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Blue Pattern Flower in Common Bean Expressed by Interaction of *Prp*^{i}*-2* with a New Gene *t*^{bp}

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Abstract. **The inheritance of blue pattern flower (BPF) expression was investigated in common bean (*Phaseolus vulgaris* L.). The BPF trait was derived from accession line G07262, and the flowers express blue banner petal and white wings with blue veins. Crosses between a BPF stock and three other parents, *t p*^{mic} long micropyle stripe BC_3 5–593, *t z Fib* arcus BC_4 5–593, and *t Z bip*^{ana} *Fib* marginata BC_3 5–593, all segregated in F_2 for BPF or white flowers in a 9:7 ratio, respectively. Progeny tests in F_3 from two of the crosses supported the hypothesis that two complementary dominant genes control BPF expression and permitted a genetic linkage estimate of cM = 32.4 ± 7.91 map units between *p*^{mic} and one of the two genes for BPF. A cross between *t z fib* virgarcus BC_3 5–593 and *T Prp*^{i}*-2 V* BC_2 5–593 demonstrated that *t Prp*^{i}*-2* did not express BPF. Two crosses, *T Prp*^{i}*-2 V* BC_2 5–593 *t p*^{mic} BC_3 5–593 and 5–593 × a BPF stock, segregated in F_2 for plants expressing BPF in a 3/16 frequency. The combined data demonstrated that a new gene, *t*^{bp} (bp = blue pattern), interacts with *Prp*^{i}*-2* to express BPF and that *P* is linked with *Prp*^{i}*-2* by 32 map units. The dominance order at the *T* locus is *T* > *t*^{bp} > *t*. The pedigree source of the *t*^{bp} gene and the heterogeneity of PI 632736 (*t p*^{mic} long micropyle stripe BC_3 5–593) are discussed.**

Bassett (2005) reviewed the literature relating to a gene [*c*^{u} *Prp*^{i}] for intensified anthocyanin expression (IAE) in a syndrome of plant organs (flower, pod, stem, and leaf) in common bean. The important commercial effect of [*c*^{u} *Prp*^{i}] is the change of pod color from green (with [*C prp*]) to dark purple pods. The gene [*c*^{u} *Prp*^{i}] was the first IAE gene to be reported and was investigated by many bean geneticists over several decades. A second gene for IAE (*Prp*^{i}*-2*) was reported by Bassett (2005). The source of *Prp*^{i}*-2* was the Centro Internacional de Agricultura Tropical (CIAT) accession line G07262, which was reported to have genotype *t p*^{mic} *Prp*^{i}*-2* (Bassett, 2005). The gene *t* controls the expression of partly colored seedcoat patterns and *p*^{mic} expresses a short, white micropyle stripe (Bassett, 2003, 2007). The genotype *t p*^{mic} expressed a long, white micropyle stripe (Fig. 1) in the seedcoat (Bassett, 2005). In the genotype *Prp*^{i}*-2 v*, the *v* gene blocks the expression of IAE. Similarly, with *t Prp*^{i}*-2*, the *t* gene was reported to block IAE in all plant organs except flowers, which were white with blue veins in the wing petals (Bassett, 2005). This tentative hypothesis for blue wing veins expression was based on preliminary data and requires further research for confirmation.

This article reports the inheritance of flower color and pattern controlled by *Prp*^{i}*-2* interacting with *t*^{bp}, a new gene at the *T* locus for flower color and partly colored seedcoat patterns, where *bp* represents *blue pattern* flower (Fig. 2).

Materials and Methods

Development of recurrent parent line 5–593. In 1985, a program was initiated to develop genetic tester stocks for the colors and patterns of common bean seedcoats by backcrossing selected genes (usually recessive alleles), singly and in combination, into a recurrent parent 5–593. The Florida dry bean breeding line 5–593 has the seedcoat genotype *T P* [*C r*] *Z J G B V Rk* (Bassett, 2007), which expresses shiny, unpatterned black seedcoats. Details of the backcross procedure for developing genetic tester stocks were previously described (Bassett, 1994). In recent years, numerous genetic tester stocks have been developed in the 5–593 genetic background (usually to the BC_3 level) and are available for experimental use at the Plant Introduction (PI) Station, Pullman, WA, upon request. A list of the genetic tester stocks used in this research is provided in Table 1.

Development of a blue pattern flower line in 5–593 background. The CIAT accession line G07262 is heterogeneous for flower color pattern (Bassett, 2005). A plant was selected (selection no. 1) from this accession with the following flower pattern: 1) broken blue veins on nearly white wing petals with a blush of blue color and 2) blue banner petal (Fig. 2). The blue color expressed is highly variable from plant to plant in segregating materials. This ''blue'' color is really in the violet range of colors, but is blue-shifted compared with the bishops violet typical for genotype *T P V* (Bassett, 2007). When viewed from 1 m, the flower of selection no. 1 appears to have a pale blue banner and white wings with obvious blue veins. This same plant (selection no. 1) was used in a previous article by Bassett (2005) and was demonstrated to have genotype *t p*^{mic} *Prp*^{i}*-2*. A white banner and blue veins on otherwise white wing petals was tentatively attributed to genotype *t Prp*^{i}*-2*, but the inheritance of blue banner color and blue veins in wing petals (blue pattern flowers) was not pursued.

We have developed a complete genetic hypothesis (Table 2) for the interaction of the gene *Prp*^{i}*-2* and a new hypothetical gene *t*^{bp}, which will be tested in experiments described later. We

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also describe the development of a new genetic stock with the blue pattern flower (Fig. 2) in BC_3 to 5–593.

In 1994, the cross 5–593 × G07262 was made, and the F_1 progeny expressed intense bishops violet flower and purple pods. In the F_2, a selection was made for a plant with blue pattern flower (BPF) and seedcoats with the long micropyle stripe (Fig. 1). In 1995, an F_3 progeny plant with BPF and long micropyle stripe seeds was crossed with *t z fib* virgarcus BC_2 5–593. An F_2 progeny of 74 plants was planted in the field, and every plant had partly colored seedcoats or long micropyle stripe. Thus, the progeny was known to be homozygous *tt*. A single plant selection for BPF and long micropyle seedcoat was made and designated *t* p^{mic} blue pattern BC_1 5–593.

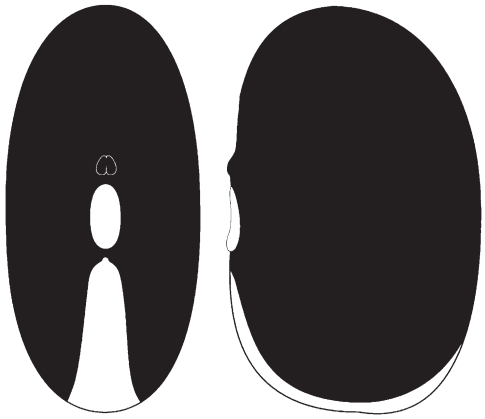

Fig. 1. A ventral view (left seed) and a side view (right seed) of a long, white micropyle stripe in common bean; with *C J*, expressed by genotype *t* p^{mic}.

Fig. 2. Blue pattern flower in common bean with blue veins on the wing petals and a blue standard petal; with *P V*, expressed by genotype t^{bp} Prp^{i}*-2*.

In 1999, a double backcross operation was made, viz., *t* p^{mic} BC_3 5–593 × F_1 (*t* p^{mic} BC_3 5–593 × *t* p^{mic} blue pattern BC_1 5–593). In 2001, seed from the BC_3-F_1 of blue pattern to 5–593 was planted in the greenhouse and observed to segregate for blue pattern or white flowers. Nine of the F_1 plants expressed BPF and were selected, and their F_2 progenies were planted in the field in 2001 at Gainesville, FL. Segregation data for flower color and pattern were recorded.

Test crosses with genetic stocks having arcus or marginata pattern seedcoats. In 2003 a BC_3-F_3 progeny from the double backcross described earlier was observed to be true breeding for BPF. This population is designated as 03–585 (Table 1) or elsewhere as t^{bp} p^{mic} Prp^{i}*-2* blue pattern BC_3 5–593. In 2005, two test crosses were made at Prosser, WA, between t^{bp} p^{mic} Prp^{i}-2 blue pattern BC_3 5–593 and two genetic testers, viz., *t z Fib* arcus BC_4 5–593 and *t Z* bip^{ana} *Fib* marginata BC_3 5–593. The F_2 from both crosses was grown in the field at Prosser and data were recorded for flower color and pattern. From those F_2 populations, 124 plants were randomly selected for F_3 progeny tests grown at Prosser in 2006. All seeds from each F_2 parent were planted in the field plots. The population sizes of the F_3 progenies ranged from 3 to 136 plants. Data were recorded for flower color and pattern for 4264 F_3 plants. The F_3 progenies with too small a population size were not included in the data analyses to reduce the risk of a sampling error for the variables under consideration. The data were analyzed to find the number of true breeding progenies for BPF or white flower, as well as the number of progenies segregating for BPF or white flowers. Using the tables and formulas of Allard (1956), the data were also analyzed to calculate linkage between the *P* gene and either of the two dominant genes for BPF. In effect, the F_3 progenies

Table 1. List of genetic tester stocks of common bean used in crosses and their PI numbers at the Western Regional Plant Introduction Station at Pullman, WA, with genotype hypothesis for the Prp^{i}*-2* and *T* genes.

PI no.	Genotype in GRIN[z]	Hypothetical genotype Prp^{i}*-2 T*	Additional description
608674	*T Fib P V*	prp^{i}*-2 T*	Purple flower
608702[y]	*t z fib* virgarcus BC_3 5–593	prp^{i}*-2 t*	
632736[x]	*t* p^{mic} long micropyle stripe BC_3 5–593	prp^{i}*-2* t^{bp} or *t*	White flower
639270	*t z Fib* arcus BC_4 5–593	prp^{i}*-2 t*	
638664	*t Z* bip^{ana} *Fib* marginata *Fib* BC_3 5–593	prp^{i}*-2 t*	
03–585[w]	Not submitted for a PI number yet; originally, *t* p^{mic} blue pattern BC_3 5–593	Prp^{i}*-2* t^{bp}	Blue pattern flower (Fig. 2) and long micropyle stripe
608700	*t Z fib* self-colored BC_2 5–593	prp^{i}*-2*	
638669	*T* Prp^{i}*-2 V* BC_2 5–593	Prp^{i}*-2 T*	IAE syndrome[v]

[z]GRIN = Germplasm Resources Information Network.
[y]This stock is the BC_3 version of virgarcus, not the BC_2 version actually used experimentally.
[x]This PI is apparently heterogeneous at *T*, with some undetermined frequencies for t^{bp} or *t* (See Tables 3 and 8). With respect to blue pattern flower expression, the t^{bp} gene is cryptic (not expressed) with prp^{i}*-2*.
[w]Plot number of a true breeding blue pattern BC_3-F_3 of unknown genotype for blue pattern flower, but known to carry a recessive allele at *T* (presumed to be *t*) and genotype p^{mic}.
[v]IAE = intensified anthocyanin expression (i.e., dark purple flowers and purple flower buds, pods, petioles, stems, and leaf lamina).

Table 2. Genetic hypothesis for expression of flower color and pattern in common bean controlled by the interaction of two genes: *Prp*^{i}-2 and t^{bp}, with *P V* homozygous in the background.

Segregation in the F_2			
Genotypes	Frequency[z]	Phenotypes[y]	Expected phenotypes in F_2
Prp^{i}-2 *Prp*^{i}-2 t^{bp} t^{bp}	1	Blue pattern	All blue pattern
Prp^{i}-2 *Prp*^{i}-2 t^{bp} *t*	2	Blue pattern[y]	3 blue pattern; 1 white
Prp^{i}-2 *Prp*^{i}-2 *t t*	1	White	All white
Prp^{i}-2 *prp*^{i}-2 t^{bp} t^{bp}	2	Blue pattern[y]	3 blue pattern; 1 white
Prp^{i}-2 *prp*^{i}-2 t^{bp} *t*	4	Blue pattern[y]	9 blue pattern; 7 white
Prp^{i}-2 *prp*^{i}-2 *t t*	2	White	All white
prp^{i}-2 *prp*^{i}-2 t^{bp} t^{bp}	1	White	All white
prp^{i}-2 *prp*^{i}-2 t^{bp} *t*	2	White	All white
prp^{i}-2 *prp*^{i}-2 *t t*	1	White	All white

[z]The distribution is in units of 1/16 due to dihybrid gene interaction, with combined frequencies of nine blue pattern flowers (Fig. 2) and seven white flowers.

[y]We attempted to classify the observed distribution of banner colors into two classes (dark blue and light blue), but without success. Our speculative hypothesis is that genotypes *Prp*^{i}-2 *Prp*^{i}-2 t^{bp} *t*, *Prp*^{i}-2 *prp*^{i}-2 t^{bp} t^{bp}, and *Prp*^{i}-2 *prp*^{i}-2 t^{bp} *t* express progressively paler blue color in the banner petal due to a combination of dosage effects at both genes that are not equal. Blue pattern = the banner petal expresses various shades of blue, whereas the wing petals are nearly white (pale blue) with blue veins.

enabled us to determine the exact genotype at *P* for each F_2 parent and to correlate this with the genotype for BPF.

Test crosses with genetic stocks having virgarcus pattern seedcoat or IAE. In 2007, the test cross was made between *t z fib* (*prp*^{i}-*2*) virgarcus BC_3 5–593 and PI 638669, which expresses IAE with genotype *T Prp*^{i} *-2 V* BC_2 5–593. The F_2 was grown at Prosser in 2008, and data were recorded on plant pigmentation and flower color and pattern. The objective of this test cross was to determine the expression of genotype *t Prp*^{i}-*2* when synthesized from a cross between genetic stocks with known genotypes.

Test crosses to determine the role of *T* or a third gene in BPF. Two additional test crosses were made in 2007: 1) *T Prp*^{i} *-2 V* BC_2 5–593 × t^{bp} p^{mic} (*prp*^{i}-*2*) BC_3 5–593 (PI 632736) and 2) 5–593 (PI 608674, with *T prp*^{i}-*2*) × t^{bp} p^{mic} (*Prp*^{i}-*2*) BC_3 5–593 blue pattern BC_3 5–593. The F_2 of both crosses was grown at Prosser in 2008, and data were recorded for plant pigmentation and flower color and pattern. The first test cross was used to test the expression of the (expected) genotype *t Prp*^{i}-*2*, but PI 643736 was found to be heterogeneous at *T* (*t* and t^{bp}). The second cross was used to determine if 5–593 carried any additional genes that may affect BPF expression [i.e., genes other than *t* and *Prp*^{i}-*2* reported by Bassett (2005) from G07262].

Results and Discussion

Presenting the final genetic hypothesis from the beginning. To make the results easier to present and follow, we will provide our final hypothesis and its gene symbol from the beginning of this section. The genetic hypothesis is fully supported by later presentation. Our original hypothesis was that three genes were required for BPF expression, viz., *t, Prp*^{i}-*2*, and *Bpf* (blue pattern flower). Not until the 2008 field data were obtained was the *Bpf* gene hypothesis (a third gene) falsified and the t^{bp} hypothesis required to fit all the data over many years. We omit the *Bpf* gene symbol throughout the presentation, but two genes other than *t* were assumed to be necessary for BPF expression until the 2008 data were obtained.

Genetic data supporting a two-gene interaction for BPF. The F_1 progeny from the cross 5–593 × G07262 expressed intense bishops violet flower and purple pods (data not shown). Those flower and pod color attributes are expressions of the gene *Prp*^{i}-*2* (Bassett, 2005). Further breeding work with the F_2 selection for BPF demonstrated that *Prp*^{i}-*2* is necessary for expression of blue veins on white wing petals (Bassett, 2005). The F_2 segregation observed in F_1 progeny selected for BPF expression from the double backcross *t* p^{mic} (*prp*^{i}-*2*) BC_3 5–593 × F_1 [*t* p^{mic} (*prp*^{i}-*2*) BC_3 5–593 × t^{bp} p^{mic} *Prp*^{i}-*2* blue pattern BC_1 5–593] fit the expected values for complementary dominant gene action, viz., a 9:7 ratio for BPF to white flower, respectively (Table 3). Thus, we can be certain that one of the dominant genes is *Prp*^{i}-*2*, but the identity of the other has not been demonstrated. If the genetic model of two complementary dominant genes is confirmed, then the tentative genetic hypothesis of Bassett (Table 4 in Bassett, 2005) for blue vein flower expression is insufficient.

The double backcross presented in Table 3 segregated in F_1 for nine BPF plants and an unrecorded number of white flower plants (data not shown). The parental genotypes given in the heading of Table 3 are consistent with the observed segregation in F_2 (Table 3). If PI 632736 had genotype t^{bp} in this experiment, then the F_2 would segregate 3 BPF (*Prp*^{i}-*2*/-) to 1 white flower (*prp*^{i}-*2 prp*^{i}-*2*), which was not observed. Thus, the F_2 data support the hypothesis that PI 632736 has genotype *t* in this experiment.

A genetic tester stock for BPF was developed in BC_3 to the 5–593 genetic background, viz., *t* p^{mic} blue pattern BC_3 5–593 (03–585 in Table 1). When this stock was test-crossed to two partly colored seedcoat pattern stocks, arcus and marginata, which are also in BC_3 to 5–593, the F_2 progeny segregated in a

Table 3. Segregation in common bean for flower color and pattern in the F_2 from nine selected F_1 progeny expressing blue pattern flowers (BPF) from the cross *t* p^{mic} (*prp*^{i}-*2*) BC_3 5–593 × F_1 [*t* p^{mic} (*prp*^{i}-*2*) BC_3 5–593 × t^{bp} p^{mic} *Prp*^{i}-*2* blue pattern BC_1 5–593].[z]

Flower type (no.)					
Blue pattern *Prp*^{i}-*2*/- t^{bp}/-	White *prp*^{i}-*2 prp*^{i}-*2* and/or *t t*	χ^2 (9:7)	*P*	χ^2 (3:1)	*P*
28	16	0.976	0.32	3.030	0.08
22	24	1.326	0.25	18.12	<0.001
27	21	0.00	1.00	9.00	0.003
25	25	0.794	0.37	16.67	<0.001
29	14	2.189	0.14	1.310	0.25
30	17	1.097	0.30	3.128	0.08
26	21	0.017	0.90	9.709	0.002
28	21	0.016	0.90	8.333	0.004
20	26	3.049	0.08	24.38	<0.001
235	185	0.015	0.90	81.27	<0.001

[z]The nine selected F_1 progeny with BPF expression (Fig. 2) had the hypothetical genotype *Prp*^{i}-*2 prp*^{i}-*2* t^{bp} *t*.

Table 4. Segregation in common bean for flower color and pattern in the F_2 from crosses: 1) *t*^{bp} *p*^{mic} *Prp*^{i}-2 blue pattern BC_3 5–593 × *t z Fib* arcus BC_4 5–593 (*prp*^{i}-*2*) and 2) *t*^{bp} *p*^{mic} *Prp*^{i}-2 blue pattern BC_3 5–593 × *t Z bip*^{ana} *Fib* marginata BC_3 5–593 (*prp*^{i}-*2*).

	Flower type (no.)			
Cross no.	Blue pattern[z] *Prp*^{i}-*2*/- *t*^{bp}/-	White *prp*^{i}-*2 prp*^{i}-*2* and/or *t t*	χ^2 (9:7)	*P*
1	58	40	0.343	0.56
2	20	14	0.092	0.76
Total	78	64	0.433	0.51

[z]The banner petal expresses various shades of blue, whereas the wing petals are nearly white (pale blue) with blue veins (Fig. 2).

9:7 ratio for BPF to white flower (Table 4). Thus, the genetic model for two complementary dominant genes was further supported with this F_2 segregation data, but requires confirmation by F_3 progeny tests. The F_3 progeny tests of 124 randomly selected F_2 parents (from both crosses) were analyzed for patterns of segregation. Among the F_2 parents with BPF, eight were true breeding for BPF and 62 segregated for blue pattern or white flower (Table 5). The progeny sizes in F_3 are not sufficient to make statistically significant distinctions between the segregation ratios 3:1 and 9:7 for blue pattern to white flowers. Thus, this aspect of the model presented in Table 2 cannot be rigorously tested. All 54 F_2 parents with white flowers were true breeding for white flower (Table 5). The observed frequency of F_3 progeny classes, 8 true breeding blue pattern flowers, 62 segregating progenies for blue pattern or white flowers, and 54 true breeding white flowers, fit the expected ratio of 1:8:7 for the same F_3 progeny classes, respectively (Table 5). On the basis of the experimental support from the observed segregation in F_2 and F_3 progenies, there is clear evidence that a second dominant gene (besides *Prp*^{i}-*2*) is necessary for BPF expression. Also, the data in Tables 3, 4, and 5 demonstrate that 5–593 does not carry some unknown third gene expressing BPF with genotype *t Prp*^{i}-*2*, but the possibility remains that line 03–585 for BPF (Table 1) may carry such a hypothetical third gene.

Considerations for naming the trait blue pattern flower. Before proposing a gene symbol for the second dominant gene, further description of its action is needed. In the segregating populations presented in Tables 3, 4, and 5, plants with BPF had banner petals with highly variable levels of expression of blue color. Casual inspection of a progeny row gives the impression of roughly two degrees of blue color, which may be labeled dark blue and light blue. We made classification for dark and light blue levels of color (data not shown), but no Mendelian ratio or hypothesis consistently described the data. There may be genuine genetic interactions within and between the two genes conditioning the degree of blue color expression, but the colors are too close and too variable due to nongenetic forces to be classified without significant error. At a low frequency, some BPF segregants express such a pale light blue color in the banner that they might be better described as blue vein flowers. Thus, blue veins on white wing petals is the more reliable of the two aspects of BPF expression. On the other hand, if one stands back and observes a progeny row from more than 3 m distance, the blue veins are hardly visible, but the blue banner color is obvious. The best compromise is to select a more generic name, viz., blue pattern, which gives due regard to banner and wing aspects of the BPF pattern.

Table 5. The distribution in common bean of 124 F_3 progenies among segregating and nonsegregating classes and the F_2 parent flower colors derived from the crosses: 1) *t*^{bp} *p*^{mic} *Prp*^{i}-*2* blue pattern BC_3 5–593 × *t z Fib* arcus BC_4 5–593 (*prp*^{i}-*2*) and 2) *t*^{bp} *p*^{mic} *Prp*^{i}-*2* blue pattern BC_3 5–593 × *t Z bip*^{ana} *Fib* marginata BC_3 5–593 (*prp*^{i}-*2*).

	F_3 progenies in each flower color class (no.)	
Flower type of F_2 parent	Observations (no.)[z]	Class description
Blue pattern[y]	8	True breeding for blue pattern flower
	62	Segregating for blue pattern[y] or white flower
White	54	True breeding for white flower

[z]For the data 8, 62, and 54, the χ^2 (1:8:7) = 0.009, *P* = 0.93. Combining true breeding or segregating F_3 progenies with blue pattern F_2 parents, the data 70 and 54 give the χ^2 (9:7) = 0.002, *P* = 0.96.
[y]This pattern expresses blue (highly variable hue) banner petal and nearly white (pale blue) wing petals with blue veins (Fig. 2).

Table 6. Calculation of genetic linkage in common bean between the *P* locus and the blue pattern flower (Fig. 2) gene *t*^{bp} (schematic symbol *B*) or the intense purple gene *Prp*^{i}-2 (schematic symbol *C*), using the combined F_3 progeny data (110 progenies) derived from the crosses: 1) *t*^{bp} *p*^{mic} *Prp*^{i}-*2* blue pattern BC_3 5–593 × *t z Fib* arcus BC_4 5–593 (*prp*^{i}-*2*) and 2) *t*^{bp} *p*^{mic} *Prp*^{i}-*2* blue pattern BC_3 5–593 × *t Z bip*^{ana} *Fib* marginata BC_3 5–593 (*prp*^{i}-*2*).[z]

Genotype of F_2 parents	F_3 progenies (no.)[y]
Blue pattern genotypes	
P P B C	13
P p^{mic} *B C*	46
p^{mic} *p*^{mic} *B C*	9
White flower genotypes	
P P B c (b C, b c)	15
P p^{mic} *B c (b C, b c)*	23
p^{mic} *p*^{mic} *B c (b C, b c)*	4

[z]Linkage was calculated by the maximum likelihood method, using the tables and formulas of Allard (1956), giving 32.4 ± 7.91 cM.
[y]The genotype at *P* in the F_2 parent was determined by F_3 progeny tests.

Calculation of linkage between *P* and one of the two BPF genes. The F_3 progeny data (Table 5) allowed us to calculate linkage on the basis of a 1:2:1 ratio (at the *P* locus) interacting with a 9:7 ratio (at the *Prp*^{i}-*2* locus and some other unidentified locus, later demonstrated to be *T*), i.e., type of data no. 22 in the presentation by Allard (1956). We found a recombination fraction of 32.4 ± 7.91 cM (Table 6). Thus, the *P* gene is linked to one of the two genes for BPF, but we do not know which one. We will return to this question later.

Determination that *T*^{bp} is the second gene (besides *Prp*^{i}-*2*) for BPF. The cross between the virgarcus (seedcoat pattern) genetic stock with *t z fib prp*^{i}-*2* and the IAE syndrome stock with *T Prp*^{i}-*2* segregated for only three phenotypic classes, none of which expressed BPF (Table 7). Thus, the genotype *t Prp*^{i}-*2* has been demonstrated to be insufficient for BPF expression. Genotype *t Prp*^{i}-*2* was also insufficient for expression of blue veins on wing petals with a white (or nearly white) banner petal, as tentatively proposed by Bassett (2005).

Two crosses, 1) IAE syndrome stock PI 638669 × PI 732736 and 2)

Table 7. Segregation in common bean for plant pigmentation and flower color in the F_2 from the cross *t z fib* (*prp*^{i}*-2*) virgarcus BC_2 5–593 (white flower and no plant pigmentation) × *T Prp*^{i}*-2 V* BC_2 5–593 (pigmented plants and dark purple flowers).[z]

Plant description[z]	Genetic hypothesis	Observations (no.)[y]
Pigmented plant and dark purple flower	*Prp*^{i}*-2*/- *T*/-	245
No plant pigmentation and standard purple flower	*prp*^{i}*-2 prp*^{i}*-2 T*/-	80
No plant pigmentation and white flower	*Prp*^{i}*-2*/- *t t* or *prp*^{i}*-2 prp*^{i}*-2 t t*	88

[z]The *Prp*^{i}*-2* gene expresses a syndrome of effects throughout the plant, viz., intensified anthocyanin expression, resulting in dark purple flowers and purple color in flower buds, pods, petioles, stems, and leaf lamina.
[y]For the data 245, 80, and 88, the χ^2 (9:3:4) = 3.030, P = 0.22.

Table 8. Segregation in common bean for plant pigmentation and for pattern and color in the flowers from the crosses: 1) *T Prp*^{i}*-2 V (P)* BC_2 5–593 (pigmented plants and dark purple flowers) × t^{bp} p^{mic} (*prp*^{i}*-2*) BC_3 5–593 (no plant pigmentation and white flowers; PI 632736) and 2) *T prp*^{i}*-2* 5–593 (no plant pigmentation and purple flowers) × t^{bp} p^{mic} (*Prp*^{i}*-2*) blue pattern BC_3 5–593 (no plant pigmentation and blue pattern flower).[z]

	Pigmented plants,	Plants without pigmentation (no.)				
	dark purple flower (no.)	Purple flowers (no.)	Blue pattern flower[y] (no.)	White flower (no.)	χ^2	
Cross no.	*Prp*^{i}*-2*/- *T*/-	*prp*^{i}*-2 prp*^{i}*-2 T*/-	*Prp*^{i}*-2*/- t^{bp} t^{bp}	*prp*^{i}*-2 prp*^{i}*-2* t^{bp} t^{bp}	(9:3:3:1)	*P*
1	162	52	55	13	1.385	0.71
2	206	64	54	21	2.522	0.47

[z]The *Prp*^{i}*-2* gene expresses a syndrome of effects throughout the plant, viz., intensified anthocyanin expression, resulting in dark purple flowers and purple color in flower buds, pods, petioles, stems, and leaf lamina.
[y]See Fig. 2.

blue pattern stock 03–585 × 5–593, segregated in F_2 in a 9:3:3:1 ratio for the same four phenotypic classes, and both segregated for a BPF class at a 3/16 frequency (Table 8). Thus, we have a rigorous demonstration that only two genes are required for BPF expression and that the second gene (besides *Prp*^{i}*-2*) must be at the *T* locus. If two genes other than *t* (one being *Prp*^{i}*-2*) were required for BPF expression, we would expect to see a trigenic segregation ratio, but this was not observed (Table 8). Therefore, a new recessive allele at *T* is required. In Tables 3 and 4, this new allele was dominant to *t* and was necessary for BPF expression, whereas in Table 8, the new allele is recessive to *T*. We propose the gene symbol t^{bp} for this gene, which exhibits the dominance order $T > t^{bp} > t$, where the letters bp stand for *blue pattern*.

With the identity of the second gene (other than *Prp*^{i}*-2*) for BPF established, we need to discuss further the data in Table 6, where p^{mic} is linked to *Prp*^{i}*-2* or t^{bp}. From the linkage map for common bean, we know that *P* is located in linkage group B7, whereas *T* is located in linkage group B9 (Bassett, 2007). Those linkage groups have been associated with chromosomes (Pedrosa et al., 2003), demonstrating that p^{mic} cannot be linked to t^{bp}. Thus, the data provide an estimate of linkage of 32.4 ± 7.91 cM between the *P* locus and *Prp*^{i}*-2*

The origin of t^{bp} in the genetic stock PI 632736 was investigated from pedigree records. The segregation data in Table 3 demonstrate that PI 632736 must have genotype *t* (at some unknown frequency) to permit the observed segregation in F_2, whereas the segregation data in Table 8 (cross no. 1) demonstrate that PI 632736 must also carry genotype t^{bp} (at some unknown frequency) to permit expression of BPF. Examination of pedigree records indicated that the origin of *t* or the t^{bp} gene in PI 632736 was from PI 451801 or 'Early Wax' snap bean. Because PI 632736 has genotype *prp*^{i}*-2*, the presence of t^{bp} went undetected during the development of the genetic stock. The goal in developing a genetic marker stocks is to select against all marker genes that are not those deliberately chosen. This goal can be thwarted when a marker gene, either in the donor or the 5–593 recurrent parent, is not detectable (cryptic) because a gene necessary for its expression is not present. The result is undetected heterogeneity for a (cryptic) marker gene.

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