

Inheritance of Yellow Corona and Hilum Ring in Seedcoats of Mayocoba Market Class Common Beans with Genotype $P [C r] gy J g b v^{lae} Rk$

Mark J. Bassett¹

Horticultural Sciences Department, University of Florida, Gainesville, FL 32611

ADDITIONAL INDEX WORDS. *Phaseolus vulgaris*, seedcoat genetics, Mayocoba dry beans

ABSTRACT. The inheritance of corona and hilum ring color of common bean (*Phaseolus vulgaris* L.) was investigated in the reciprocal cross ‘Wagenaar’ (a Canario market class dry bean) × ‘Mayocoba’ (Mayocoba market class dry bean), where both parents were known to have seedcoat color genotype $P [C r] gy J g b v^{lae} Rk$. ‘Wagenaar’ has greenish yellow (GY) seedcoat (due to gy) except for purple (dark) corona (due to v^{lae}) and reddish brown hilum ring (due to J), whereas ‘Mayocoba’ has an entirely GY seedcoat. Seeds produced on the F_1 progeny plants had GY corona and reddish brown hilum ring. The F_2 segregated for three phenotypic classes, the two parental classes and the F_1 class, but the segregation did not fit a 1:2:1 segregation ratio due to disturbed segregation. F_3 progeny tests of 35 randomly selected F_2 parents demonstrated that the two parental classes were true breeding and the F_1 class segregated again (as in the F_2) for the same three phenotypic classes. In spite of variable expressivity of GY color and disturbed segregation, the data support a single gene hypothesis, for which the tentative symbol *Chr* is proposed. *Chr* is dominant for changing purple corona to GY, but recessive for changing reddish brown hilum ring to GY. Thus, only one gene, *Chr*, controls the difference in seedcoat color between the market classes Canario and Mayocoba. An allelism test between *Chr* and *Z* (hilum ring color factor) is needed before a formal proposal for *Chr* can be made.

Prakken (1970) summarized the genetics of seedcoat colors in common bean (*Phaseolus vulgaris* L.) other than red colors, and he reconciled the various systems of gene symbols used by various researchers. 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. One of the colors in the first table is pale greenish yellow (canary), which was also called schamois by Lamprecht (1932). Thus, two distinct seedcoat colors were attributed to only one genotype. Bassett et al. (2002) discovered a new gene (Gy) producing greenish yellow seedcoat color and established that [pale] greenish yellow seedcoats have genotype $P [C r] gy J g b v^{lae} Rk$, whereas the genotype of schamois (same as schamois) is $P [C r] Gy J g b v^{lae} Rk$.

Schamois color seeds also have reddish brown hilum ring (Fig. 1), which is controlled (expressed) by J (Prakken, 1970). Color illustrations of greenish yellow seedcoats (market class Azufrado Peruano) and schamois seedcoat color (market class Jalinho) were provided by Voysest (2000, p. 181-182).

Nine genes control seedcoat color in common bean, and very complicated epistatic interactions occur among those genes (Bassett et al., 2002; Prakken, 1972). For this paper, only a brief introduction to the genetics of seedcoat color is needed. The two cultivars tested in this paper both carried the dominant (wild type) allele at the P , C , J , and Rk loci, and those dominant alleles do not alter the color. Similarly, the two cultivars tested both carried the recessive r allele at the R locus for dominant red color, which is closely linked to C . The genes G , B , and V are color modifying genes: G (from *Gelbe*, a German word) for yellow with $G b v$, B for mineral brown with $G B v$ and grayish brown with $g B v$, and V for black (anthocyanin pigments) with $G B V$ (and $g B$

V) and dark brown purple with $G b V$. With $g b v$, the seedcoat is nearly colorless, shamois or cream color. Gy is also a color modifying gene that with $g b v$ changes shamois (Gy) to greenish yellow (gy), and the Gy locus is closely linked to C (Bassett et al., 2002; McClean et al., 2002). The dark corona colors of v^{lae} and the brown to black hilum ring of J are both epistatic to gy/gy (Bassett et al., 2002).

The cultivars of the Mayocoba and Canario market classes all have pink flowers with genotype v^{lae} , which is known to have the pleiotropic effect of producing dark corona colors (Bassett, 1995; Voysest, 2000). The color of the corona is almost black with $G B v^{lae}$, but dark gray to dark purple with $G b v^{lae}$ and $g b v^{lae}$. The Mayocoba market class seeds have genotype $P [C r] gy J g b v^{lae}$

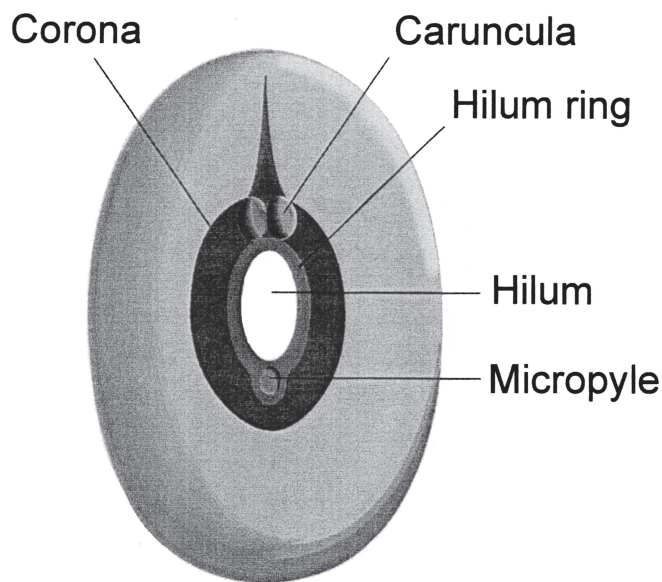


Fig. 1. Ventral view of a common bean seed illustrating the dark (black or dark purple) corona region of the seedcoat expressed by the gene v^{lae} . The hilum ring structure (a physical ridge) is located just inside the corona.

Received for publication 9 Dec. 2002 Accepted for publication 29 May 2003. This research was supported by the Florida Agricultural Experiment Station and a T-STAR grant, and approved for publication as journal series R-09078. ¹Professor.

Rk, and (when grown under ideally cool conditions) have greenish yellow color extending over the entire seedcoat, including the corona and hilum ring (Fig. 1). The failure to express dark corona color (due to v^{lae}) and reddish brown hilum ring (due to *J*) is in apparent violation of known genetic rules for seedcoat color. This paper investigates the hypothesis that a single gene (tentative gene symbol *Chr*) controls the expression of the greenish yellow corona and hilum ring of Mayocoba cultivars in the presence of v^{lae} .

Materials and Methods

Seeds of 'Wagenaar' were obtained from H. Dijkstra, Collection Manager, Centre for Genetic Resources, Wageningen, The Netherlands. The seedcoat genotype of 'Wagenaar' is $P [C r] gy J g b v^{lae} Rk$ and has greenish yellow seedcoat except for purple corona and reddish brown hilum ring (Bassett et al., 2002). Seeds of the Mayocoba market class (presumed to be the 'Mayocoba' cultivar) were obtained from the Los Angeles market by a source that cannot be disclosed due to contractual agreement (condition of employment as an expert witness). The seedcoat genotype for the 'Mayocoba' cultivar is the same (for all known seedcoat color genes) as that of 'Wagenaar' given above; but the greenish yellow seedcoat color covers the entire seedcoat of 'Mayocoba', including corona and hilum ring, whereas 'Wagenaar' has dark corona and reddish brown hilum ring (Bassett et al., 2002). Therefore, there must be one or more unknown genes controlling this difference in corona and hilum ring color.

In Fall 1999, reciprocal crosses were made between 'Wagenaar' and 'Mayocoba', and the F_1 generation was grown in the greenhouse in Winter 2001. Data were recorded for the seedcoat color of the F_2 seed, especially in the corona and hilum ring. Reciprocal F_2 progenies were grown in the field in Spring 2001, and data were recorded for seedcoat color of seeds sampled from each F_2 plant. From the cross 'Wagenaar' x 'Mayocoba', 35 randomly selected F_2 plants were progeny tested in the field in Spring 2002. Thirty seeds per plot were planted for F_2 parents with greenish yellow corona and hilum ring, and 50 seeds per plot were planted for the other two classes of F_2 parents: 1) those with dark corona and reddish brown hilum ring or 2) yellow corona and reddish brown hilum ring. Data were recorded for seedcoat color of seeds sampled from each F_3 plant.

Results and Discussion

The seedcoats of the F_2 seeds produced on the reciprocal F_1 progeny from the cross 'Wagenaar' x 'Mayocoba' had the same color: greenish yellow (GY) over the entire seedcoat except for reddish brown hilum ring (data not shown). The GY color in the corona region shows some variable expressivity, but is more stable in the corona compared with the remainder of the seedcoat.

The F_2 of the reciprocal crosses segregated into three phenotypic classes (Table 1). The genetic hypothesis is that the observed segregation is controlled at a single locus with the expected ratio of 1:2:1 for the three classes listed in Table 1. For the cross 'Wagenaar' x 'Mayocoba', the chi-square value is large, but not quite large enough to reach statistical significance, whereas for the reciprocal cross, the chi-square was large enough to indicate a significant disturbance in segregation at the hypothetical single gene controlling the three classes. When the reciprocal cross data were combined, the chi-square value for

the 1:2:1 ratio was greatly reduced, indicating that there was a reciprocal difference in the direction of disturbance of the segregation (Table 1). With respect to the expected frequency values, cross 1 gave a surplus of Mayocoba class phenotypes (yellow corona and hilum ring), and cross 2 gave a shortage of Mayocoba class phenotypes. These results may be due to maternal effects of the parents.

The tentative gene symbol for the gene controlling color in corona and hilum ring is *Chr* (Table 1), where *Chr* signifies *corona* and *hilum ring*. The action of *Chr* is dominant with respect to changing the corona color from dark purple to the GY of $P [C r] gy J g b v^{lae} Rk$, but the same gene acts recessively to change the hilum ring color from reddish brown to GY ("yellow") (Table 1). The segregation for yellow corona vs. dark corona is significantly disturbed in both crosses 1 and 2, but segregation for dark hilum ring vs. yellow hilum ring is normal in both crosses although cross 2 just barely qualifies with $P = 0.053$ (Table 1).

The F_3 progenies from 35 randomly selected F_2 parents from the cross 'Wagenaar' x 'Mayocoba' demonstrated the expected segregation patterns for a trait controlled by a single gene (Table 2). All F_2 parents with yellow corona and hilum ring were true breeding in F_3 progenies. All F_2 parents with dark corona and hilum ring were true breeding in F_3 progenies. Thus, the two parental classes were true breeding.

All F_2 parents with yellow corona and dark hilum ring (the phenotype of the original F_1) had F_3 progenies that segregated into the same three phenotypic classes as the F_2 , but the segregation was significantly disturbed with respect to the expected 1:2:1 ratio (Table 2). The segregation for yellow corona vs. dark corona was normal, but the segregation for yellow hilum ring vs. dark hilum ring was highly significantly disturbed (Table 2).

The distinction between seeds with yellow corona and hilum ring vs. the other two classes is truly Mendelian, but the classification of seeds with yellow corona and dark hilum ring vs. dark corona and hilum ring is difficult because of variable expressivity of the dark (anthocyanin) colors in the corona of the *chr/chr* class (Tables 1 and 2). The variability involves both spatial distribution of dark color in the corona as well as intensity of color expression. Nevertheless, the frequency of the three expected genotypes at the *Chr* locus in the F_2 parents (of the F_3 progeny tests) gave a good fit to a 1:2:1 ratio (Table 2).

In spite of the variable expressivity of dark color in the corona and the apparent disturbed segregation at the *Chr* locus, the F_3 data fit a single gene hypothesis. If a second gene (independent of *Chr*) controlled hilum ring color with v^{lae} , then the two parental classes would not always be true breeding in F_3 tests. Therefore, the gene *Chr* (in the presence of v^{lae}) suppresses expression of dark colors (anthocyanins) in the corona by dominant gene action and reddish brown color in the hilum ring by recessive gene action.

'Wagenaar' is a member of the Canario market class, having GY color and dark corona (Voyses, 2000). Thus, a single gene (*Chr*) controls the seedcoat color distinction between the Mayocoba market class and the Canario market class.

No formal proposal of the gene symbol *Chr* will be made because there is an unresolved question about possible allelism between *Chr* and *Z*. The *Z* locus controls hilum ring (HR) color expression with the genotype $j z$ (Bassett et al., 1999; Prakken, 1970). The Mayocoba class beans all have genotype *J* and could not express a HR color change with *J z*, where *j* is required for *z* expression. However, one might hypothesize a unique and undiscovered allele at *Z*, viz., Z^{chr} , where the superscript stands

Table 1. Segregation for seedcoat color in the hilum ring and corona in the F₂ from the crosses 1) 'Wagenaar' *chr/chr* x 'Mayocoba' *Chr/Chr* and 2) the reciprocal cross in common bean.^z

Cross no.	Yellow ^y corona and hilum ring <i>Chr/Chr</i>	Yellow ^y corona, dark hilum ring ^x <i>Chr/chr</i>	Dark corona ^w and hilum ring ^x <i>chr/chr</i>	χ^2 1:2:1	<i>P</i>
1	93	180	69	4.316	0.12
2	32	85	55	6.174	0.046
1 and 2	125	265	124	0.502	0.78

^zCombining the classes *Chr/Chr* and *Chr/chr*, cross 1 data 273, 69 give $\chi^2(3:1) = 4.246$, $P = 0.039$; cross 2 data 117, 55 give $\chi^2(3:1) = 4.465$, $P = 0.035$; and crosses 1 and 2 (combined) data 390, 124 give $\chi^2(3:1) = 0.210$, $P = 0.65$. Combining the classes *Chr/chr* and *chr/chr*, cross 1 data 249, 93 give $\chi^2(3:1) = 0.877$, $P = 0.35$; cross 2 data 140, 32 give $\chi^2(3:1) = 3.752$, $P = 0.053$; crosses 1 and 2 (combined) data 389, 125 give $\chi^2(3:1) = 0.127$, $P = 0.72$.

^yYellow = greenish yellow color controlled by *gy*.

^xDark hilum ring color is reddish brown.

^wDark corona color ranges from black to pale gray to purple and often is not expressed in the entire corona.

Table 2. Segregation for seedcoat color in the hilum ring and corona in F₃ progenies of randomly selected F₂ parents from the cross 'Wagenaar' *chr/chr* x 'Mayocoba' *Chr/Chr* in common bean.^z

Genotype of F ₂ parent ^y	No. of F ₃ progenies ^x	Yellow ^w corona and hilum ring <i>Chr/Chr</i>	Yellow ^w corona, dark hilum ring ^v <i>Chr/chr</i>	Dark corona ^u and hilum ring ^v <i>chr/chr</i>	χ^2 1:2:1	<i>P</i>
<i>Chr/Chr</i>	10	254				
<i>Chr/chr</i>	17	254	316	201	32.35	<0.001
<i>chr/chr</i>	8			317		

^zCombining the *Chr/Chr* and *Chr/chr* classes, for the data 570, 201 the $\chi^2(3:1) = 0.471$, $P = 0.49$. Similarly, combining the *Chr/chr* and *chr/chr* classes, for the data 517, 254 the $\chi^2(3:1) = 25.95$, $P < 0.001$.

^yThe phenotypes of the F₂ parents correspond exactly to those of the F₃ classes with the same genotypes.

^xFor the data 8, 17, 10 the $\chi^2(1:2:1) = 0.057$, $P = 0.88$.

^wYellow = greenish yellow color controlled by *gy*.

^vDark hilum ring is reddish brown.

^uDark corona color ranges from black to pale gray to purple and often is not expressed in the entire corona.

for *corona* and *hilum ring* color. *Z^{chr}* is dominant to *Z* and can express GY corona color (with *gy J*) by dominant epistatic gene action with respect to *J*. With *gy J*, *Z^{chr}* acts like a recessive gene for GY color expression in the HR.

Currently, the laboratory of P.E. McClean (North Dakota State Univ., Fargo) is developing a molecular marker for the putative *Chr* locus (McClean, personal communication). McClean was not able to find polymorphism between 'Wagenaar' and 'Enola' using either the STS (sequence tagged site) or RAPD (random amplified polymorphic DNA) markers for the *Z* locus (McClean, personal communication). Once a RAPD marker for the putative *Chr* locus is developed, converted to an STS marker, and mapped in the BAT x Jalo mapping system, one can ask the question whether the marker is independent of the already mapped *Z* locus (McClean et al., 2002).

Testing for allelism between *Z* and *Chr* by the classical genetic test cross approach is quite difficult because of the complexity of the genetic interaction involved with *z* and *gy* expression. Only stocks recessive at *T* or *J* (or both) will express *z* in seedcoats, and *gy* expresses most reliably with the shamois genotype *g b v* (or *v^{lae}*). Thus, finding or constructing parental lines for the test cross is difficult, and analysis of the data for F₁ and F₂ generations will be challenging. Thus, a molecular genetic approach to the allelism test is preferable.

Literature Cited

- Bassett, M.J. 1995. The dark corona character in seedcoats of common bean cosegregates with the pink flower allele *v^{lae}*. J. Amer. Soc. Hort. Sci. 120:520-522.
- Bassett, M.J., C. Shearon, and P. McClean. 1999. Allelism found between two common bean genes, hilum ring color (*D*) and partly colored seedcoat pattern (*Z*), formerly assumed to be independent. J. Amer. Soc. Hort. Sci. 124:649-653.
- Bassett, M.J., R. Lee, C. Otto, and P.E. McClean. 2002. Classical and molecular genetic studies of the strong greenish yellow seedcoat color in 'Wagenaar' and 'Enola' common bean. J. Amer. Soc. Hort. Sci. 127: 50-55.
- Lamprecht, H. 1932. Beiträge zur Genetik von *Phaseolus vulgaris*. Zur Vererbung der Testafarbe. Hereditas 16:169-211.
- McClean, P.E., R.K. Lee, C. Otto, P. Gepts, and M.J. Bassett. 2002. Molecular and phenotypic mapping of genes controlling seedcoat pattern and color in common bean. J. Hered. 93:148-152.
- Prakken, R. 1970. Inheritance of colour in *Phaseolus vulgaris* L. II. A critical review. Meded. Landbouwhogeschool Wageningen 70-23:1-38.
- Prakken, R. 1972. Inheritance of colours in *Phaseolus vulgaris* L. III. On genes for red seedcoat colour and a general synthesis. Meded. Landbouwhogeschool Wageningen 72-29:1-82.
- Voysest, O.V. 2000. Mejoramiento Genético del Frijol (*Phaseolus vulgaris* L.). Legado de Variedades de América Latina 1930-1999. Centro Internacional de Agricultura Tropical, Cali, Colombia. Publicación CIAT No. 321.