A New Gene for Flower Color Pattern, White Banner (*wb*), in Progeny of an Interspecific Hybrid between Common and Scarlet Runner Beans

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Abstract. A new gene for flower color pattern, designated white banner (WB), appeared in material derived from the cross 'Harvester' snap bean (*Phaseolus vulgaris* L.) × Plant Introduction (PI) accession 273666 of scarlet runner bean (*P. coccineus* L.). The WB character has a white banner petal and pale violet wings (veronica-violet 639/2). The inheritance of the mutant was studied in crosses involving dry bean breeding line 5-593, which has bishops-violet (wild-type) flowers, and genetic stocks *v* BC₂ 5-593 (white flowers) and *blu* BC₂ 5-593 (blue flowers). Segregation in F₂ and F₃ progenies from the cross *v* BC₂ 5-593 × WB supported the hypothesis that WB is controlled by a single recessive gene that is nonallelic with the *V* locus. An allelism test with *blu* BC₂ 5-593 gave evidence that WB is not allelic with the *blu* locus. The gene symbol *wb* is proposed for the gene producing WB.

The genetics of flower color in common bean was reviewed recently by Leakey (1988) in a book chapter, which has helpful illustrations [after Prakken (1972)] of color patterns on the wing and banner petals. [Note: Leakey has pointed out a typographical error in the diagram of his paper: "Amended genotype proposed" for the all-white flower type code 1 should read *p p T Rk*, *P t t Rk*, or *P T rk rk*.] In this paper, all color names and numeric designations are taken from the Horticultural Colour Chart of the Royal Horticultural Society (1938). A recessive allele at either *P* or *T* will produce an all-white flower. In the presence of *P* and *T*, the *V* locus can express a series of colors (wing petal only): *V/V* gives bishops-violet, *V/v* gives cobalt-violet, *v^{lae}/v^{lae}* gives rose-purple, and *v/v* gives white (Bassett et al., 1990). Either *P/- T/- v^{lae}/v^{lae}* or *P/- T/- v/v* with *rk^d/rk^d* gives red veins in the wing petals (Prakken, 1972). In the presence of *P* and *T* with *v*, *Rst/-* gives a red-tipped banner petal (Prakken, 1972). The interactions of *Sal* (from *P. coccineus*) with *V* and *v* are fully described by Bassett et al. (1990). Recently, an induced mutant for blue (methyl-violet) flower color was reported to be controlled by *blu/blu* (Bassett, 1992).

This paper presents evidence for the inheritance of a genetic variant for flower color pattern, designated "white banner," that appeared in segregating progenies derived from an interspecific hybrid.

Materials and Methods

In 1977, a cross was made between the 'Harvester' snap bean (*p/p*) and the *P. coccineus* Plant Introduction (PI) accession 273666, which has vine habit and scarlet flower color. Scarlet flower color is probably due to *Sal Am v* (my unpublished data). In the resulting F₂ population, selections were made for bush (determinate) habit. Two such selections, designated 273666 #12 (white flowers with red veins, *P/- T/- vlv rk^d/rk^d*) and 273666 #23 (camellia-rose flowers, *P/- T/- Sal/Sal v/v*) were crossed.

Breeding line 5-593 has determinate plant habit, bishops-violet flowers (*P T V*), and shiny black seeds. A genetic stock, *v* BC₂ 5-

593, was produced by backcrossing the recessive allele *v* into the 5-593 recurrent parent, giving white flowers (*P T v*) and mineral brown seeds. The complete seed coat color genotype of 5-593 is *P T Mar C D J G B V Rk* (my unpublished data).

In 1988, the breeding line 5-593 was crossed with F₁ (273666 #23 × 273666 #12), which probably had the genotype *P/P T/T Sal/sal Am/am v/v Rk/rk^d* and may have been heterozygous for a gene controlling white banner. The F₂ population was planted in the field in Spring 1989. Selections were made for segregants with unique flower colors: white banner petals and pale violet wings (Veronica-violet 639/2). This new flower color pattern was named white banner (WB). In 1989, crosses were made between the genetic stock *v* BC₂ 5-593 and F₃ progeny of the WB selections. In Spring 1990, F₂ progenies of the resulting F₁ plants were planted in separate field plots, 90-717 through 90-732 and 90-740 through 90-744.

In 1990, the genetic stock *blu* BC₂ to 5-593 (*P T V blu*) (Bassett, 1992) was crossed with an F₃ selection from 90-718 with WB *V/v* flowers. In Spring 1991, F₂ progenies from the resulting F₁ plants were planted in separate field plots, 91-132 through 91-137. In Fall 1990, remnant seed of F₂ stock 90-718 were planted in the greenhouse, and F₃ seed were produced on 39 unselected F₂ progeny. The F₃ seed were planted in the field in Spring 1991 in plots 91-601 through 91-639. The second backcross to 5-593 was made by the cross 5-593 × F₃ 90-718 WB flowers. The BC₂-F₂ seed were planted in the field in Spring 1991 in plots 91-640 through 91-642.

Classification for flower color was made in all the segregating progenies planted in the field in 1990 and 1991, and notes were made on the flower color of all parental material and F₁ progeny described above.

Results and Discussion

The cross *v* BC₂ 5-593 × F₃ WB flower segregants produced F₁ progeny with cobalt-violet flower color, which is interpreted as a nonallelic response showing the genotype *V/v*. The hypothesis of nonallelism between the *V* locus and the locus controlling the WB character is supported by F₂ segregation for three flower color classes (Table 1). Two of these classes were parental and the third was wild type, which is interpreted as a two-factor segregation. The F₂ populations were tested for goodness of fit to a 9:3:4 segregation ratio, and 19 of the 20 populations gave a satisfactory

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Table 1. Segregation for flower color in the F₂ from the cross *v* BC₂ 5-593 x F₃ white banner flower segregants.

Plot no.	Segregation classes and genotypes			χ^2 (9:3:4)	P value
	Wild type ^z (V/- Wb/-)	White banner (V/- wb/wb)	White flower (v/v -/-)		
90-717	31	4	13	3.45	0.18
90-718	30	7	12	0.74	0.69
90-719	27	7	16	1.627	0.44
90-721	27	4	12	2.519	0.28
90-722	35	4	8	6.598	0.04
90-723	23	6	19	5.676	0.06
90-724	29	5	15	2.60	0.27
90-725	32	7	8	2.74	0.25
90-726	32	3	11	5.14	0.08
90-727	27	3	16	5.478	0.07
90-728	24	3	10	2.784	0.25
90-729	25	4	13	2.582	0.28
90-730	14	4	2	2.489	0.29
90-731	27	3	10	3.60	0.17
90-732	27	8	11	0.116	0.94
90-740	24	6	12	0.667	0.72
90-741	23	6	16	2.921	0.23
90-742	31	5	9	3.128	0.21
90-743	27	8	10	0.274	0.87
90-744	20	5	13	2.012	0.37
Totals	535	102	236	28.623	<0.001
Expected ^y	491.06	163.69	218.25		

^zWild-type colors include bishops-violet (V/V), cobalt-violet (V/v), and (in some plots) various red colors produced by interactions of *Sal* and V, v (Bassett et al., 1990).

^yThe expected values are based on the segregation ratio 9:3:4.

fit (Table 1). On the basis of these results and other data presented below, the gene symbol *wb* is adopted for the WB character. However, when the data were combined and tested, the χ^2 (9:3:4) = 28.623, $P < 0.001$. An examination of the deviations from expected values indicates that there was a large deficiency of WB

Table 2. Genetic model for flower color segregation in F₂ progeny from crosses between *v* Wb and V wb and the expected segregation in F₃ progeny tests of each genotype in the F₂.

F ₂ genotypes	Fre- quency ^c	F ₂ phenotypes	Expected ^y segre- gation in F ₃
Wb/Wb V/V	1	Bishops-violet (BV)	True-breeding for BV
Wb/Wb V/v	2	Cobalt-violet (CV)	3 (BV + CV) : 1 white
Wb/Wb v/v	1	White	True-breeding for white
Wb/wb V/V	2	Bishops-violet (BV)	3BV:1whitebanner(WB)
Wb/wb V/v	4	Cobalt-violet (CV)	9 (BV + CV) : 3 WB : 4 white
Wb/wb v/v	2	White	True-breeding for white
wb/wb V/V	1	White banner (WB)	True-breeding for WB
wb/wb V/v	2	White banner (WB)	3 WB : 1 white
wb/wb v/v	1	White	True-breeding for white

^cEach value is the numerator (n) of the expected frequency (n/16) in the F₂, in which the expected ratio of phenotypic classes is 9 (BV + CV):3 WB:4 white.

^yThe expected ratio of segregation classes in the F₃ (from random F₂ plants) is 1 true-breeding for BV : 2 [3 (BV + CV):1 white] : 2 (3 BV:1 white banner) : 4 [9 (BV + CV):3 WB:4 white] : 1 true-breeding for WB : 2 (3 WB:1 white) : 4 true-breeding for white.

segregants (Table 1). An analysis of segregation at the V and Wb loci gave the following results: For the V/- and v/v classes, the segregation was 671 and 247, respectively, and χ^2 (3:1) = 1.779, $P = 0.18$. For the Wb/- and wb/wb classes, the segregation was 807 and 111, respectively, and χ^2 (3:1) = 81.582, $P < 0.001$. Thus, segregation was normal at the V locus, but there is reduced transmission of the recessive allele at the Wb locus. Because the wb allele appears to have originated from the *P. coccineus* PI accession 273666, it is possible that wb is linked to genes that give poor transmission. Disturbed ratios of this type are common in interspecific crosses between *P. vulgaris* and *P. coccineus* (Smartt, 1970).

Some of the F₂ populations also segregated for *Sal*, but those data were omitted to avoid unnecessary complication of the presentation (Table 1); i.e., the segregation at wb and V could be classified in the presence of *Sal* without reference to *Sal*. The interaction of *Sal* and wb V produces a unique phenotype. The banner petal is variable in color (perhaps due to *Sal*/*Sal* vs. *Sal*/*sal*); heliotrope 636/1, 2, or 3; and the wings are heliotrope 636/2 or cobalt-violet 634/2. These hues are slightly redder than rose-purple because of the action of *Sal*.

Although the combined data in Table 1 show a disturbed 9:3:4 ratio, not all of the contributing progenies give high χ^2 values. If the disturbance is due to linked genes from the *P. coccineus* parent PI 273666, then F₂ progenies with χ^2 values <1 may have broken the linkage between wb and these genes. Plot 90-718 has $\chi^2 = 0.74$, and, therefore, the hypothetical linkage may have been broken in this stock. To test this idea, remnant seed were grown in the greenhouse and the progeny were classified for flower color. When the new data were added to that in Table 1, the combined data were 53 plants with V/- Wb/- flowers, 16 with V/- wb/wb flowers, and 20 with v/v -/- flowers, which gives χ^2 (9:3:4) = 0.428, $P = 0.81$. The goodness of fit to the ratio improves with added sample size. It is concluded that the parent of plot 90-718 is free of the factors producing the disturbed segregation in Table 1.

To test the hypothesis that WB flower color is controlled by a single recessive gene, wb, F₃ progeny tests were made of the 39 F₂ plants grown from remnant seed of 90-718. The expected frequencies of the various segregation classes in F₂ and F₃, based on a two-factor model, are presented in detail (Table 2). All the various expected F₃ segregation classes were observed, and there was good agreement with their expected frequencies (Table 3). The combined data involving the two types of F₃ progenies segregating at the Wb locus gave acceptable fits to the expected ratios, but the probability values are somewhat low, viz., 0.21 and 0.12. This raises some doubt about the Wb locus being entirely free of the hypothetical linked genes or pleiotropic effects of wb that may reduce transmission somewhat.

A second backcross was made between 5-593 and segregants carrying wblwb V/v in BC₁ to 5-593. The three resulting F₂ progenies all segregate for v, and they give no indication of any disturbance in the segregation for wb (Table 4). There is no support for the possibility that wb may have pleiotropic effects that reduce its transmission rate with respect to the rate for the wild-type allele Wb.

A stock with WB flowers was also crossed to the blue flower marker character to test for allelism. The F₁ progeny had either cobalt-violet or bishops-violet flowers, which is interpreted as an indication of nonallelism. The F₂ progeny from the allelism test give a good fit either a two-factor segregation ratio, involving only wb and blu, or a three-factor segregation ratio involving wb, blu, and v (Table 5). Clearly, wb is nonallelic with blu.

In summary, the WB character is confirmed to be controlled by a single recessive gene that is nonallelic with either V or blu. The

Table 3. Segregation for bean flower color in F_3 progeny tests of 39 unselected F_2 plants from the cross $Wb \times BC_2$ 5-593 $\times$ F_3 9-523-4 #1 $wb \times V$ (from remnant seed of 90-718, Table 1).

Plot no.	F_2 parent	Classification of F_3 progeny ^z			Ratio tested	χ^2 value	P value
		Violet ^y (V/- Wb /-)	White banner (V/- wb / wb)	White (v/v -/-)			
1-634	V Wb	40					
1-639		38					
1-618	V/v Wb			16	3:1	0.022	0.88
1-619		58		13	3:1	1.695	0.19
1-620		50		22	3:1	1.185	0.28
1-625		54		19	3:1	0.041	0.84
1-626		54		14	3:1	0.706	0.40
1-629		57		14	3:1	1.056	0.30
1-630 ^x	V Wb / wb	54	21		3:1	0.360	0.55
1-631 ^x		26	10		3:1	0.148	0.70
1-632 ^x		31	5		3:1	2.370	0.12
1-633 ^x		30	8		3:1	0.316	0.57
1-635 ^x		31	7		3:1	0.877	0.35
1-636 ^x		28	9		3:1	0.009	0.92
1-637 ^x		32	6		3:1	1.719	0.19
1-638 ^x		30	8		3:1	0.316	0.57
1-617 ^w	V/- Wb /-	34	11	13	9:3:4	0.215	0.90
1-621 ^w		43	11	18	9:3:4	0.619	0.73
1-622 ^w		41	17	15	9:3:4	1.381	0.50
1-623 ^w		43	7	19	9:3:4	3.354	0.19
1-624 ^w		45	10	20	9:3:4	1.444	0.49
1-627 ^w		41	9	16	9:3:4	1.340	0.51
1-628 ^w		45	11	13	9:3:4	2.324	0.31
1-603	V wb		31				
1-609			38				
1-601	V/- wb		22	8	3:1	0.044	0.83
1-602			22	12	3:1	1.922	0.17
1-604			22	8	3:1	0.044	0.83
1-605			31	8	3:1	0.419	0.52
1-606			28	9	3:1	0.009	0.92
1-607			28	10	3:1	0.035	0.85
1-608			25	9	3:1	0.039	0.84
1-610	v/v -/-			29			
1-612				29			
1-613				29			
1-614				29			
1-615				29			
1-616				26			

^zFor the χ^2 test for the goodness of fit of the F_3 segregation classes to the expected (Table 2) the χ^2 (1:2:2:4:1:2:4) = 4.897, P = 0.56.

^yThe violet flower class includes both bishops-violet (V/V) and cobalt-violet (V/v).

^xFor the progenies segregating for violet and white banner flowers the totals were 262 and 74, respectively, and the χ^2 (3:1) = 1.587, P = 0.21.

^wFor the progenies segregating for violet, white banner, and white flowers the totals were 292, 76, and 114, respectively, and the χ^2 (9:3:4) = 4.244, P = 0.12.

flower type of wb is distinguished easily from wild-type and all other flower color variants and, thus, makes a valuable addition to the marker genes available in common bean.

The relationship of wb to rk^d has not been explored in the experiments described above, and some discussion of the effects of rk^d on flower color pattern is necessary. The genotype $v \times rk^d$ produces flowers with a white banner petal and wing petals of pure white, except for very fine red veins (Leakey, 1988; Prakken,

Table 4. Segregation for flower color in the F_2 from the cross 5-593 $\times$ $wb \times V/v \times BC_1$ 5-593.

Plot no.	Flower color classes			χ^2 (9:3:4)	P value
	Violet ^z	White banner ^y	White		
1-640	20	9	9	0.608	0.74
1-641	21	5	9	0.467	0.79
1-642	22	6	10	0.222	0.90
MISSING?	63	20	28	0.039	0.98

^zThe violet flower class includes bishops-violet (V/V) and cobalt-violet (V/v).

^yThe white banner class includes the genotypes $wb \times V$ /-

Table 5. Segregation for flower color in F_2 progenies from the allelism test cross between $V \times blu \times BC_2$ 5-593 $\times$ F_3 V/v wb .

Plot no.	Flower color classes				Ratio tested	χ^2 value	P value
	Violet ^z	Blue	White banner ^y	White			
1-132 ^x	27	4	10		9:3:4	2.447	0.29
1-134 ^x	29	10	9		9:3:4	1.009	0.60
1-135 ^x	24	11	8		9:3:4	1.775	0.41
1-137 ^x	28	11	7		9:3:4	2.589	0.27
1-133 ^w	24	6	6	11	27:9:12:16	1.879	0.60
1-136 ^w	18	4	9	14	27:9:12:16	1.617	0.66

^zThe violet flower class includes bishops-violet (V/V) and cobalt-violet (V/v).

^yThe white banner class includes the genotypes blu /- wb and $blu \times wb$.

^xThe totals for the violet, blue, and white banner classes were 108, 36, and 34, respectively, and the χ^2 (9:3:4) = 3.303, P = 0.19.

^wThe totals for the violet, blue, white banner, and white classes were 42, 10, 15, and 25, respectively, and the χ^2 (27:9:12:16) = 1.396, P = 0.71.

1972). The genotype $wb \times v$ produces pure-white flowers, including the wings (Tables 1-4). Therefore, wb cannot be a synonym for rk^d . Without experimental evidence, one cannot rule out the possibility that wb may be another allele at the Rk locus, but this seems a highly improbable departure from the known effects of rk and rk^d . An allelism test for that hypothesis would be very difficult to perform (perhaps impossible) because the red seed coat color of rk and rk^d is recessive and can only be classified reliably (expressed) with $b \times v$ (Prakken, 1972), whereas the flower color pattern effects of wb are not expressed with v . If wb produced red seed coats with $b \times v$, it might be possible to develop a very indirect allelism test, but it would be very laborious to perform.

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