Flower Colors in Common Bean Produced by Interactions of the *Sal* and *V* Loci and a Gametophyte Factor *Ga* Linked to *Sal*

Mark J. Bassett¹, Xue Lin-Bao², and L. Curtis Hannah¹

Vegetable Crops Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL 32611

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Abstract. Inheritance of red flower color was investigated in crosses using Lamprecht's lines M0169 and M0056, which are derived from *Phaseolus coccineus* L., and Univ. of Florida *P. vulgaris* L. breeding line 5-593. Based on segregation in the F₂ populations from 5-593 x M0169 and 5-593 x M0056, we hypothesize that the genotypes for flower colors are *sal/sal V/V* for 5-593 and *Sal/Sal v/v* for M0169 and M0056. The backcross 5-593 x F₁ (5-593 x M0056) segregated for four flower colors in about equal frequencies, and F₂, F₃, and F₄ progeny tests of the backcross plants provided confirmation of all the genotypes in the digenic model. The two recombinant true-breeding colors/genotypes were white (*sal/sal v/v*) and china rose (*Sal/Sal V/V*). We hypothesize that the large deficiency of plants carrying the *Sal* allele in segregating populations is due to a gametophyte factor linked to *Sal*. We propose the gene symbol *Ga* for the gametophyte factor locus, which achieves complete selection for pollen carrying *Ga* on female plants carrying *Ga*, i.e., no pollen carrying *ga* achieves fertilization. The linkage between *Ga* and the marker locus *Sal* is 17 CM (centiMorgan).

The genetics of red flower colors in *Phaseolus vulgaris* is incomplete. Tjebbes (1925) reported a red flower locus with a series of alleles in *P. coccineus*: *Ad* dominant to *Au* and both dominant to *a*. The red hues controlled by *Ad* and *Au* are very close, and *a* gives white flowers. *AdAd* is self-sterile and *AuAu* is partially sterile. Lamprecht (1948a) reported the existence of four dominant genes in *P. coccineus* that control various red hues in flowers, i.e., *Am*, *Sal*, *Beg*, and *No*. He demonstrated that the latter three genes (in the presence of *P*, *T*, *v*) each produce a different red hue independently of each other, whereas *Am* has expression only in the presence of *Sal*. However, neither Lamprecht nor any other researcher has published data showing joint segregation of gene combinations, such as *Sal Beg* or *Sal No*; hence, the possibility that *Beg* and *No* are really alleles at the *Sal* locus has not been ruled out. The gene combination *Sal Am* produces scarlet red. The colors produced by all other combinations of the dominant genes from *P. coccineus* remain speculative or uninvestigated. The interactions of *V* with the four red color genes also remain largely uninvestigated. Closing these voids in the genetics of flower color will be difficult in experiments where two or more genes segregate simultaneously. In such segregating populations, many of the progeny genotypes will have hues that are too close to classify without excessive errors (M.J.B., unpublished data). Ibrahim and Coyne (1975) crossed several *P. coccineus* plant introduction lines with several cultivars of *P. vulgaris* and obtained an F₂ segregation ratio of 3:1 for scarlet : white flowers when *P. vulgaris* was used as female. In reciprocal crosses with *P. coccirreus* as female, only geranium pink and white flowers were observed in the F₂ progeny.

This paper presents results on the interaction of the *Sal* and *V* loci and proposes genotypes for the various colors observed.

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¹Professor.

²Visiting Student, Peoples Republic of China.

Materials and Methods

The flower color names and numeric designations we used are taken from the *Horticultural Colour Charts* (Royal Horticultural Society, 1938). Lines M0169 and M0056 from Lamprecht's collection, now available as plant introduction lines 527711 through 527878 at Pullman, Wash., were selected as sources of the gene *Sal* for salmon red flower color. Lamprecht's (1948a) cross V0214 x M0056 was reported to exhibit certation (competitive advantage of one pollen genotype over another, resulting in unequal chances of fertilization) in the segregation of *Sal* and *sal*. Line M0169 had flower color nearly identical to M0056. The wing petal color of M0169 is carmine-rose 621/0 and that of M0056 is camellia-rose 622/1. Line 5-593 is a bush breeding line with black seeds, and the wing petals are bishops-violet 34/2 (genotype VV).

The crosses 5-593 x M0169 and 5-593 x M0056 were made in 1987. Flower color was recorded in the F₁ and F₂ populations. Selected F₂ plants with white flowers were progeny-tested in the field in 1988. The backcross test 5-593 x F₁ (5-593 x M0056) was made in 1988. Most of the BC₁-F₁ plants were progeny-tested in the field, but one remaining class was progeny-tested in the greenhouse. In 1989, selected plants from the greenhouse BC₁-F₂ were progeny-tested in F₃ and, in some cases, in F₄. These tests included plants with camellia-rose, magenta-rose, and mallow-purple flower colors.

Results and Discussion

The wing petals of F₁ 5-593 (violet) x M0169 (red) were china-rose 024/1 and those of F₁ 5-593 x M0056 were magenta-rose 027/2. The F₂ (both crosses) were classified for three flower color classes: "red", violet, and white (Table 1). The "red" class was a composite of several close red hues that could not be clearly distinguished. The violet class included two close colors.

Our hypothesis is that *Sal* is epistatic (dominant epistasis) to the *V* locus, and, in the presence of *Sal*, one of several red colors will be produced, depending on the genotype at *V* and whether the dominant allele at *Sal* is homozygous or not (Table

Table 1. Genetic hypothesis for the interaction of *Sal* and *V* in F_2 populations derived from the cross 5-593 x M0056 and the flower colors corresponding to each genotype.

Genotype	Wing petal color ^a
<i>Sal/Sal V/V</i>	China-rose 024/1
<i>Sal/Sal V/v</i>	Magenta-rose ^y 027/2
<i>Sal/sal v/v</i>	Camellia-rose 622/1
<i>Sal/sal V/V</i>	Mallow-purple 630/0
<i>Sal/sal V/v</i>	Magenta-rose ^y 027/2
<i>Sal/sal v/v</i>	Camellia-rose 622/1
<i>sal/sal V/V</i>	Bishops-violet 34/2
<i>sal/sal V/v</i>	Cobalt-violet 634/1
<i>sal/sal v/v</i>	White

^aColor names and numeric designation for hue and chroma are taken from The "Royal Horticultural Society (1938).

^yA range of hues was observed for these two genotypes varying from magenta 27/2 to hues redder than magenta-rose 027/2, but no reliable classification could be made within this range.

Table 2. Segregation for flower color (wing petals only) in F_2 populations from two crosses between violet flowers (5-593) and red flowers (M0169 and M0056).

Cross	Flower color classes			χ^2 12:3:1	<i>P</i>
	Red	Violet	White		
5-593 x M0169	249	95	13	16.96	<0.001
5-593 x M0056	188	70	25	11.20	0.004
Combined data	437	165	38	20.83	<0.001

1). In the absence of a dominant allele at *Sal*, the flowers will either be bishops-violet for *V/V*, cobalt-violet for *V/v*, or white for *v/v* (Table 1). The F_2 data were tested for goodness of fit to a 12:3:1 ratio for red : violet : white flower color (Table 2). The data clearly do not fit this ratio for either cross, but the failure could be due to the certation effect reported by Lamprecht (1948a) in his crosses with M0056. There is a shortage of-red plants and a surplus of violet plants, both effects possibly resulting from certation. Using the maximum likelihood method of Allard (1956), tests for linkage between *Sal* and *V* gave an estimate of 34.7 ± 9.02 CM (centiMorgan) for the F_2 from 5-593 x M0169 and 50.9 ± 8.83 CM for the F_2 from 5-593 x M0056. We cannot explain the apparent linkage disturbance in the first cross, but we doubt that any significant linkage exists because of the complete absence of linkage disturbance in the second cross; i.e., the result is not repeatable for the same genotypes in a different cross.

Our hypothesis to explain the certation effect is that the *Sal* locus is linked to another locus controlling microgametophytic function. Disturbed ratios of this type have been reported in maize and shown to be the result of a gametophyte factor linked to the marker gene, e.g., the linkage (25 cM) of the *sugary* locus with a gametophyte factor (Emerson, 1934) and the linkage (12 cM) of the *brittle* locus with another gametophyte factor (Burnham, 1936; Longley, 1961). We developed a model that fits the F_2 data for 5-593 x M0056 very well (Table 3). This model assigns the following gametic frequencies to the pollen: 0.15 for *Sal V*, 0.15 for *Sal v*, 0.35 for *sal V*, and 0.35 for *sal v*. The same four gametes in the egg have equal frequencies, 0.25, assuming normal Mendelian segregation. When the same model is applied to the F_2 data for 5-593 x M0169, the fit is very poor (Table 3). Most of the deviation from expected in the latter case is due to a large deficiency of white flower segregants; a deficiency in the double recessive class sometimes oc-

Table 3. A gametophyte effect model to explain certation at the *Sal* locus, assuming gamete frequencies in the pollen of 0.15 for *Sal* and 0.35 for *sal*.

Cross	Type of data	Flower color classes			Total χ^2	<i>P</i>
		Red	Violet	White		
5-593 x M0056	Observed	188	70	25	0.339	0.84
	Expected	183.95	74.29	24.76		
	χ^2	0.089	0.247	0.002		

Table 4. Segregation for flower color in the F_1 of the backcross 5-593 X F_1 (5-593 X M0056).^a

Hypothesized genotypes	Flower color classes	No. plants		χ^2 value	<i>P</i>
		Observed	Expected		
<i>Sal/sal V/V</i>	Mallow-purple 630/0	14	15	0.067	
<i>Sal/sal V/v</i>	Magenta-rose 027/2	11	15	1.067	
<i>sal/sal V/V</i>	Bishops-violet 34/2	14	15	0.067	
<i>sal/sal V/v</i>	Cobalt-violet 634/1	21	15	2.400	
Total		60	60	3.6	0.31

^aThe hypothesized parental genotypes are *sal/sal V/V* for 5-593 and *Sal/Sal v/v* for M0056.

curs in digenic segregations. Clearly, the certation effect reported by Lamprecht (1948a) for his cross with M0056 has been confirmed by the data involving the cross 5-593 x M0056.

We continued the investigation by making the backcross 5-593 x F_1 (5-593 x M0056). The hypothetical genotypes for the parents are *sal/sal V/V* for 5-593 and *Sal/Sal v/v* for M0056. If the model is correct, the BC- F_1 should segregate for four flower color classes. The observed segregation gave an acceptable fit with the theoretical expectations (Table 4). If the sum of the red flower classes is compared to the sum of the violet flower classes, a surplus of violet flowers is observed, i.e., 25 red vs. 35 violet. This deviation from a 1:1 expected ratio of red : violet is not significant ($\chi^2 = 1.667$, $P = 0.20$). For the BC- F_1 , 120 seeds were planted. Due to the effects of segregation for genes causing crippling and lethality (possibly *D1-1*, *D1-2* or *cr-1*, *cr-2*), =30 seedling lethals and 30 crippled seedlings were observed (Coyne, 1965; Finke et al., 1986; Shii et al., 1980). In summary, half of the population never flowered and could not be classified.

The 14 bishops-violet plants (Table 4) were progeny-tested, and all, totaling 607 BC- F_2 plants, bred true for bishops-violet flower color (data not shown). These results support the hypothesized genotype *sal/sal V/V*. The 21 cobalt-violet plants (Table 4) were also progeny-tested, and the progeny in all plots segregated for three flower color classes (Table 5). The data are consistent with a 1:2:1 ratio for the three color classes, and the hypothesis that cobalt-violet has the genotype *sal/sal V/v* is supported. Eleven of the 14 mallow-purple plants (Table 4) were progeny-tested, and the progeny in all plots segregated for three color classes (Table 5). Clearly, the data do not fit a 1:2:1 ratio for the three color classes, and the deviation is the result of a large deficiency of china-rose segregants. The certation effect that makes the *Sal* allele have a transmission disadvantage with respect to the *sal* allele is clearly confirmed. The data also

Table 5. Combined BC-F₂ segregation data from 21 BC-F₁ plants with cobalt-violet flower color and 11 BC-F₁ plants with mallow-purple flower color, and 11 BC-F₁ plants with magenta-rose flower color from the backcross 5-593 x F₁ (5-593 x M0056).

Parental BC-F ₁ flower color	BC-F ₂ flower color classes	Hypothesized genotype ^a	No. plants		χ^2 ratio	χ^2 value	<i>P</i>
			Observed	Expected			
Cobalt-violet	Bishops-violet	<i>sal/sal V/V</i>	244	244	1:2:1	0.000	<0.37
	Cobalt-violet	<i>sal/sal V/v</i>	470	488		0.664	
	White	<i>sal/sal v/v</i>	262	244		1.328	
	Total		976			1.992	
Mallow-purple	China-rose	<i>Sal/Sal V/V</i>	99	179.25	1:2:1	35.928	<0.001
	Mallow-purple	<i>Sal/sal V/V</i>	375	358.50		0.759	
	Bishops-violet	<i>sal/sal V/V</i>	243	179.25		22.673	
	Total		717			59.359	
Magenta-rose	Camellia-rose	<i>Sal/- v/v</i>	80	93.75	3:9:1:2:1	2.017	<0.001
	Red ^a	<i>Sal/- V/-</i>	226	281.25		10.854	
	Bishops-violet	<i>sal/sal V/V</i>	42	31.25		3.698	
	Cobalt-violet	<i>sal/sal V/v</i>	90	62.50		12.100	
	White	<i>sal/sal v/v</i>	62	31.25		30.258	
	Total		500			58.926	

^aThe magenta-rose, china-rose, and mallow-purple classes were combined because a few plants were difficult to classify without ambiguity.

support the hypothesized genotype *Sal/sal V/V* for mallow-purple.

The segregation data from the BC₁-F₂ from the 11 mallow-purple BC₁-F₁ plants were also analyzed as 11 separate progenies, combining the china-rose and mallow-purple classes into a red class and testing for goodness of fit to a 3:1 ratio of red vs. bishops-violet flowers. Four of the progenies had *P* values <0.05 due to a shortage of "red" plants and an excess of bishops-violet. The distribution of proportions of the 11 progenies that were bishops-violet ranged from 0.27 to 0.45. Therefore, the entire distribution was skewed above the expected proportion of 0.25 (for a 3:1 ratio).

The 11 BC-F₁ plants with magenta-rose flower color (Table 4) were tested in the greenhouse to allow a more intensive effort to discriminate between similar red hues. These progenies segregated again for all the same color classes observed in the original F₂ from 5-593 x M0056 (Tables 3 and 5). A complete classification without ambiguity of all colors was not possible even with the aid of color charts in a sheltered environment and the opportunity to label all plants and check the color designation repeatedly. For the colors magenta-rose, china-rose, and mallow-purple, a few plants in this range of colors were difficult to classify without ambiguity. These colors were combined in a group designated simply as "red". The classification of the BC-F₂ differed from the classification of the original F₂ by separating out the camellia-rose segregants from the red class and splitting the violet class into its components, bishops-violet and cobalt-violet. Using these five classes and our model (Table 1), the expected frequencies for the five classes are 3:9:1:2:1 (Table 5). The observed data gave a very poor fit to the model, and this failure is due primarily to certation at the salmon locus. This can be demonstrated by comparing the combined data for the two red classes with the combined data for the violet and white classes, which gives $\chi^2(3:1) = 50.789$ and $P < 0.001$. However, if one does a chi-square test separately on the violet and white classes, $\chi^2 = 5.134$ and $P = 0.08$, which is an acceptable fit. The appearance of both camellia-rose and white segregants in all 11 BC-F₂ progenies supports the hypothesis that the genotype of the magenta-rose class in the BC-F₁ is *Sal/sal VV*.

The genetic model predicts four true-breeding genotypes/colors, but, thus far, only one, *sal/sal V/V* for bishops-violet, has been demonstrated. Ten white F₂ segregants, six from 5-593x M0056 and four from 5-593 x M0169, were progeny-tested in F₃, and all plots, totaling 415 plants, were true-breeding for white (data not shown).

The third true-breeding class is china-rose. No china-rose plants were saved from the progeny test of mallow-purple BC-F₁, but new china-rose segregants were derived from a genotype not yet demonstrated, *Sal/Sal V/v*, which was usually designated magenta-rose "china" to distinguish it from the bluer magenta-rose. A greenhouse progeny test (BC-F₃) of a plant of this type gave eight magenta-rose, eight china-rose, and four camellia-rose progeny. The remnant seed tested in the field in plot 9-235 gave six camellia-rose and 46 "red" (magenta and china combined) progeny. The genotype of this plant is confirmed by the absence of any violet or white segregants, while segregating for camellia-rose. Seven of the eight china-rose BC-F₃ plants were progeny-tested in the field, giving a total of 237 plants classified in the seven plots. All plots were true-breeding for china-rose (data not shown). Besides 9-235, six additional progeny tests of BC-F₃ magenta-rose "china" plants were made. The combined data segregated for 47 camellia-rose and 161 "red", giving a good fit to the expected 1:3 ratio ($\chi^2 = 0.641$, $P = 0.42$).

The fourth true-breeding class is camellia-rose. In 1989, 44 BC-F₂ segregants with camellia-rose flower color were progeny-tested in BC-F₃ field plots, involving a total of 1080 plants. Plants in seven plots were true-breeding for camellia-rose and 37 segregated for two classes, plants with either camellia-rose or white flowers. Testing the expected ratio of 1:2 for true-breeding to segregating plots, a poor fit is shown by the large chi-square ($\chi^2 = 6.016$, $P = 0.01$). The data from the segregating plots were combined, and the observed segregation was 571 camellia-rose and 325 white-flowered plants. This proportion gave a poor fit to the expected 3:1 ratio for camellia-rose and white ($\chi^2 = 60.72$, $P < 0.001$). Once again, certation at the salmon locus resulted in a shortage of camellia-rose plants. The question remains whether certation is due to a pleiotropic effect of the *Sal* locus or is produced by a linked locus for a gametophyte effect. For each segregating progeny, the ratio of

Table 6. The frequency distribution for the ratio of white flower segregants to total plants in progeny tests of 37 BC-F₂ camellia-rose plants that segregated in BC-F₃ for camellia-rose and white progeny.

No. BC-F ₃ progenies in each class of ratio (white flower/total)												
Upper class limits												
0.13	0.17	0.21	0.25*	0.29	0.33	0.37	0.41	0.45	0.49	0.53	0.57	
1	2	2	3	2	4	0	8	7	2	5	1	

*The mean ratio expected in the absence of certation.

white-flowered segregants to total plants was calculated. The frequency distribution of these ratios appears to be bimodal (Table 6). The classes ranging from 0.13 to 0.33 appear to be distributed more or less normally about 0.25, the expected mean in the absence of certation. There are 14 progenies in this region of the distribution. There is a break in the distribution at class 0.37. A separate group of 23 progenies are distributed in the range from 0.41 to 0.57, which deviate greatly from the expected 0.25 mean. The most probable explanation of these data is that the latter 23 progenies resulted from the linkage of *Sal* with a gametophyte factor, for which the gene symbol *Ga* is proposed. The 14 progenies distributed around 0.25 resulted from segregation of *Sal* alleles that were freed from the linked gametophyte factor by the crossing-over that occurred in the BC-F₂ parents. Nine of the 11 BC-F₂ progenies derived from magenta-rose parents (Table 6) exhibited (individually) a shortage of *Sal* segregants (data not shown); thus, it must be assumed that these BC-F₂ parents carried the original parental (M0056) linkage arrangement, *ga Sal/Ga sal*, which will be explained below.

A reduction in the transmission rate of *Sal* alleles is demonstrated above, but it is not obvious whether reproduction is blocked before or after fertilization. We favor the hypothesis that the block occurs before fertilization due to a gametophyte factor, because a zygotic lethal effect would lead to consequences not observed. If a zygotic lethal effect were involved, this would lead to missing seeds in the pods at random positions, similar to chromosome translocation heterozygotes (Ashraf and Bassett, 1986). No such missing seeds in pods were observed in the parental plants that produced self-progeny showing certation.

The data in Table 6 can be used to estimate the two parameters involved in generating the non-Mendelian frequency of white-flowered plants. Gametophyte factors have been described in other plant species in which selection occurs during pollination. For example, Emerson (1934) described such a genetic system in maize and provided an exhaustive treatment of resultant data. In his material, pollen containing one allele of a gene termed *Ga* (gametophyte factor) are given a selective advantage over *ga* pollen in the fertilization process if the female plant contains at least one dose of the *Ga* allele. Action of the *Ga* locus is made apparent by non-Mendelian ratios of a linked gene. The data presented here concerning the unexpected ratios observed with *sal* can be explained by such a mechanism. Specifically, we propose that the *sal* allele is linked in repulsion to a gametophyte factor allele, *Ga*. On stiler tissue containing the *Ga* allele, selection occurs for *Ga* pollen. The homologous chromosome in this particular cross, which contains the dominant allele at the pigment gene, *Sal*, is linked in repulsion to the recessive allele at the *Ga* locus, *ga*.

If one assumes that selection for *Ga* is complete (no *ga* pollen achieve fertilization) and that linkage between *Ga* and *sal* is complete (no recombination between these genes), then one would

expect 50% white-flowered plants in the selfed generations presented in Table 6. Values less than 50% would be obtained if 1) recombination occurs between *Ga* and *sal* and/or 2) some *ga* pollen can achieve fertilization. Following the method of Emerson (1934), the data presented in Table 6 allow one to estimate the value of both of these functions.

Emerson (1934) discovered that the genetic analysis of progeny derived by self-pollination of a plant exhibiting altered ratios allows one to estimate the position of the *Ga* factor, as well as the relative strength of selection for *Ga* pollen on females containing the *Ga* allele. The formulas for estimating these functions are presented and explained below.

Although the frequency of progeny exhibiting the mutant phenotype is a function of both recombination and the degree of selection for the *Ga* allele, the frequency of *Ga/ga* heterozygotes within the selfed progeny from a *Ga/ga* heterozygote is independent of selection and is, in fact, equal to 50%. Using the symbols of Emerson (1934), let *p* equal the frequency of *Ga* pollen achieving fertilization and *q* the frequency of *ga* pollen achieving pollination. If *Ga* and *ga* are transmitted at equal frequencies through the female, then the frequency of *Ga/ga* heterozygotes will be $p/2 + q/2$. The first term in this expression represents the situation in which *Ga* is transmitted through the male, whereas the second term describes the frequency of *Ga* transmission through the female. Since *Ga* and *ga* are the only types of pollen achieving fertilization, $p + q$ must equal 1. Substitution of $1 - p$ for *q* leads to the conclusion that the frequency of *Ga/ga* heterozygotes is equal to $1/2$. Intuitively, one comes to the same conclusion if one considers cases where $p = 1$ (complete selection) or $p = 0.5$ (no selection). In the former case, only *Ga* is transmitted through the male and the resulting progeny would be composed of only two genotypes, *Ga/Ga* and *Ga/ga*. These would occur in a 1:1 ratio and the heterozygous class would make up 50% of the total. Similarly, if there is no selection, we would obtain *Ga/Ga*, *Ga/ga*, and *ga/ga* in a 1:2:1 ratio. Again, the heterozygous class would make up 50% of the progeny.

The frequency of *Ga/ga* heterozygotes maintaining the original, or parental, linkage relationship (in this case, *ga Sal/Ga sal*) is solely a function of the rate of recombination between the two genes. Let *x* equal the recombination fraction. If the genes *Ga* and *sal* are 100× map units apart, then the frequency of production of gametes containing the parental arrangement of alleles at these two loci would be $1 - x$. The genotype *ga Sal/Ga sal* can be produced in two ways: the *ga Sal* chromosome can be transmitted through the male parent or through the female parent. Among all the 16 fertilization events possible in the self-pollination of a *ga Sal/Ga sal* heterozygote, the two fertilization events mentioned above would occur with the frequency of $q(1 - x)^2/2 + p(1 - x)^2/2$. Since $q = 1 - p$, the expression simplifies to $(1 - x)^2/2$. Since *Sal/sal* heterozygotes make up 50% of the total progeny, the frequency of *Sal/sal* heterozygotes maintaining the parental linkage relationship with the *ga* locus (i.e., *ga Sal/Ga sal*) would be $(1 - x)^2$. *Sal/sal* heterozygotes maintaining the parental linkage arrangement with the *ga* locus can easily be separated from the nonparental types since the former will produce > 25% white-flowered plants upon self-pollination.

Before one can calculate the linkage from the data in Table 6, it is necessary to remove any data that failed to show certation because the linkage was broken in BC-F₂, rather than BC-F₃. We determined that BC-F₂ parents #4 and #10 had already broken the *Ga-sal* linkage. When the BC-F₃ progeny from these

two parents (five progenies in all) were removed from Table 6, 32 BC-F₂ progenies remained, rather than the original 37. Among these 32, 22 *Sal/sal* heterozygotes had maintained the parental arrangement of the *Ga* and *ga* alleles and 10 showed no evidence of certation. Thus, $22/32 = (1 - x)^2$ and we calculate the value of x to be 0.17, giving an estimate of 17 cM for the map distance between *Sal* and *Ga*. The same ratio is set equal to $(1 - x)^2$, regardless of whether the marker gene and gametophyte loci are linked in repulsion or coupling phase.

Once the map position of the *Ga* locus is identified relative to the marker gene, the intensity of selection conditioned by *Ga* can be calculated from the frequency of one of the genotypic classes within the F₂ population. Of the 16 possible fertilization events resulting from selfing the heterozygote above, four will be *sal/sal*: *Ga sal/Ga sal* plants will occur with the frequency of $p(1 - x)^2/2$, *ga sal/ga sal* plants will occur at the frequency of $x(q/2)$, and *Ga sal/ga sal* plants can occur in two ways with the following frequencies, $(1 - x)p/2$ and $(1 - x)q/2$. Substitution of $1 - p$ for q and combining the above frequencies leads to the equation for the frequency of plants with white flowers, which is equal to $(p - 2px + x)/2$. This formula is appropriate when there is repulsion-phase linkage between the marker and gametophyte loci, as with our data (Table 6). When the linkage is in coupling phase, one must set the ratio equal to $2px + 1 - p - x$.

Among the 22 segregating plants in Table 6 with elevated ratios of white-flowered plants, the average frequency of plants with the recessive phenotype is 43.890. From this and from the estimate of x , we can calculate a value of p equal to 1.07. Since the maximum value for p is 1, we conclude that selection is virtually complete for the *Ga* allele over the *ga* allele. Deviation from the theoretical limit of 1 maybe a reflection of the fairly large variation in the observed value of the percentage of recessive phenotypes, a phenomenon that is common in the maize studies of gametophyte factors.

Lamprecht's line M0056 was derived from a cross between *P. vulgaris* and *P. coccineus* (formerly *multiflorus*), hence the letter M for *multigaris* (Lamprecht's term for interspecific materials). It is well established that genes from *P. coccineus* are lost through negative selection in interspecific germplasm with *P. vulgaris* cytoplasm (Lamprecht, 1935, 1941, 1948b, 1948c; Manshardt and Bassett, 1984; Smartt, 1970; Thomas, 1964). Our paper has elucidated a specific process by which this elimination of a *P. coccineus* allele is achieved. The *Ga* allele in *P. vulgaris* 5-593 is able to block fertilization of pollen carrying the *ga* allele from *P. coccineus* and reduce transmission of genes linked to this locus, e.g., *Sal*.

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