A New Allele (V^{wf}) at the V Locus for Flower and Seedcoat Color in Common Bean

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ABSTRACT. The inheritance of flower and seedcoat color was studied using Lamprecht line M0137 (PI 527845) of common bean (*Phaseolus vulgaris* L.) as the source of a new allele, V^{wf} , at the V locus. The cross M0137 $c^{res} V^{wf} \times C v BC_2$ 5-593 (a genetic tester stock) was studied in progeny of the F_1 , F_2 , F_3 , and F_4 generations. The observed segregation for flower and seed colors was consistent with the hypothesis that M0137 carried a new allele, V^{wf} , that produced (in the presence of $P C J G B$) white flowers and black seeds rather than the white flowers and mineral-brown seeds produced (in the presence of $P C J G B$) by v . The V/V^{wf} genotype produced cobalt-violet flowers, the same as V/v . A test cross of $F_3 V^{wf} \times t BC_1$ 5-593 bipunctata demonstrated that V^{wf} is not allelic with t , a gene that can produce white or colored flowers and self-colored or partly colored seeds, depending on background genotype.

There are three alleles known at the V locus in common bean (*Phaseolus vulgaris*), viz., V , v^{lae} , and v (Leakey, 1988; Prakken, 1970). The alleles at the V locus have pleiotropic effects on flower and seedcoat colors (Prakken, 1970). For example, with $TPCJGB$, the V allele confers wild-type purple (bishops violet) flower color and black seedcoat color (Prakken, 1970). With $TPCJGB$, the v^{lae} allele confers pink flower color and mineral-brown seedcoats with a black corona, and the v allele confers white flower color and mineral-brown seedcoats without black corona (Bassett, 1995; Prakken, 1970). All the genes controlling the color of seedcoats and other plant organs have been defined and described in comprehensive reviews (Leakey, 1988; Prakken, 1970, 1972). The objective of this paper is to present evidence that there is a fourth allele at V that has unique pleiotropic effects on flower and seedcoat color.

Materials and Methods

Florida dry bean breeding line 5-593 has determinate habit, purple flowers, and shiny, pure black seedcoats. The seedcoat genotype of 5-593 is $TP [C r] D J G B V Rk$ (Bassett, 1994a; Prakken, 1970, 1972).

In 1985, a program was initiated to develop genetic tester stocks, each with one or more recessive marker genes for seedcoat color or pattern backcrossed into the recurrent parent 5-593. Details of the backcross procedure are described by Bassett (1994b). One of the tester stocks developed is designated $v BC_2$ 5-593, which indicates that the v allele is in BC_2 to the recurrent parent 5-593, and the line is homozygous for all the genes that produce the mineral-brown seedcoat color.

The $t BC_1$ 5-593 bipunctata stock is a line with partly colored seedcoats. The bipunctata pattern was derived from Lamprecht line V0005 ('Incomparable', now PI 527712), and has two black dots on a pure white background. The development of the bipunctata stock was made easier by the fact that the donor parent had a black seedcoat like 5-593 and had no other marker genes that needed to be removed by selection. Good illustrations of partly colored

seedcoat patterns have been published by Lamprecht (1934), Leakey (1988), and Schreiber (1940).

In 1989, I began a study of the germplasm collection left by Herbert Lamprecht (now available under PI accession numbers 527711 through 527878). About 30% of the accessions in the collection were studied by means of crosses to genetic tester stocks that I had developed. The most important of the tester stocks was $v BC_2$ 5-593, which has the genotype $TPCJGB v$ (Bassett, 1994a, 1994b, 1995). The tester stock carries dominant alleles at the two loci (T and P) other than V that can confer white flower color in common bean (Leakey, 1988; Prakken, 1970). Thus, the F_1 plants from a cross of $v BC_2$ 5-593 with any pure line stock (the unknown) with unknown genetic constitution at V will reveal which allele is present in the unknown at V . For example, if the unknown carries V , the F_1 will have the genotype V/v , which has the flower color cobalt violet (Bassett et al., 1990). If the unknown carries v^{lae} , the F_1 will have the genotype v^{lae}/v , which has the flower color pale pink; and if the unknown carries v , the F_1 will have the genotype v/v , which has the flower color pure white (Prakken, 1970).

One of the Lamprecht accessions chosen for genetic investigation was M0137 (PI 527845), where the 'M' indicates multigaris, which is Lamprecht's term for a line derived from an interspecific hybrid between *P. vulgaris* and *P. coccineus* L. Line M0137 has determinate plant habit, white flowers, and seedcoats with tiny black dots on a cartridge buff background. There were no genetic notes left by Lamprecht for line M0137.

Line M0137 was crossed with $v BC_2$ 5-593 and the F_2 was planted in the field in Spring 1992. Data were taken on flower and seedcoat color and pattern in the F_1 and F_2 . Selection was made in the F_2 for plants with white flowers and unpatterned black seeds. A progeny test (14 F_3 plants) was made of such an F_2 selection in

Table 1. A listing of the pleiotropic effects on flower and seedcoat color and pattern (with background genotype $TPCJGB$) of the three known alleles at the V locus, plus a new allele, V^{wf} , hypothesized to be carried by M0137.

Allele at	Phenotypic expression	
V locus	Seedcoat color	Flower color
V	Black	Bishops violet
v^{lae}	Mineral brown with black corona	Pink
v	Mineral brown with no corona	White
V^{wf}	Black	White

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Table 2. Segregation for seedcoat color and genotype^z in the F₂ from the cross M0137 x v BC₂ 5-593.

Unpatterned black C V ^{wf}	Unpatterned mineral brown C v	Black dots on cartridge buff ^y c ^{res} V ^{wf}	Brown dots on cartridge buff ^x c ^{res} v	χ^2 9:3:3:1 ^w	P value
72	31	22	9	1.9602	0.58

^zAll F₂ plants had white flowers; hence, segregants with black seeds are hypothesized to have a previously unreported allele, V^{wf}, that produces white flowers, but maintains the black seedcoat.

^yThe light pattern color is cartridge buff on which the resperus pattern of black dots appear.

^xThe dots are mineral brown in the resperus pattern on cartridge buff background.

^wAnalysis with Mather's (1957) orthogonal contrasts gives: $\chi^2_C = 0.249$, $P = 0.618$; $\chi^2_v = 1.682$, $P = 0.20$; $\chi^2_L = 0.03$, $P = 0.86$.

the greenhouse in Fall 1992, and an F₄ progeny test was made of each F₃ plant in the field in Spring 1993. Data were taken on flower and seedcoat color and pattern in the F₃ and F₄.

One of the F₃ progeny plants with white flowers and unpatterned black seeds was crossed with another genetic tester stock, t BC₁ 5-593 bipunctata x F₃ V^{wf}. The F₂ was planted in the field in Spring 1994. Data were taken on the F₁ and F₂ as above.

Results and Discussion

The F₁ plants from the cross M0137 x v BC₂ 5-593 had pure white flowers and unpatterned black seedcoats. The white flowers would normally be interpreted to mean that M0137 carries v, but, if that were true, then the seedcoat color would be mineral brown, not black. The proposed hypothesis is that M0137 carries an unreported allele at the V locus that confers white flowers, but does not have a pleiotropic effect on seedcoat color as v does (Table 1).

The F₂ plants from the cross M0137 x v BC₂ 5-593 all had white flowers, but segregated for four phenotypic classes of seedcoat color (Table 2). There was a good fit to the expected 9:3:3:1 segregation ratio, where the wild-type C allele was dominant to the c^{res} allele and the V^{wf} allele was dominant to v (Table 2). One can see from the analysis of orthogonal contrasts that there was a modest shortage (not significant) of the V^{wf} allele (Table 2).

One of the F₂ selections with white flowers and unpatterned black seedcoats was progeny tested in the greenhouse, and seed was produced on 14 F₃ plants, which were each progeny tested in

the field. The F₃ segregated for 8 plants with black seedcoats and 6 plants with mineral-brown seedcoats, which showed a modest shortage (nonsignificant) of plants with V^{wf}/– (Table 3). Among the 8 black-seeded F₃ plants, the F₄ progeny test produced 5 segregating progenies and 3 nonsegregating progenies, which gave a good fit to the expected 2:1 ratio of segregating to nonsegregating progenies (Table 3). The combined F₄ segregating progenies gave a satisfactory fit to a 3:1 segregation ratio of black-to mineral-brown-seeded types, but there was a modest (nonsignificant) shortage of black-seeded plants (Table 3). All the above data is clearly consistent with the hypothesis of a single-factor segregation, where the dominant allele produces a previously unreported phenotype.

The F₁ plants from the cross t BC₁ 5-593 bipunctata x F₃ V^{wf} had cobalt-violet flowers and self-colored black seeds (data not shown). The hypothesis is that the cobalt-violet flowers are the result of the heterozygous genotype V/V^{wf}. Thus, V/V^{wf} produces the same flower color as V/v (Bassett et al., 1990), i.e., the flower color effect of V^{wf} is the same as v. In contrast, the black seedcoat color produced (with P C J G B) by V^{wf} is the same as V.

The cross t BC₁ 5-593 bipunctata x F₃ V^{wf} provides an allelism test for the alternative hypothesis that V^{wf} is really t on a genetic background that fails to produce partly colored seeds (Bassett and Blom, 1991) and produces colored flowers (Bassett, 1993). Under the alternative hypothesis, F₃ V^{wf} has the genotype t Z and t BC₁ 5-593 bipunctata has the genotype t z. The Z locus controls the expression of virgarcus (z/z) pattern with respect to piebald and

Table 3. Segregation for seedcoat color in the F₃ and F₄ from an F₂ parent (from M0137 x v BC₂ 5-593) with white flowers and unpatterned black seedcoats.

F ₃ parent seedcoat color ^z	Seedcoat colors of F ₄ progeny		χ^2 3:1	P value
	Black	Mineral brown		
Black	21	5	0.462	0.50
Black	20	6	0.051	0.82
Black	24	6	0.40	0.53
Black	26	3	3.322	0.07
Black	19	9	0.762	0.38
Subtotal	110	29	1.269	0.26
Black	26	0		
Black	28	0		
Black	29	0		
Mineral brown	0	28		
Mineral brown	0	29		
Mineral brown	0	29		
Mineral brown	0	23		
Mineral brown	0	22		
Mineral brown	0	23		

^zThe segregation for seedcoat color in the F₃ gave 8 black and 6 mineral brown, χ^2 (3:1) = 2.381, $P = 0.12$. Within the 8 progeny with black seed there was segregation for 5 plants that segregated in F₄ at V and 3 plants that were true breeding in F₄ at V; χ^2 (2:1) = 0.063, $P = 0.80$.

Table 4. Segregation for flower color and seedcoat pattern in the F₂ from the cross *t* BC₁ 5-593 bipunctata (*t z* V)^z × F₃ V^{wf} (TZV^{wf}).^z

Flower color	Seedcoat pattern	Genotype	Frequency ^y
Bishops violet	Self-colored ^x	<i>T</i> / <i>-</i> <i>V</i> / <i>V</i>	17
Cobalt violet	Self-colored ^x	<i>T</i> / <i>-</i> <i>V</i> / <i>V</i> ^{wf}	28
White	Self-colored ^x	<i>T</i> / <i>-</i> <i>V</i> ^{wf} / <i>V</i> ^{wf}	14
White	Partly colored ^w	<i>t</i> / <i>t</i> <i>-</i> / <i>-</i>	20

^zThe *Z* locus and genetic effects symbolized are those of Schreiber (1940), where *t z* gives restricta [same as Lamprecht's (1934) *virgatus*], *t Z/z* gives ambigua, and *t Z/Z* gives expansa [same as Lamprecht's (1934) *minimus*]. The genetics of the bipunctata pattern is ignored here for simplicity because it is not needed for the conclusions made.

^yFor the data 17, 28, 14, and 20, the χ^2 (3:6:3:4) = 0.46, *P* = 0.93.

^xSelf-colored black seeds, i.e., the entire seedcoat is colored.

^wVarious partly colored seedcoat patterns were observed.

sellatus patterns (Lamprecht, 1934; Sax and McPhee, 1923; Surface, 1916). Schreiber (1940) provided a broader experimental basis for the genetics of partly colored seeds and redefined the *Z* locus effects in a new genetic model. According to Schreiber (1940), with *l*, *t Z* gives expansa (same as the *minimus* of Lamprecht, 1934), *t Z/z* gives ambigua, and *t z* gives restricta (same as the *virgatus* of Lamprecht, 1934). Bipunctata is produced by *t z* with *bip arc*, according to Lamprecht (1940a). Thus, the cross F₃ V^{wf} (*t Z*) × *t* BC₁ 5-593 bipunctata (*t z*) would produce *t Z/z* or ambigua in F₁ if the alternative hypothesis were correct; but, since the F₁ was self-colored, the alternative hypothesis was not supported. The F₂ from the cross F₃ V^{wf} × *t* BC₁ 5-593 bipunctata gave a good fit to the hypothesis of two-factor segregation at *V* and *T* (Table 4). Thus, V^{wf} must be an allele at *V* and not a *t* allele (either new or standard).

The inheritance of seedcoat color in common bean has been extensively studied by many investigators over several decades (as reviewed by Prakken, 1970, 1972). It may seem surprising that an allele at such an important locus for seed color as *V* could have escaped discovery for such a long time. It is my hypothesis that the V^{wf} allele did not originate in *P. vulgaris*, but in *P. coccineus*. As described above, M0137 was derived from a cross involving *P. coccineus*.

The V^{wf} allele plays an important role in *P. coccineus* by interacting with the gene for red flower color, *Sal*, and permitting pure red colors (M.J. Bassett, unpublished data), while allowing the seedcoat to be black or other various blue to purple colors that would be possible with *V* in *P. vulgaris* (Prakken, 1970). Lamprecht (1948) presented most of the data on his experimental work with the inheritance of red flower colors derived from *P. coccineus* in a single paper and commented on his previous work (Lamprecht, 1940b). All of his crosses with red-flowered materials carried either *v*^{lae} or *v* along with one of the genes for red color (Lamprecht, 1948). He described the flower color produced by *Sal v* as Salmon red and said that "almost the same colour is produced when the gene *v*^{lae} is present," i.e., is produced by *Sal v*^{lae}. The interactions of *Sal* with *V* were described by the present author (Bassett et al., 1990).

Over one-third of the *P. coccineus* accessions in the PI collection at Pullman, Wash., have black or purple seeds, or at least a portion of the seeds of each of those accessions has such colors. If those materials were *P. vulgaris*, they would carry *V* and have the corresponding bluish purple flower colors that are the pleiotropic effects of *V* (Bassett et al., 1990). Instead, the nonwhite flower colors are mostly, if not entirely, in the range of pure (nonbluish) red colors described by Lamprecht (1940b). Such pure red flowers and purple to black seedcoats can only be achieved by having V^{wf}

accompany the gene(s) for red flower color. Thus, *P. coccineus* has maintained the presumed adaptive value of the dark seedcoat colors without sacrificing the presumed adaptive values of the pure red flower colors.

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