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

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**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 $P\{C\, r\} g y\, J\, g\, b\, v^{lae}\, Rk$. ‘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 $Rk$), whereas ‘Mayocoba’ has an entirely GY seedcoat. Seeds produced on the F₁ progeny plants had GY corona and reddish brown hilum ring. The F₂ segregated for three phenotypic classes, the two parental classes and the F₁ class, but the segregation did not fit a 1:2:1 segregation ratio due to disturbed segregation. F₂ progeny tests of 35 randomly selected F₂ parents demonstrated that the two parental classes were true breeding and the F₁ class segregated again (as in the F₂) 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 $P\{C\, r\} g y\, J\, g\, b\, v^{lae}\, Rk$, whereas the genotype of shamois (same as schamois) is $P\{C\, r\} g y\, J\, g\, b\, v^{lae}\, Rk$.

Shamois 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 shamois 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 $g\, b\, V$) and dark brown purple 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 $P\{C\, r\} g y\, J\, g\, b\, v^{lae}$.

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and 'Mayocoba' in corona and hilum ring color. Therefore, there must be one or more unknown genes controlling this difference in 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 F1 generation was grown in the greenhouse in Winter 2001. Data were recorded for the seedcoat color of the F1 seed, especially in the corona and hilum ring. Reciprocal F2 progenies were grown in the field in Spring 2001, and data were recorded for seedcoat color of seeds sampled from each F2 plant. From the cross 'Wagenaar' × 'Mayocoba', 35 randomly selected F2 plants were progeny tested in the field in Spring 2002. Thirty seeds per plot were planted for F2 parents with greenish yellow corona and hilum ring, and 50 seeds per plot were planted for the other two classes of F2 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 F2 plant.

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\_cr 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 'Mayacoba' 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 'Mayacoba', 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.

Results and Discussion

The seedcoats of the F1 seeds produced on the reciprocal F1 progeny from the cross 'Wagenaar' × '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 F2 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 genotype P [C r] gy J g b v\_cr Rk, but has greenish yellow seedcoat except for reddish brown hilum ring (Bassett et al., 2002). Seeds of the Mayocoba market class (presumed to be the 'Mayacoba' cultivar) demonstrated the expected segregation patterns for a trait controlled by a single gene (Table 2). All F2 parents with yellow corona and hilum ring were true breeding in F2 progenies. All F2 parents with dark corona and hilum ring were true breeding in F2 progenies. Thus, the two parental classes were true breeding.

All F2 parents with yellow corona and dark hilum ring (the phenotype of the original F1) had F2 progenies that segregated into the same three genotypic classes as the F2, 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 chr1chr 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 F2 parents (of the F2 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 F2 data fit a single gene hypothesis. If a second gene (independent of Chr) controlled hilum ring color with v\_cr, then the two parental classes would not always be true breeding in F2 tests. Therefore, the gene Chr (in the presence of v\_cr) 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 (Voysey, 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^br, 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.

<table>
<thead>
<tr>
<th>Cross no.</th>
<th>Yellow* corona and hilum ring Chr/Chr</th>
<th>Yellow* corona and hilum ring Chr/chr</th>
<th>Dark corona* and hilum ring Chr/chr</th>
<th>χ²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>93</td>
<td>180</td>
<td>69</td>
<td>4.316</td>
<td>0.12</td>
</tr>
<tr>
<td>2</td>
<td>32</td>
<td>85</td>
<td>55</td>
<td>16.74</td>
<td>0.046</td>
</tr>
<tr>
<td>1 and 2</td>
<td>125</td>
<td>265</td>
<td>124</td>
<td>0.502</td>
<td>0.78</td>
</tr>
</tbody>
</table>

*Combining the classes Chr/Chr and Chr/chr, cross 1 data 273, 69 give χ²(3:1) = 4.246, P = 0.039; cross 2 data 117, 55 give χ²(3:1) = 4.465, P = 0.035; and crosses 1 and 2 (combined) data 390, 124 give χ²(3:1) = 0.210, P = 0.65. Combining the classes Chr/chr and chr/chr, cross 1 data 249, 93 give χ²(3:1) = 0.877, P = 0.35; cross 2 data 140, 32 give χ²(3:1) = 3.752, P = 0.053; crosses 1 and 2 (combined) data 389, 125 give χ²(3:1) = 0.127, P = 0.72.

†Yellow = greenish yellow color controlled by gy.

‡Dark hilum ring color is reddish brown.

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

<table>
<thead>
<tr>
<th>Genotype of F₂ parent*</th>
<th>No. of F₂ progenies†</th>
<th>Yellow* corona and hilum ring Chr/Chr</th>
<th>Yellow* corona and hilum ring Chr/chr</th>
<th>Dark corona* and hilum ring Chr/chr</th>
<th>χ²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chr/Chr</td>
<td>10</td>
<td>254</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chr/chr</td>
<td>17</td>
<td>254</td>
<td>316</td>
<td>201</td>
<td>32.35</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>chr/chr</td>
<td>8</td>
<td></td>
<td>317</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Combining the Chr/Chr and Chr/chr classes, for the data 570, 201 the χ²(3:1) = 0.471, P = 0.49. Similarly, combining the Chr/chr and chr/chr classes, for the data 517, 254 the χ²(3:1) = 25.95, P < 0.001.

†The phenotypes of the F₂ parents correspond exactly to those of the F₂ classes with the same genotypes.

‡For the data 8, 17, 10 the χ²(1:2:1) = 0.057, P = 0.88.

§Yellow = greenish yellow color controlled by gy.

‖Dark hilum ring is reddish brown.

for corona and hilum ring color, Zchr is dominant to Z and can express GY corona color (with gy) by dominant epistatic gene action with respect to J. With gy J, Zchr 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 b v (or v b). Thus, finding or constructing parental lines for the test cross is difficult, and analysis of the data for F₂ and F₃ generations will be challenging. Thus, a molecular genetic approach to the allelism test is preferable.

Literature Cited


