) and "marbled" by Nakayama (1964). With either pattern name, the dark pattern color is expressed because of *C* (and remaining seedcoat color genotype), and the light pattern color (cartridge buff) is expressed because of c^u (same as c^u/c^u). Full color illustration of cartridge buff color and the seedcoat patterns controlled by the *C* locus was provided by Leakey (1988, see especially p. 604).

The attributes of the *C* locus provide a difficult challenge for development of a single genetic tester stock that can determine the seedcoat color genotype by the protocol of Bassett (1992). The c^u allele was chosen as the best tester allele because it is the most recessive of all *C* alleles. The anticipated test cross

F_1 seedcoat phenotypes (Bassett, 1992) were nonpatterned black (nonallelic interaction where the variety carries *C*) and cartridge buff (allelic interaction where the variety carries c^u). In this paper I present the results of test crosses between the genetic tester stock c^u BC₃ 5-593 and 20 varieties, 18 of which were of known genotype at *C*.

Materials and Methods

Table 1 presents the list of varieties studied, sources of the seed, and seedcoat colors. The varieties were chosen for one of two reasons: 1) because the genotypes for seedcoat color (or at least the genotype at *C*) were previously determined; or 2) the variety contributed to the representation of the complete range of possible interactions encountered. For 18 of the varieties tested, the genotype at the 'complex *C* locus' is known, and the sources of that information are cited (Table 2). The variety 'Wax Digo' has particular importance because it carries the "standard" recessive allele at *c*, which produces mottled seedcoat colors when heterozygous, *C/c* (Lamprecht, 1932). In Prakken's (1970) summary of seedcoat color genetics, the Group VI color series gives the "shiny dark pattern colors" produced by *C J*, whereas substitution of the standard *c* for *C* produces the *c J* Group V color series, which Prakken calls the "shiny background colors." Each seedcoat color with *C* is changed to a slightly paler color with *c*; hence, the *C/c* mottling is subtle. To my knowledge, no commercial dry bean varieties grown in the United States are known to have a *c/c* genotype.

The genetic tester stock used in the test cross program described below is c^u BC₃ 5-593. The tester carries only the recessive alleles for the seedcoat color genes indicated in the name, 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 $P [C r] D J G B V Rk$ (Bassett, 1994b, 1996a). The c^u allele in c^u BC₃ 5-593 was derived from Prakken's "allrecessive" tester (Bassett, 1994b, 1996a). In the 5-593 genetic background, the c^u allele produces cartridge buff seedcoat color, and C/c^u produces a nearly black seedcoat with widely dispersed tiny flecks of cartridge buff.

The 20 varieties listed in Table 1 were crossed to c^u BC₃ 5-593 in the greenhouse over a period of several years, and the F_1 progeny were either grown (most commonly) in the greenhouse or in the field in various years. Data were taken on the seedcoat color and pattern in the F_1 progeny. The genotypes at seedcoat color loci other than *C* are not given (Table 2) because they do not contribute any useful information for interpreting the F_1 phenotypes of the test crosses. Data were taken on attributes of the seed from F_1 test cross plants immediately after harvest.

The genetic tester stock $g B v$ BC₁ 5-593 was developed from the cross 'Calima' ($[C^{ma} R] J g b v Rk$) \times $b v$ BC₃ 5-593 by selection in the field (Spring 1994) for the segregants with

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Table 1. Seedcoat phenotypes of parental bean varieties of common bean studied in test crosses and the sources of the seed.

Parental varieties	Seedcoat phenotype ^z
Akasando ^v , Commodore ^x , G23623 ^w	Oxblood red
Jacobs Cattle ^v	Oxblood red/white; partly colored
Montcalm ^u , Garnet ^u , Hueta ^u , UI-37 ^u , Rufus ^u	Garnet brown (Dark Red Kidney or Small Red classes)
Redkloud ^v	Testaceous (Light Red Kidney class)
Sutter Pink ^t	Pink (Pink class)
5-593 ^s	Black
Opal ^f	Silvery gray
Wax Digo ⁱⁿ (PI 226936) ^q , Masterpiece ^f , Prim ^p , Citroen ^o	Pale greenish yellow or creamish pale buff
Wagenaar ^o	Greenish yellow
PI 527735 (V0400) ^q , PI 527808 (V0874) ^q	White

^vThe red color names (oxblood, garnet brown, testaceous, and pink) are from Smith (1939), and the remaining names follow Prakken (1970, 1972).

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Table 2. Genotypes at the *C* locus for the seedcoats of common bean varieties (all pure lines) tested and references to research supporting the genotype.

Parental varieties	<i>C</i> locus genotype	Reference
Montcalm, Redkloud, Sutter Pink	<i>c</i> ^u	Bassett, 1998a
Wax Digo ⁱⁿ	<i>c</i>	Lamprecht, 1932
PI 527734, PI 527808	<i>c</i>	Stig Blixt ^t
Garnet, Rufus, Hueta ^u , UI-37	<i>C</i>	Bassett, 1998a
5-593	<i>C</i>	Bassett, 1994b
Prim	<i>C</i>	Bassett, 1999
Masterpiece	<i>C</i>	Nakayama, 1961
Wagenaar, Citroen	<i>C</i>	Prakken, 1972
Akasando	<i>C, R</i>	Nakayama, 1961
Commodore	<i>R</i>	Smith and Madsen, 1948
Jacobs Cattle	[? <i>R</i>]	Bassett, 1998a
G 23623, Opal	?	(Genotype not known)

^tFrom genetic notes transcribed by Blixt^t from Lamprecht's (1932) seed packet data after Lamprecht's death; information now in the common bean genetic stock collection at Pullman, Wash. See the Genetic Resources Information Network (GRIN) to access the data.

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pale greenish yellow seedcoats ([*C r*] *J g b v*) in the *F*₂ progeny. A true breeding *F*₃ pale, greenish-yellow progeny was used to back-cross to 5-593. The *F*₂ was grown in the field in Spring 1995 and selection was made for plants with seedcoats of buffy citrine color with genotype *P C J g b v*. Thus, the *g B v* *BC*₁ 5-593 stage of development was obtained in Spring 1995. Under field conditions at Gainesville, Fla., the buffy citrine color is a pale gray rather than the gray greenish brown of winter-grown greenhouse plants or plants grown under much more temperate summer conditions at higher latitudes.

To test the hypothesis that the putative "buffy citrine" may actually be due to some recessive *c* allele, the cross *g B v* *BC*₁ 5-593 × *c*^u *BC*₃ 5-593 was made in Fall 1995 in the greenhouse. The *F*₂ seed was produced in Winter 1996, and the *F*₂ was planted in the field in Spring 1996. The cross *c*^u *BC*₃ 5-593 × *v* *BC*₃ 5-593 was also made in Fall 1995 in the greenhouse. The *F*₂ seed was produced in Winter 1996, and the *F*₂ was planted in the

field in Spring 1996. Data were taken on flower color and seedcoat color and pattern in *F*₁ and *F*₂ progenies for both the above crosses.

In 1996 and 1997 the remaining two back-crosses to 5-593 were made to develop the *g B v* *BC*₃ 5-593 genetic tester stock. This stock has been sent to the Western Regional Plant Introduction Station at Pullman, Wash., to be included in the genetic stock collection for common bean, i.e., be given a PI accession number and maintained in the permanent germ-plasm collection.

Results and Discussion

In extensive test crosses of common bean varieties with the *c*^u *BC*₃ 5-593 genetic tester, seven different phenotypic classes were observed among the test cross *F*₁ progenies (Table 3). The first phenotype is the result of simple allelism, giving the cartridge buff of the tester, i.e., the variety tested carries *c*^u (Bassett, 1998a). The second phenotype (Table 3) is due to a recessive *c* allele, but not the same allele as the

tester. When the test cross *F*₁ progeny express seedcoats with brown tinged with grayish indigo, the *c* allele present in the variety tested must be either the standard *c* or some other recessive *c* not *c*^u (Table 3).

The third phenotypic class (Table 3) is the result of nonallelism. The unpatterned black *F*₁ progenies from crosses with the Small Red market class parents, 'Garnet', 'Rufus', 'Hueta^u', and 'UI-37', are nonallelic. A fourth phenotypic class (Table 3) resulted from the crosses with 5-593 and G23623, which produced *F*₁ progeny with black seedcoats having a highly restricted pattern, viz., widely distributed tiny flecks of cartridge buff. Thus, the *C* allele in 5-593 and G23623 produces a *F*₁ heterozygote with very limited patterning. The flecks are so small that they can only be verified under 15× magnification. The flecks otherwise may be mistaken for dust, tiny particles of debris, or minute seedcoat damage.

The question remains whether the *C/c*^u heterozygote having tiny cartridge buff flecks with *V/-* will produce a typical marbling pattern with *v/v*. Illustration of the marbling pattern was given in Bassett (1996b). Conclusive evidence was obtained from the data from two crosses: *g B v* *BC*₁ 5-593 × *c*^u *BC*₃ 5-593 and *c*^u *BC*₃ 5-593 × *v* *BC*₃ 5-593, where *g B v* *BC*₁ 5-593 and *v* *BC*₃ 5-593 carry the *C* allele from 5-593. The tiny cartridge buff flecks observed with *V/-* were not observed with *v/v* (Table 4).

The fifth test cross phenotype (Table 3) is the result of a nonallelic interaction, giving black/cartridge buff marbling. This type of interaction was previously reported by Nakayama (1960, 1961, 1964) for *C* × *c*^u crosses. The marbling pattern was expressed with all possible genotypic combinations at *G*, *B*, and *V*.

The pattern descriptors, mottle and marble, are terms of art. The *C/c* interaction produces mottling, which is a subtle patterning between two colors that are close in hue and also varies greatly from seed to seed in the relative proportions of "dark pattern" to "light pattern" color (Prakken, 1970). On the other hand, the *C/c*^u interaction produces marbling, which can be a high or low contrast patterning depending on the hue of the "dark pattern" color controlled by the genotype at *G*, *B*, and *V*. Also, the marbling pattern has relatively constant proportions (from seed to seed) of "dark pattern" to "light pattern" color. Illustration of mottling and marbling patterns was given by Bassett (1996b).

The marbling pattern produced by the *C/c*^u interaction is hardly distinguishable from the same pattern produced by a dominant "allele" at the *C* locus that produces a true-breeding marbling (Prakken, 1970). Various symbols have been used for the dominant marbling allele by various authors over many decades: *C*^{ma}, *M*, or some tightly linked combination of *C* and *M* indicated by a curving line above the two letters and joining them. The same 'complex *C* locus' also controls anthocyanin color patterning in all plant parts, e.g., hypocotyl, cotyledon, seedcoat, stem, petiole, leaf lamina, flower bud, and banner petal (see Prakken, 1970, for a review).

Table 3. Parental common bean varieties test crossed with the c^u BC₃ 5-593 tester, the seedcoat phenotypes of the F₁ progeny, and the genetic interpretation of the test cross results, i.e., the putative allele at the *C* locus.

Parental varieties tested	Test cross F ₁ seedcoat		C locus genotype
	Class no.	Phenotype	
Montcalm, Redcloud, Sutter Pink	1	Cartridge buff	c^u
Wax Digoïn, PI 527735, PI 527808	2	Brown tinged with grayish indigo ²	c
Garnet, Rufus, Huetaar, UI-37	3	Unpatterned black	C
5-593, G23623	4	Black with widely distributed tiny cartridge buff flecks ³	C
Masterpiece, Wagenaar, Prim, Citroen	5 ^x	Black/cartridge buff; marbled pattern	C
Akasando, Commodore, Jacobs Cattle	6 ^w	Black, dark purple, or navy blue/cartridge buff (sometimes tinted various colors); marbling pattern	[? R]
Opal ($C^{st} j$)	7 ^v	Black/cartridge buff; stripe pattern	C^{st}

²The c^u/c interaction produces pale grayish brown at Gainesville, but the description of Prakken (1970, 1972) is given because it is more representative of seedcoat expression in the higher latitude temperate zone.

³The C allele producing tiny cartridge buff flecks with C/c $V/-$ does not express tiny fleck pattern with C/c v/v (Table 4).

^xThis class of seedcoat pattern was previously reported by Nakayama (1960, 1961) and was interpreted as a C/c^u interaction.

^wMarbling ("marble stripes") was previously reported by Nakayama (1964), for the interaction of [$C R$]/ c^{ui} , with [$C R$] from 'Akasando' and c^{ui} from 'Blue Butter'.

^vThe genotype j/j obscures (prevents expression of "dark pattern" color) whatever dominant seedcoat pattern is otherwise expressed with J (Prakken, 1972).

Table 4. Segregation (with genetic hypothesis) for flower color and seedcoat color and pattern in the F₂ from two common bean crosses: 1) $g B \nu BC_3$ 5-593 \times c^u BC₃ 5-593; and 2) c^u BC₃ 5-593 \times ν BC₃ 5-593.

Cross no.	<i>V/-</i> purple flowers		<i>v/v</i> white flowers			χ^2 ratio tested	χ^2	<i>P</i>
	<i>C/-</i> Black seeds ²	c^u/c^u Cartridge buff seeds	<i>C/- G B</i> Mineral brown seeds	<i>C/- g B</i> Buffy citrine seeds	c^u/c^u Cartridge buff seeds			
1	177	54	32	[32, both classes combined] ³		36:12:9:7	2.939	0.40
2	ND ^x	ND ^x	30		8	3:1	0.316	0.57

²No separate classification was made for the seed with C/c^u , giving tiny cartridge buff flecks.

³Under field growing conditions the underdeveloped buffy citrine color could not be unambiguously distinguished from cartridge buff.

^xND = data not shown.

Nakayama (1965), working with the cross 'Sanpaku' ($P C j g b \nu^{lac}$) \times 'Ever Green' ($P c^u j g b \nu$), demonstrated that the c^u allele in 'Ever Green' had mutated into a new, completely recessive allele c^r , i.e., does not produce marbling with C/c^r .

The results in Table 3 demonstrate that dominant C alleles have also acquired mutations, allowing expression of either C/c^u marbling or C/c^u unpatterned color. Thus, a geneticist must be very careful to test any putative c^r allele with appropriate testers, such as 'Masterpiece' or 'Akasando' (Table 3).

The sixth test cross phenotype (Table 3) is the result of a cross between a variety carrying unpatterned dominant red (or partly colored dominant red/white in the case of 'Jacobs Cattle') and the c^u BC₃ 5-593 tester (Bassett, 1996b, 1998a). The coloring of the marbled pattern can be quite variable among varieties, and the presence of [? R] needs to be confirmed with a test cross with either $b \nu$ BC₃ 5-593 or $g b \nu$ BC₃ 5-593 (Bassett, 1996b, 1998a).

The seventh test cross phenotype (Table 3) is the result of a cross between a variety with a seedcoat pattern controlled at C and the c^u BC₃ 5-5-593 tester, where the seedcoat pattern of test cross F₁ progeny is identical with that of the variety tested (data not shown). Great variation is possible for seedcoat patterns controlled at C , with almost continuous variation between such types as marbled, stripes, pinto,

etc. The possible variations in the types of stripes is so great and finely graded in differences that no descriptive catalog of the differences seems possible.

Any C locus pattern may be carried cryptically due to epistasis by p , t , or j (Prakken, 1970, 1972). The only variety tested that carries a dominant C locus pattern was 'Opal' (Table 3). The seedcoat pattern controlled by C^{st} in 'Opal' is obscured by the action of j (Bassett, unpublished data). In marbled seedcoats the action of j cannot completely suppress the pattern expression, but does weaken it to a faint expression level (Bassett, unpublished data; Prakken, 1972). For seedcoat patterns with less extensive "dark pattern color" zones the pattern is completely obliterated, as in 'Opal'.

In general, the test cross protocol for determining seedcoat color in common bean (Bassett, 1992), as it is applied to any given locus, results in the conclusion that the variety being tested carries either the dominant or the recessive allele at that locus. For the C locus the results of the test cross have more than two allelic possibilities. Two distinct recessive allelic classes (Table 3, classes 1 and 2) can be distinguished, viz., the c^u allele, which includes the c^r allele, and the c allele, which includes the standard c and possibly others. The C locus results also included five dominant allelic classes (Table 3, classes 3 through

7). Class 3 is completely unpatterned, class 4 is only slightly patterned, and class 5 is marbled. Class 6 carries the dominant gene R for red (oxblood), which results in marbling pattern, but both the "dark pattern color" and the "light pattern color" are not typical for class 5 C alleles. The most reliable indicator of class 6 is the tinting of the cartridge buff zone with various colors.

Class 7 is a special case where a dominant pattern allele at C has been entirely or nearly obscured by the interaction of the recessive allele at the J locus (Table 3). The result of the test cross is to make the underlying (unexpressed) pattern visible by removing the j effect. Varieties that carry visible (with J) dominant C patterns do not need the test cross to reveal the genotype at C for those who know how to identify those patterns. There are also recessive seedcoat pattern genes in common bean: partly colored patterns dependent on t for expression (Prakken, 1970), and three patterns, each determined by a different recessive allele at the stippled locus (Bassett, 1996c, 1998b). Thus, when a variety with a seedcoat pattern is test crossed with c^u BC₃ 5-593 and the F₁ progeny show the same pattern observed in the patterned parent, then the pattern must be controlled at the C locus.

The F₁ classes 3–6 are interpreted as being allelic with C because this is the simplest hypothesis consistent with the data. Various loci closely linked together within the 'complex C locus' of Prakken (1970) are probably playing a role in the seedcoat pattern expression, but the data produced by this protocol are not adequate to determine those genotypes. Genes not linked to C are probably not influencing the observed results because such interactions have not been reported during decades of genetic investigations, many of which were capable of exposing them (Prakken, 1970).

Literature Cited

- Bassett, M.J. 1991. A revised linkage map of common bean. *HortScience* 26:834–836.
- Bassett, M.J. 1992. Development of a protocol for determining the genotype of seedcoat color and color pattern in common bean. *Annu. Rpt. Bean Improv. Coop.* 35:191–192.
- Bassett, M.J. 1994a. Tight linkage of purple pod character and the complex C locus in common bean. *J. Hered.* 85:288–290.
- Bassett, M.J. 1994b. The genotype for seedcoat color of breeding line 5-593. *Annu. Rpt. Bean Improv. Coop.* 37:244–245.
- Bassett, M.J. 1996a. 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.
- Bassett, M.J. 1996b. A complex C region genotype [? R] that with $G B \nu^{lac}$ produces dark seal brown seedcoat color in common bean. *J. Amer. Soc. Hort. Sci.* 121:594–598.
- Bassett, M.J. 1996c. New genes, *stp* and *stp^{hbw}*, for flower color and seedcoat pattern in common bean. *J. Amer. Soc. Hort. Sci.* 121:388–392.
- Bassett, M.J. 1998a. A test cross protocol for determining the genotype of dark red colors in common bean. *J. Amer. Soc. Hort. Sci.* 123:1048–1052.
- Bassett, M.J. 1998b. A third recessive allele, *stp^{mic}*,

- for seedcoat pattern at the *Stp* locus in common bean. J. Amer. Soc. Hort. Sci. 123:404–406.
- Bassett, M.J. 1999. The seedcoat color genotype of 'Prim' and the manteca and coscorrón market classes of common bean. HortScience 34:336–337.
- Feenstra, W.J. 1960. Biochemical aspects of seedcoat colour inheritance in *Phaseolus vulgaris* L. Meded. Landbouwhogeschool, Wageningen 60(2):1–53.
- Lamprecht, H. 1932. Beiträge zur Genetik von *Phaseolus vulgaris*. I. Hereditas 16:169–211.
- Leakey, C.L.A. 1988. Genotypic and phenotypic markers in common bean, p. 245–327. In: P. Gepts (ed.). Genetic resources of *Phaseolus* beans. Kluwer Academic Press, Boston.
- Nakayama, R. 1960. Genetical studies on kidney beans (*Phaseolus vulgaris*). V. On the inheritance of seed-coat color I. 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.
- Nakayama, R. 1964. Genetical studies on kidney beans (*Phaseolus vulgaris*). VII. A modifier of flower color and its relation to *c^w* gene. Bul. Fac. Agr. Hirosaki Univ. 10:1–13.
- Nakayama, R. 1965. Genetical studies on kidney beans (*Phaseolus vulgaris*). VIII. A new allele at the *C* locus. Bul. Fac. Agr. Hirosaki Univ. 11:55–58.
- 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.
- Prakken, R. 1974. Inheritance of colours in *Phaseolus vulgaris* L. IV. Recombination within the 'complex locus *C*'. Meded. Landbouwhogeschool, Wageningen 74-24:1–36.
- Smith, F.L. 1939. A genetic analysis of red seedcoat color in *Phaseolus vulgaris*. Hilgardia 12:553–621.
- Smith, F.L. and C.D. Madsen. 1948. Seed-color inheritance in beans. J. Hered. 39:191–194.