Allelism between the P and Stp Genes for Seedcoat Color and Pattern in Common Bean

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ABSTRACT. The P locus in common bean (Phaseolus vulgaris L.) can express complete absence of color (white) in seedcoats and flowers with p (with B V) or a pale grayish white seedcoat and nearly white flower with p\textsuperscript{m}, but P has never been considered a seedcoat pattern locus. Genes controlling seedcoat colors and patterns have been backcrossed into the recurrent parent 5-593 with black seedcoats and violet flowers. The cross, p BC, 5-593 x \textit{stp} BC, 5-593 (black seeds with a long white micropyle stripe and hilum arcs), failed to show evidence of genetic complementation in either F\textsubscript{1} or F\textsubscript{2} progeny, leading to the hypothesis that \( P \) and \( Stp \) are allelic. Five cross combinations between two recessive \( P \) alleles (p BC, 5-593 and \( p_{m} \) BC, 5-593) and three recessive alleles at the stipped seedcoat gene \( Stp \) (\( stp \) BC, 5-593, \( stp^{\text{mic}} \) BC, 5-593, and \( stp^{\text{hbw}} \) BC, 5-593) expressed no genetic complementation in seedcoats and flowers of \( F_{2} \) progeny and confirmed the allelism hypothesis. New gene symbols are proposed for the recessive alleles at \( P \) for \( stp \), \( p_{m} \) for \( stp^{\text{mic}} \) and \( p_{m} \) for \( stp^{\text{hbw}} \). The dominance order at \( P \) is \( P > p_{m} > p_{m} > p_{m} > p \). Crosses were made between self-colored BC, 5-593 and three other parents—\( p_{m} \) BC, 5-593, \( stp^{\text{mic}} \) BC, 5-593, and \( stp^{\text{hbw}} \) BC, 5-593—to explore interactions between the pattern genes \( T \) and \( P \); and segregation for seedcoat patterns in \( F_{2} \) was discussed. The hypothesis was proposed that the \( T \) locus regulates expression at \( P \), or the biosynthetic step regulated by \( P \).

Prakken (1970) summarized the genetics of seedcoat color (other than the red colors) in common bean (\textit{Phaseolus vulgaris} L.), and he reconciled the different gene symbols used by various researchers for the same gene. Subsequently, Prakken (1972) published his extensive work with red seedcoat colors and organized the entire body of seedcoat color genetics (Prakken, 1970, 1972) into two tables, one for the yellow-black series of colors and the other (a text table) for the red colors. The tables present the colors expressed with genotype \( P_{n}P_{n} \) together with all combinations of the other eight genes (\( C, R, D, J, G, B, V, \) and \( Rk \)) in the seedcoat color system. Two of the eight genes, the pattern gene \( C \) and the gene \( R \) for dominant red color, are very tightly linked (Prakken, 1972). To express the nearly unbreakable linkage between the two genes, they are usually presented in brackets, \( [C R] \) (Bassett, 1991). Recently, a ninth gene (\( Gy \) for greenish yellow) for seedcoat color was reported by Bassett et al. (2002), but this gene is known to be closely linked to \( C \) (McClenan et al., 2002) and with further experimental work may prove to be another gene (like \( R \)) located within the complex \( C \) locus as described by Prakken (1974). Also, the \( D \) locus was recently discovered to be allelic with the \( Z \) gene, which interacts with \( T \) (\( T \) for totally colored seedcoat) to produce various partly colored seedcoat patterns (Bassett et al., 1999).

Seedcoat Color Genetics

The genetic stocks employed in this paper all carried the genotype \( [C R] J G B V Rk \), which expresses black seedcoat except where altered by \( p \) or other pattern genes. The \( C \) locus has a very large multiple allelic series of dominant genes controlling seedcoat patterns, and \( c^{*} \) expresses a cartridge buff (pale beige) seedcoat. Patterns controlled by \( C \) have a dark pattern color contrasted with cartridge buff as the light pattern color, unless modified by alleles for recessive red colors controlled by the red kidney locus \( Rk \). The genotype \( C/c \) expresses subtle seedcoat mottling effects, whereas \( c/c \) genotypes have slightly paler colors than the same background genotypes with \( C/C \). The \( J \) locus (with \( j/j \)) expresses loss of color in the hilum ring, reduced color expression in the corona, and loss of seedcoat shininess. According to Bassett (1996a), \( j/j \) also expresses immature seedcoat colors, i.e., a paler version of whatever color the seedcoat color genotype with \( J \) would have expressed. The \( Z \) locus interacts with \( J \) to produce (with \( j/z/c \)) the loss of color in the corona region of the seedcoat in addition to the hilum ring. The genes \( G, B, \) and \( V \) are color modifying genes; \( G \) (from \textit{Gelbe}, yellow in German) for yellow with \( G b V \), \( B \) for brown expressing mineral brown with \( G B V \) and buffy citrine with \( G b V \), and \( V \) for violet to black (anthocyanin pigments) expressing dark brown violet with \( G b V \) and black with \( G B V \). With \( g b v \), the seedcoat is shamois. The red kidney locus \( Rk \) controls recessive red seedcoat colors teseaceous (light red kidney) and garnet brown (dark red kidney), which have the most stable expression with \( c^{*} \). The gene \( R \) expresses dominant red (oxblood) color, which is slightly bluer than garnet brown (Bassett, 1998a).

History of the \( P \) Locus

The recessive allele \( p \) expresses (with genotype \( P/p \)) a white seedcoat. Shull (1908) was the first to report the existence of a dominant gene necessary to express seedcoat color, and Emerson (1909) gave this gene the symbol \( P \). Lamberprecht (1936) discovered a second ground factor gene designated \textit{griseoalbus} (for gray-white seedcoat), which he gave the gene symbol \( Gri \). The term ground factor means that \( Gri \) (and \( P \)) are necessary for seedcoat color expression. Bassett (1994) discovered that \( Gri \) is allelic with \( P \), and gave the recessive allele the gene symbol \( p^{m} \). The current view of the role the \( P \) gene plays in seedcoat chemistry will be given at the end of the paper.

Bassett (1996b) discovered a new seedcoat gene (with gene symbol \( Stp \) for stipped) for pattern in seedcoats and flowers and described two recessive alleles at this locus \( stp \) and \( stp^{\text{mic}} \). A third recessive allele, \( stp^{\text{hbw}} \), was later reported by Bassett (1998b). Allelism tests were made between \( Stp \) and the two other genes known to express seedcoat pattern, viz., \( C \) and \( T \), and found that \( Stp \) was
nonallelic (Bassett, 1996b). The P locus was not known to produce patterns in seedcoats. This paper presents evidence for the allelism of P and Stp and investigates the dominance relationships among five recessive genes: stp, stp<sup>pm</sup>, stp<sup>mic</sup>, p, and p<sup>m</sup>. The paper also presents descriptions of interactions of t with stp and stp<sup>pm</sup> as expressed in altered seedcoat patterns.

Materials and Methods

**Materials and Test Crosses.** The genetic stocks used were constructed by backcrossing selected recessive marker genes for seedcoat color or pattern into the recurrent parent 5-593, a Florida dry bean breeding line with black seedcoats due to genotype T<sub>P</sub>C<sub>r</sub>Z<sub>J</sub>G<sub>V</sub>R<sub>k</sub> (Bassett, 2001). The P locus genetic stocks included p BC<sub>3</sub> 5-593 [white seed with (pale yellowish) brown micropyle stripe] and p<sup>m</sup> BC<sub>3</sub> 5-593 (light gray with B V). The Stp locus genetic stocks included stp BC<sub>3</sub> 5-593 (Fig. 1), stp<sup>pm</sup> BC<sub>3</sub> 5-593 (Fig. 2), stp<sup>mic</sup> BC<sub>3</sub> 5-593 (Fig. 3), and t stp<sup>pm</sup> BC<sub>3</sub> 5-593 (Fig. 4).

To test for allelism between P and Stp, the cross p BC<sub>3</sub> 5-593 x t stp<sup>pm</sup> BC<sub>3</sub> 5-593 was made in Fall 2000, and the F<sub>1</sub> generation was grown in the field in Spring 2001. Data were recorded for color and pattern of seedcoats and flowers. To test for the interactions of t with stp and stp<sup>pm</sup>, the crosses t self-colored BC<sub>3</sub> 5-593 x stp BC<sub>3</sub> 5-593 and stp<sup>pm</sup> BC<sub>3</sub> 5-593 were made in Fall 2000, and the F<sub>1</sub> generation was grown in the field in Spring 2001. Data were recorded for color and pattern of seedcoats and flowers.

To further test for allelism between P and Stp and establish the dominance order among the putative five recessive alleles at P, the following test crosses were made: p BC<sub>3</sub> 5-593 x stp BC<sub>3</sub> 5-593, p BC<sub>3</sub> 5-593 x stp<sup>pm</sup> BC<sub>3</sub> 5-593, p BC<sub>3</sub> 5-593 x stp<sup>mic</sup> BC<sub>3</sub> 5-593, and p<sup>m</sup> BC<sub>3</sub> 5-593 x stp<sup>pm</sup> BC<sub>3</sub> 5-593. The F<sub>1</sub> progenies from the test crosses between the two known recessive alleles at P and the three known recessive alleles at Stp were grown in the greenhouse in Winter 2002, and descriptive data were recorded for color and pattern of seedcoats and flowers.

Results and Discussion

For the cross p BC<sub>3</sub> 5-593 x t stp<sup>pm</sup> BC<sub>3</sub> 5-593, the F<sub>1</sub> seeds expressed the white micropyle stripe pattern on black seeds typical of genotype Stp<sup>pm</sup> (Fig. 3). The lack of complementation between P and Stp supported the hypothesis of nonallelism. The segregation observed in the F<sub>2</sub> generation for flower color and seedcoat color

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**Fig. 1.** Drawings of seeds with the stippled pattern controlled by p (formerly stp): upper seeds show the most extensive dark pattern color; lower seeds show the least extensive dark pattern color.

**Fig. 2.** Drawings of seeds with the stippled pattern controlled by p<sup>m</sup> (formerly stp<sup>pm</sup>).
Table 1. Segregation for flower color and seedcoat pattern in the F2 from the cross p BC3 5-593 (T/t) x t stpBC3 5-593 (tpw).

<table>
<thead>
<tr>
<th>Violet flowers</th>
<th>White flowers</th>
</tr>
</thead>
<tbody>
<tr>
<td>T/t pmpw/ -</td>
<td>T/t p/m -</td>
</tr>
<tr>
<td>Black seed</td>
<td>White seed</td>
</tr>
<tr>
<td>with white</td>
<td>White seed</td>
</tr>
<tr>
<td>MS—</td>
<td>two-points</td>
</tr>
<tr>
<td>with white MS—</td>
<td>with brown</td>
</tr>
<tr>
<td>and fibula arcs</td>
<td>two-points</td>
</tr>
<tr>
<td>239</td>
<td>37</td>
</tr>
</tbody>
</table>

MS = micropyle stripe.

For the genotype T/t pmpw, the observed value of 37 was a surplus over the expected value of 27.94, giving χ² = 2.94. Similarly, the surplus of T/t p/m vs. t t pmpw, T/t p/m vs. T/t pmpw, and t t p/m, the data 239, 96, 112 gave χ² = 2.388, P = 0.30. For T/t vs. t t, the data 335, 112 gave χ² = 3.1 = 0.001, P = 0.98. For pmpw/- vs. p p, the data 314, 133 (a surplus over the expected 111.75) gave χ² = 5.388, P = 0.02.

or pattern is presented in Table 1. The observed data involved five phenotypic classes and fit the proposed genetic model, but the chi-square test for segregation at the P locus gave a significant deviation from expected values (Table 1). There was a surplus of for p/p plants and a shortage of for pmpw/- plants. This shortage may be due to lethality of pmpw genotypes.

**Phenotype of pmpw.** For the F1 plants from the cross p BC3 5-593 x stp BC3 5-593, the wings of the flowers were white, but the banner petal had the same pattern as stp BC3 5-593 (Fig. 5) except that the color was distinctly paler, and the violet banner tip was more narrow. The F2 seeds had the same pattern as stp (Fig. 1), but the dotting on the micropyle end of the seed was more dispersed. Thus, stp is an allele at P and is almost completely dominant to p. I propose the new gene symbol pmpw for stp.

**Phenotype of pmpw.** For F1 plants from the cross p BC3 5-593 x stpBC3 5-593, the wings of the flowers were pale violet with a small patch of white in the center. The violet color of the wings was more narrow. The F2 seeds had the same pattern as stp BC3 5-593, the wings of the flowers were pale violet with a small patch of white in the center and a white peripheral band ≈0.5 mm wide or less. The data presented in a previous paper (virgarcus).

Now that the previous gene stp is known to be an allele at P with new gene symbol pmpw, the data presented in a previous paper (Bassett, 1998b) for interactions stp BC3 5-593 x stp BC3 5-593 was not made, the dominance of stp over pmpw is assumed because of the dominance of stp over p. The dominance order stp BC3 5-593 x stp BC3 5-593 was previously established (Bassett, 1998b); and similarly the dominance order pmpw > p was previously established (Bassett, 1994). Thus, the dominance order, using the new gene symbols for the former Stp locus, is P > pmpw > stp > pmpw > p.
end of the seed (Fig. 4) and \lt;math\rangle t \lt;math\rangle \text{p}^{\text{w}} \lt;math\rangle \text{ restricts color expression to a virgarcus pattern (Bassett, 1996c) without a micropyre stripe (Fig. 6). The simplest hypothesis for the gene actions involved is that \lt;math\rangle t \lt;math\rangle , and its modifier \lt;math\rangle z \lt;math\rangle , regulate the expression at \lt;math\rangle P \lt;math\rangle or the biosynthetic step regulated by \lt;math\rangle P \lt;math\rangle (P. McClean, personal communication). Genotype \lt;math\rangle t \lt;math\rangle z \lt;math\rangle \text{p}^{\text{w}} \lt;math\rangle \text{ expresses a precisely additive restriction to the pattern of color expressed by \text{p}^{\text{w}}.\lt;math\rangle

Additional research was performed to explore the interactions of \lt;math\rangle t \lt;math\rangle with the other two recessive alleles at \lt;math\rangle S\text{tp} \lt;math\rangle . The cross \lt;math\rangle t \lt;math\rangle \text{self}-\lt;math\rangle \text{colored BC}_{1} \lt;math\rangle 5-593 \lt;math\rangle x \lt;math\rangle \text{st}p \lt;math\rangle \text{BC}_{1} \lt;math\rangle 5-593 \lt;math\rangle (\text{p}^{\text{w}}) \lt;math\rangle \text{ segregated in F}_{2} \lt;math\rangle for \lt;math\rangle t \lt;math\rangle \text{p}^{\text{w}} \lt;math\rangle \text{ recombinants at the expected frequency (data not shown). The seedcoat pattern of \text{p}^{\text{w}} \lt;math\rangle \text{ was not different from \text{p}^{\text{w}}. \lt;math\rangle The cross \lt;math\rangle t \lt;math\rangle \text{self}-\lt;math\rangle \text{colored BC}_{1} \lt;math\rangle 5-593 \lt;math\rangle x \lt;math\rangle \text{st}p^{\text{bos}} \lt;math\rangle \text{BC}_{1} \lt;math\rangle 5-593 \lt;math\rangle (\text{p}^{\text{w}}) \lt;math\rangle \text{ segregated in F}_{2} \lt;math\rangle for \lt;math\rangle t \lt;math\rangle \text{p}^{\text{w}} \lt;math\rangle \text{ recombinants at the expected frequency (data not shown). The seedcoat pattern of \text{p}^{\text{w}} \lt;math\rangle \text{ differs from \text{p}^{\text{w}} \lt;math\rangle \text{ by having much less dark pattern color and more dispersed black dotting. The white seedcoat areas outside the corona (Fig. 7) actually have a secondary pattern of pale gray dots (not shown to simplify the illustration), which give an overall light gray appearance to the seed. The pale gray dot pattern can only be observed to consist of separate dots with 15x magnification.\lt;math\rangle

Biochemistry of \text{P} in Relation to Seedcoat Color. The biochemistry of the \text{P} gene is under investigation at Michigan State University (G. Hosfield, personal communication). This research group regards \text{P} as a candidate gene for the enzyme, flavanone 3-hydroxylase (F3H) (unpublished data). F3H converts flavanone to a dihydroflavonol called dihydrokaempferol, which is then converted to kaempferol. Dihydroflavonols are the precursors to all color compounds, and in alfalfa (Medicago media), F3H is involved in the synthesis of anthocyanins and flavonols (G. Hosfield, personal communication).

Biochemical investigation of \text{P} at North Dakota State University also indicates that \text{P} is a candidate gene for the enzyme F3H (P. McClean, personal communication). His laboratory has cloned a fragment of F3H, which spans from exon 2 across intron 2 and just into exon 3. They sequenced 23 common bean genotypes \lt;math\rangle \text{named cultivars, including ‘UI-114’ (with \text{P}) and ‘Aurora’ (with \text{p}).\lt;math\rangle

The research at these two laboratories on the role of \text{P} in the biochemistry of seedcoat colors remains unpublished. Because common bean has no genetic transformation system, proving the hypothesis of \text{P} as a candidate gene for F3H will be difficult. Perhaps reviewers will accept the results of polymorphism studies as providing the necessary proof for a species without a transformation system (P. McClean, personal communication).

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