The *griseoalbus* (Gray-white) Seedcoat Color Is Controlled by an Allele (p^{gr}) at the *P* Locus in Common Bean

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Abstract. A cross was made between *gri* (gray-white seedcoat) and *p* (pure-white seedcoat) using genetic stocks *gri* BC₂ 5-593 and *p* BC₂ 5-593 developed to carry only a single recessive allele for seedcoat color in an otherwise all-dominant genetic background. The recurrent parent, 5-593, is a Florida dry-bean breeding line with bishops-violet flowers, determinate habit, small seed size, shiny black seeds, and seedcoat genotype *T Mar P [C r] D J G B V Rk*. The F₁ progeny from the above cross between *gri* and *p* had the flower color pattern and seedcoat color of the *griseoalbus* character (*gri*), but had less intense color expression. Therefore, I hypothesized that *gri* is an allele at the *P* locus (allelic interaction). The hypothesis of allelism was confirmed in the F₂, which failed to segregate for bishops-violet flowers and black seed, i.e., no complementation was evident. The symbol p^{gr} is proposed for the new allele at *P*, where the dominance series is $P > p^{gr} > p$. The gene for gray-white seeds in *gri* BC₂ 5-593 was shown to be allelic to Lamprecht's *gri* gene in V0059 (PI 527716).

The *griseoalbus* (*gri*) gene was identified by Lamprecht (1936) and was regarded by him as one of two basic genes ("groundfactors") for seedcoat colors in common bean, the other basic color gene being *p* (Emerson, 1909). *Griseoalbus* means gray-white and refers to the action of *gri* on seedcoat color. That is, whatever seedcoat color is expressed with *Gri* is reduced to gray-white by the action of *gri*. When Prakken (1970) published his critical review of all previous work with the genetics of seedcoat color, he dismissed *gri* with the statement, "... about this gene pair *Gri gri* I do not have personal experience." Recently, Bassett (1992) reported that *gri* has pleiotropic effects, producing a distinctive flower color pattern when in combination with *V* or v^{luc} . The wing petals are nearly colorless, but have a faint blue tint. In contrast, the banner petal is white except for two bishops-violet dots (often fused) in the upper middle position. The discovery of these pleiotropic effects was the result of backcrossing *gri* into the recurrent parent breeding line 5-593. This paper describes the results of an attempt to create a genetic stock with both "groundfactors" (Prakken, 1970, see p. 2), viz., with the genotype *p gri*. Hypotheses about the biochemical actions of *p* and *gri* in pigment synthesis have been proposed by Leakey (1988).

Materials and Methods

I have been developing a set of genetic stocks, each of which has a different single recessive gene for seedcoat color substituted into a genetic background that has dominant genes at all the other loci affecting seedcoat color. The backcross method has been used to create these stocks, using the Florida dry-bean breeding line 5-593 as the recurrent parent. Line 5-593 has bishops-violet flowers, determinate habit, and small and shiny black seeds with the seedcoat genotype *T Mar P Gri [C r] D J G B V Rk* (Bassett, 1992; Bassett and Blom, 1991; Bassett, unpublished data; Prakken, 1970).

For each seedcoat color marker gene, the initial cross was marker source parent $\times$ 5-593. Selections were then made in the F₂ for plants homozygous for the marker. The first backcross was made with several F₃ progeny originating from selected F₂ plants, and the resulting F₁ plants were harvested separately. Subsequent segregating populations (usually four) resulting from the backcrosses to 5-593 were selected to produce populations that segregated for only the single recessive marker (i.e., homozygous for other seedcoat color marker genes or other characters). The above procedure was repeated (second backcross) when no population was found that had only the one desired marker substitution. The development of the BC₂ stock with *gri* resulted in the line designated *gri* BC₂ 5-593 (Bassett, 1992). Genetic stock *gri* BC₂ 5-593 has gray-white seeds and flowers with patterned color: the nearly white wing petals have a faint blue tint and the standard is white except for two bishops-violet dots (often fused) in the upper center position. Similarly, a line designated *p* BC₂ 5-593 was developed, using the snap bean cultivar Triumph as the source of *p*. Genetic

stock *p* BC₂ 5-593 has pure-white flowers and seedcoats.

Once stocks with an array of single recessive genes were developed, it was easy to construct cross progeny with substitutions for two recessive genes by mating the single-gene stocks (e.g., *j* BC₂ 5-593 $\times$ *p* BC₂ 5-593).

To create a genetic tester stock with the genotype *p gri* the cross *p* BC₂ 5-593 $\times$ *gri* BC₂ 5-593 was made. Four plants of the F₁ generation and four plants of *gri* BC₂ 5-593 were grown in the greenhouse. The F₂ progenies were grown in four separate plots (one for each F₁ parent) in the field in Spring 1992. Data were taken on flower color (and pattern) and seedcoat color for each F₁ and F₂ plant.

The genetic stock *gri* BC₂ 5-593 was developed from Lamprecht's line V0400 (now PI 527735) (Bassett, 1992). To make certain that the *gri* gene that I derived from V0400 is the same as the one Lamprecht reported, I made an allelism test using the reciprocal crosses V0059 $\times$ *gri* BC₂ 5-593 and *gri* BC₂ 5-593 $\times$ V0059. The genotype for seedcoat color of V0059 is *P gri C ins J G b v^{luc} r*, according to Lamprecht (1936), where *ins* is the same as *d*, according to Prakken (Prakken, 1970). Four F₁ plants were grown for each of the reciprocal crosses as described above. Data were taken on the flower color (and pattern) and seedcoat color of each plant.

Bean plants were grown in greenhouse culture in peat-vermiculite potting mix in 3.7-liter pots that were nestled 2 to 3 cm into the surface of soil-filled benches. Plants were fertilized weekly with Peters Excel Cal Mag 15N-5P-15K (Grace-Sierra Horticultural Products Co., Milpitas, Calif.). The greenhouse was at 22 to 28C day/10 to 15C night. The field soil type was Pomona sand. In the field, bean seeds were sown in raised beds (20 cm high $\times$ 60 cm wide) in two rows 30 cm apart with in-row plant spacing of 20 cm.

Results and Discussion

The F₁ plants from *p* BC₂ 5-593 $\times$ *gri* BC₂ 5-593 were expected to express bishops-violet flowers and shiny black seeds due to complementation of the two nonallelic recessive genes. The observed flower and seed colors were very different. The flowers had pure-white wing petals and banner petals with two (fused) violet dots that were intermediate in intensity between pure white and the bishops-violet dots of *gri* BC₂ 5-593. The seeds were gray-white, but more pale than the gray-white of *gri* BC₂ 5-593, i.e., intermediate in intensity. The hypothesis tested was that the intermediate colors of the flowers and seeds are the result of an allelic interaction produced by the genotype p^{gr}/p . In this case, the new gene symbol p^{gr} represents a new allele at the *P* locus giving the *griseoalbus* phenotype first described by Lamprecht (1936) and amplified by Bassett (1992). That is, seedcoats are gray-white (with appropriate modifiers) and flowers (with *V*) possess nearly white wing petals tinted with blue and a white banner petal, except for two bishops-violet dots (often fused) in the upper middle position.

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To test the hypothesis of allelism between *p* and *gri*, the F₂ generation (i.e., from *p* BC₂ 5-593 x *gri* BC₂ 5-593) was grown and examined. No segregants were found with wild-type flower color, i.e., bishops-violet (Table 1). It was clear that there were two levels of intensity of the *gri* type of flower color pattern among nonwhite flowers because of the observed intermediate intensity of the F₁ phenotype (*p* BC₂ 5-593 x *gri* BC₂ 5-593) and the stronger intensity of *gri* BC₂ 5-593. The two intensity classes among plants with patterned flowers were combined into a single class (Table 1). The data adequately fit a 3:1 segregation ratio between *gri*-pattern flowers and pure-white flowers, respectively (Table 1). Also, there was always cosegregation for either gray-white seed with the *gri*-pattern flowers or pure-white seed with the pure-white flowers (Table 1), which is typical of the pleiotropic effects of *gri* reported by Bassett (1992). In the absence of any evidence for complementation, I concluded that the observed segregation for either colored flowers and seeds or pure-white flowers and seeds is controlled by two alleles at the *P* locus. I hypothesized that the colored flowers and seeds are the result of two genotypes, *p^{gri}/p^{gri}* and *p^{gri}/p*, whereas the pure-white flowers and seeds are the result of the genotype *p/p*.

The investigation by Lamprecht (1936), which characterized *gri* expression, was based on two crosses: V0059 (now PI 527716) x Line 146 and V0060 (now PI 527717) x Line 146. Line 146 is the all-recessive tester line with genotype *P Gri c j g b v r* (Lamprecht, 1936). Lamprecht simply assumed that the single recessive factor in V0059 and V0060 that controlled the *griseolbus* character was a gene at a locus different from *P*. He did not perform an allelism test of V0059 and V0060 with a stock carrying *p*.

Alleight plants from the allelism test crosses V0059 x *gri* BC₂ 5-593 and *gri* BC₂ 5-593 x V0059 were identical, each having the typical flower color pattern and seedcoat color of *gri* BC₂ 5-593 (data not shown). These results support the proposed hypothesis of allelism.

In summary, the proposed new allele (symbol *p^{gri}*) is partially dominant to *p* but fully recessive to *P*. Thus, the amended genotype of

Table 1. Segregation for flower color (and pattern) and bean (*Phaseolus vulgaris* L.) seed color in the F₂ from the cross *p* BC₂ 5-593 x *gri* BC₂ 5-593.^z

Phenotypic classes		χ^2 (3:1)	<i>P</i> values
<i>gri</i> -pattern flowers, ^y gray-white seed	Pure-white flowers, pure-white seed		
45	12	0.474	0.49
41	16	0.287	0.59
42	17	0.458	0.50
42	15	0.053	0.70
Totals 170	60	0.145	0.70

^zGenetic stock *p* BC₂ 5-593 has pure-white flowers and pure-white seedcoats, whereas genetic stock *gri* BC₂ 5-593 has gray-white seeds and flowers with patterned color: the nearly white wing petals have a faint blue tint and the standard is white except for two bishops-violet dots (often fused) in the upper center position.

^yThe *gri*-pattern flowers included the typical color patterns for *gri* BC₂ 5-593 (new hypothesis: *p^{gri}/p^{gri}*) and the F₁ plants (*p^{gri}/p*), but the two types (color intensity levels) were combined into a single class. No flowers with wild-type color (bishops-violet) were observed.

5-593 should be *T Mar P [C r] D J G B V Rk*. The *Gri* locus has been deleted from the array of genes controlling seedcoat color because there is no separate gene for the gray-white seedcoat character.

During the 1950s, bean breeders abandoned the development of snap bean cultivars with colored seedcoats and changed to exclusive use of the *p* allele to obtain pure-white seedcoats. This was done because processed snap bean pods with colored seeds produced a dark-colored pot liquor, which was judged undesirable in appearance. Although *p* achieved a total loss of seedcoat color with a single gene, it produced many deleterious side effects in the performance of such lines (Deakin, 1974; Dickson and Petzoldt, 1988). Pot liquor color of processed snap bean pods is a function of pod interior color factors as well as seedcoat colors (S. Magnuson, personal communication). Pods with *p* always produce clear pot liquor, but alternative seedcoat genotypes can produce either clear or colored pot liquor, depending on pod interior color factors.

Snap bean breeders should consider alternative single recessive genes that can produce clear pot liquor in processed beans with presumably less deleterious side effects (e.g., *p^{gri}* with its pale gray-white seedcoat or the alleles for cartridge buff seedcoat, *c^{cr}* or *c^w*). Snap bean pods are harvested before the seeds are mature, and the seedcoat pigments of genotypes with pale colors at maturity are not yet

apparent. Thus, the immature seedcoats are effectively colorless at harvest maturity.

The conversion from *p* to alternative single genes is not a difficult breeding task for any single stock, but it is laborious to convert an entire program. More research is needed to determine whether the alternative recessive genes for colorless immature seeds confer less deleterious secondary effects than *p*.

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