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, $t^{pmic}$ long micropyle stripe BC$_3$, 5–593, $t^{z}$ Fib arcus BC$_3$ 5–593, and $t^{z}$ bip$^{pm}$ 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$_2$ 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 $pm$ and one of the two genes for BPF. A cross between $t^{z}$ fib arcus BC$_3$ 5–593 and $T Prp^{-2}$ V BC$_3$ 5–593 demonstrated that $t Prp^{-2}$ did not express BPF. Two crosses, $T Prp^{-2}$ V BC$_3$ 5–593 $t^{pmic}$ BC$_3$. 5–593 and 5–593 $t^{bp}$ 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 $Prp^{-2}$ by 32 map units. The dominance order at the $T$ locus is $T > T^{p} > t$. The pedigree source of the $t^{bp}$ gene and the heterogeneity of PI 632736 ($t^{pmic}$ long micropyle stripe BC$_3$ 5–593) are discussed.

Bassett (2005) reviewed the literature relating to a gene [c$^{pr}$ $Prp^{i}$] 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$^{pr}$ $Prp^{i}$] is the change of pod color from green (with [C $prp$]) to dark purple pods. The gene [c$^{pr}$ $Prp^{i}$] was the first IAE gene to be reported and was investigated by many bean geneticists over several decades. A second gene for IAE ($Prp^{-2}$) was reported by Bassett (2005). The source of $Prp^{-2}$ was the Centro Internacional de Agricultura Tropical (CIAT) accession line G07262, which was reported to have genotype $t^{pmic}$ $Prp^{-2}$ (Bassett, 2005). The gene $t$ controls the expression of partially colored seedcoat patterns and $pm$ expresses a short, white micropyle stripe (Bassett, 2003, 2007). The genotype $t^{pmic}$ $Prp^{-2}$ expressed a long, white micropyle stripe (Fig. 1) in the seedcoat (Bassett, 2005). In the genotype $Prp^{-2}$ v, the v gene blocks the expression of IAE. Similarly, with $t$ $Prp^{-2}$, 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 $Prp^{-2}$ 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 $T T^{C} C^{r}$ $Z J G B V R R$ (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 $T T V$ (Bassett, 2007). When viewed from 1 m, the flower of selection no. 1 appears to have a pale bluebanner 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 $t^{pmic} Prp^{-2}$. A white banner and blue veins on otherwise white wing petals was tentatively attributed to genotype $t Prp^{-2}$, 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 $Prp^{-2}$ and a new hypothetical gene $t^{bp}$, which will be tested in experiments described later. We
also describe the development of a new genetic stock with the blue pattern flower (Fig. 2) in BC3 to 5–593.

In 1994, the cross 5–593 × G07262 was made, and the F1 progeny expressed intense bishops violet flower and purple pods. In the F2, a selection was made for a plant with blue pattern flower (BPF) and seedcoats with the long micropyle stripe (Fig. 1). In 1995, an F3 progeny plant with BPF and long micropyle stripe seeds was crossed with t z fib virgarcus BC2 5–593. An F4 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 t. A single plant selection for BPF and long micropyle seedcoat was made and designated t p^mic blue pattern BC1 5–593.

In 1999, a double backcross operation was made, viz., t p^mic BC3 5–593 × F1 (t p^mic BC3 5–593 × t p^mic blue pattern BC1 5–593). In 2001, seed from the BC3-F1 of blue pattern to 5–593 was planted in the greenhouse and observed to segregate for blue pattern or white flowers. Nine of the F1 plants expressed BPF and were selected, and their F2 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 arcurus or marginata pattern seedcoats.** In 2003 a BC3-F1 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 p^mic Prp-2 blue pattern BC3 5–593. In 2005, two test crosses were made at Prosser, WA, between t p^mic Prp-2 blue pattern BC3 5–593 and two genetic testers, viz., t z fib arcus BC4 5–593 and t z bip^mna Fib marginata BC3 5–593. The F2 from both crosses was grown in the field at Prosser and data were recorded for flower color and pattern. From those F2 populations, 124 plants were randomly selected for F3 progeny tests grown at Prosser in 2006. All seeds from each F2 parent were planted in the field plots. The population sizes of the F3 progenies ranged from 3 to 136 plants. Data were recorded for flower color and pattern for 4264 F3 plants. The F3 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 F3 progenies

| Pl no. | Genotype in GRIN^t | Hypothetical genotype | Additional description |
|--------|--------------------|-----------------------|-----------------------|
| 608674  | T Fib P V          | prp^t-2 T             | Purple flower         |
| 608702  | t z fib virgarcus BC3 5–593 | prp^t-2 t | White flower         |
| 632736* | t p^mic long micropyle stripe BC3 5–593 | prp^t-2 t or t | Blue pattern flower (Fig. 2) and long micropyle stripe |
| 608700  | t Z fib self-colored BC3 5–593 | prp^t-2 | 1AE syndrome* |
| 638669  | t Z fib self-colored BC3 5–593 | prp^t-2 V BC3 5–593 | IAE syndrome* |

^GRIN = Germplasm Resources Information Network.

This stock is the BC3 version of virgarcus, not the BC2 version actually used experimentally.

*This PI is apparently heterogeneous at T, with some undetermined frequencies for P or t (See Tables 3 and 8). With respect to blue pattern flower expression, the P^t gene is cryptic (not expressed) with prp^t.

*Plot number of a true breeding blue pattern BC3-F1 of unknown genotype for blue pattern flower, but known to carry a recessive allele at T (presumed to be t) and genotype P^mic.

*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-2 and IAE, with P V homozygous in the background.

| Genotypes | Frequency | Phenotypes | Expected phenotypes in F2 |
|-----------|-----------|------------|--------------------------|
| Prp-2\- Prp-2 pflC pflC | 1 | Blue pattern | All blue pattern |
| Prp-2\- Prp-2 pflC pflC | 2 | Blue pattern | 3 blue pattern; 1 white |
| Prp-2\- Prp-2 pflC pflC | 4 | Blue pattern | 9 blue pattern; 7 white |
| Prp-2\- Prp-2 pflC pflC | 1 | White | All white |
| Prp-2\- Prp-2 pflC pflC | 2 | White | All white |
| Prp-2\- Prp-2 pflC pflC | 2 | White | All white |
| Prp-2\- Prp-2 pflC pflC | 1 | White | All white |

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.

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-2\- Prp-2 pflC pflC, Prp-2\- Prp-2 pflC pflC, and Prp-2\- Prp-2 pflC pflC 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 F2 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-2) virgarcus BC3 5-593 and PI 638669, which expresses IAE with genotype T Prp-2\- V BC2 5-593. The F2 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-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-2\- V BC2 5-593 × pflC prp-2 (prp-2) BC3 5-593 (PI 632736) and 2) 5-593 (PI 608674, with T prp-2\- × pflC prp-2 (Prp-2) BC3 5-593 blue pattern BC3 5-593. The F2 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-2\-, but PI 643736 was found to be heterogeneous at T (and pflC). 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-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-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 pflC 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 F1 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-2 (Bassett, 2005). Further breeding work with the F2 selection for BPF demonstrated that Prp-2 is necessary for expression of blue veins on white wing petals (Bassett, 2005). The F2 segregation observed in F1 progeny selected for BPF expression from the double backcross t pflC (prp-2) BC3 5-593 × F1 [t pflC (prp-2) BC3 5-593 × pflC prp-2] blue pattern BC1 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-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 F1 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 F2 (Table 3). If PI 632736 had genotype t pflC (03-385 Table 1). When this stock was test-crossed to two partly colored seedcoat pattern stocks, arcus and marginata, which are also in BC3 to 5-593, the F2 progeny segregated in a

Table 3. Segregation in common bean for flower color and pattern in the F2 from nine selected F1 progeny expressing blue pattern flowers (BPF) from the cross t pflC (prp-2) BC3 5-593 × F1 [t pflC (prp-2) BC3 5-593 × pflC prp-2] blue pattern BC1 5-593.

| Flower type (no.) | Blue pattern | White pattern |
|-------------------|--------------|---------------|
| Prp-2\- pflC pflC | 28           | 16            | 0.976 | 0.32 | 3.030 | 0.08 |
| Prp-2\- pflC pflC | 22           | 24            | 1.326 | 0.25 | 18.12 | <0.001 |
| Prp-2\- pflC pflC | 27           | 21            | 0.00  | 1.00 | 9.00  | 0.003 |
| Prp-2\- pflC pflC | 25           | 25            | 0.794 | 0.37 | 16.67 | <0.001 |
| Prp-2\- pflC pflC | 29           | 14            | 2.189 | 0.47 | 13.10 | 0.25 |
| Prp-2\- pflC pflC | 30           | 17            | 1.096 | 0.30 | 3.128 | 0.004 |
| Prp-2\- pflC pflC | 26           | 21            | 0.016 | 0.90 | 8.333 | <0.001 |
| Prp-2\- pflC pflC | 28           | 21            | 0.016 | 0.90 | 8.333 | <0.001 |
| Prp-2\- pflC pflC | 20           | 26            | 3.049 | 0.08 | 24.38 | <0.001 |
| Prp-2\- pflC pflC | 235          | 185           | 0.015 | 0.90 | 81.27 | <0.001 |

*The nine selected F1 progeny with BPF expression (Fig. 2) had the hypothetical genotype Prp-2 prp-2 pflC pflC.*
Table 4. Segregation in common bean for flower color and pattern in the F2 from crosses: 1) *pp* *pmic* *Prp*-2 blue pattern BC3 5-593 × *tz* *Fib* arcus BC4 5-593 (*prp*-2) and 2) *pp* *pmic* *Prp*-2 blue pattern BC3 5-593 × *Z* *bip* *Fib* marginata BC3 5-593 (*prp*-2).

| Flower type (no.) | F2 progenies in each flower color class (no.) | Genotype of F2 parents | F3 progenies (no.) |
|------------------|---------------------------------------------|------------------------|------------------|
| **Blue pattern** | **White** | **prp*-2** | 3:1 | **prpmic** | **prpmic** |
| Blue pattern | White | 3:1 | 15 | 46 |
| Blue pattern | Blue | 9:7 | 4 | 9 |
| White | Blue | 1:8:7 | 15 |
| White | White | 1:8:7 | 23 |
| Blue | Blue | 1:8:7 | 4 |

9:7 ratio for BPF to white flower (Table 4). Thus, the genetic model for two complementary dominant genes was further supported with this F2 segregation data, but requires confirmation by F3 progeny tests. The F3 progeny tests of 124 randomly selected F2 parents (from both crosses) were performed for patterns of segregation. Among the F2 parents with BPF, eight were true breeding for BPF and 62 segregated for blue pattern or white flower (Table 5). The progeny sizes in F3 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 F2 parents with white flowers were true breeding for white flower (Table 5). The observed frequency of F3 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 F3 progeny classes, respectively (Table 5). On the basis of the experimental support from the observed segregation in F2 and F3 progenies, there is clear evidence that a second dominant gene (besides *Prp*-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*-1, 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 F3 progenies among segregating and nonsegregating classes and the F2 parent flower colors derived from the crosses: 1) *pp* *pmic* *Prp*-2 blue pattern BC3 5-593 × *tz* *Fib* arcus BC4 5-593 (*prp*-2) and 2) *pp* *pmic* *Prp*-2 blue pattern BC3 5-593 × *Z* *bip* *Fib* marginata BC3 5-593 (*prp*-2).

| Flower type of F2 parent | Observations (no.) | Class description |
|--------------------------|--------------------|-------------------|
| Blue pattern | 8 | True breeding for blue pattern flower |
| White | 62 | Segregating for blue pattern or white flower |
| White | 54 | True breeding for white flower |

For the data 8, 62, and 54, the *χ*² (1:8:7) = 0.009, *P* = 0.93. Combining true breeding or segregating F3 progenies with blue pattern F2 parents, the data 70 and 54 give the *χ*² (9:7) = 0.002, *P* = 0.96.

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 *pp* (schematic symbol *B*) or the intense purple gene *Prp*-2 (schematic symbol *C*), using the combined F3 progeny data (110 progenies) derived from the crosses: 1) *pp* *pmic* *Prp*-2 blue pattern BC3 5-593 × *tz* *Fib* arcus BC4 5-593 (*prp*-2) and 2) *pp* *pmic* *Prp*-2 blue pattern BC3 5-593 × *Z* *bip* *Fib* marginata BC3 5-593 (*prp*-2).

| Genotype of F2 parents | F3 genotypes (no.) |
|------------------------|--------------------|
| **Blue pattern genotypes** | **White flower genotypes** |
| *P B C* | *P pflCpflfl.* |
| *P p* | *P pflC-fl-fl.* |
| *P p* | *P pflC-fl-I.* |
| *P p* | *P flC-pflfl.* |
| *P p* | *P flC-fl-I.* |
| *P p* | *P fl-I-pflfl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
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| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
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| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
| *P p* | *P fl-I-fl-I.* |
| *P p* | *P fl-I-fl-fl.* |
Table 7. Segregation in common bean for plant pigmentation and flower color in the F₂ from the cross \( t \times \text{fib (prp}'-2\text{)} \) virgarcus BC₂ 5–593 (white flower and no plant pigmentation) \( \times T \text{Prp}'-2 \) V BC₂ 5–593 (pigmented plants and dark purple flowers).2

| Plant description | Genetic hypothesis | Observations (no.) |
|-------------------|-------------------|--------------------|
| Pigmented plant and dark purple flower | \( \text{Prp}'-2/T'/- \) | 245 |
| No plant pigmentation and standard purple flower | \( \text{prp}'-2 \text{prp}'-2 T'/- \) | 80 |
| No plant pigmentation and white flower | \( \text{Prp}'-2//t' \text{t' or prp}'-2 \text{prp}'-2 \text{t'} \text{t'} \) | 88 |

1The \( \text{Prp}'-2 \) 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.

2For the data 245, 80, and 88, the \( \chi^2 (9:3:4) = 3.030, P = 0.22 \).

Table 8. Segregation in common bean for plant pigmentation and for pattern and color in the flowers from the crosses: 1) \( T \text{Prp}'-2 \) V (\( P \)) BC₂ 5–593 (pigmented plants and dark purple flowers) \( \times \text{p}^\circ \text{p}'-2\text{mc} (\text{prp}'-2) \) BC₃ 5–593 (no plant pigmentation and white flowers; P1 632736) and 2) \( T \text{prp}'-2 \) 5–593 (no plant pigmentation and purple flowers) \( \times \text{p}^\circ \text{p}'-2\text{mc} (\text{Prp}'-2) \) blue pattern BC₃ 5–593 (no plant pigmentation and blue pattern flower).3

| Cross no. | Pigmented plants, dark purple flower (no.) | Plants without pigmentation (no.) | Purple flowers (no.) | Blue pattern flower (no.) | White flower (no.) | \( \chi^2 \) (9:3:3:1) | \( P \) |
|-----------|-------------------------------------------|----------------------------------|---------------------|-------------------------|-------------------|----------------|---|
| 1         | \( \text{prp}'-2//T'/- \)                | 162                              | 52                  | 55                      | 13                | 1.385          | 0.71 |
| 2         | 206                                       | 64                               | 54                  | 21                      | 2.522             | 0.47           |     |

1The \( \text{Prp}'-2 \) 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.

2See Fig. 2.

3Examination of pedigree records indicated that the origin of \( t \) or the \( \text{p}^\circ \) gene in PI 632736 was from PI 451801 or 'Early Wax' snap bean. Because PI 632736 has genotype \( \text{prp}'-2\text{,} \) the presence of \( \text{p}^\circ \) 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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