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FLOWER COLOR INHERITANCE IN *SALVIA SPLENDENS*

By

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ABSTRACT

FLOWER COLOR INHERITANCE IN SALVIA SPLENDENS

By

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Eight distinct flower color classes of *Salvia splendens* were intercrossed. The F_1 plants were self-pollinated to produce the F_2 generation and backcrossed to both parents. The F_2 and backcross populations were statistically analyzed and compared. Seven genes were found to control flower color inheritance. The R and L genes control the colors red, R_L_, rose, rrL_, salmon, R_ll, and pink, rrll. The Int gene had no effect on the R and L genes when dominant, but when recessive with dominant R and L, it produces rose color. The P gene controls colored, P_, versus white, pp, flowers. Purple color is produced by the V gene and burgundy color is controlled by the B gene. The E gene dilutes the colors produced by the other loci. The R, L, Int, and P genes exhibit complete dominance while the V, B, and E genes are incompletely dominant. The R, B, and E genes were discovered in this study.

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INTRODUCTION

Salvia splendens F. Sellow ex Roem. & Shult. (1) is a member of the Lamiaceae (Labiatae) or mint family. Originally from the Brazilian tropics, it is a perennial in warm regions but grown as an annual in areas experiencing freezing temperatures. *S. splendens* has racemose inflorescences and deciduous bracts. The calyx is campanulate with the tubular corolla extending 1 to 1½ inches. The lower lip of the corolla is much reduced (1). According to the most recent study, the gametophytic chromosome number is 22 (2). Commonly called Scarlet Sage, scarlet red is the original and most popular color, but once in cultivation, purple and white forms were quickly discovered. Plant breeders have expanded the color range to rose, salmon, pink, bicolors, and various shades of red.

Unlike its herbal relatives, *S. splendens* is a popular ornamental species used primarily as a bedding plant but also as a cut flower. Salvia comprises 5 to 6 % of the bedding plant crop for most growers (9). In 1984 the wholesale value of bedding plants for the top 25 states in the country was over $209 million (16). According to these figures over $10 million is spent annually on salvia alone and its popularity is growing. The objective of this study was to determine the number of genes controlling flower color inheritance in *S. splendens*. Such a determination would be quite valuable to plant breeders wishing to expand the current color range available to the gardening public.

LITERATURE REVIEW

In 1960 Paris, Haney, and Wilson (12) conducted a survey of flower color inheritance studies. They found that Vavilov's (17) theory of homologous variation was quite valid. The gene types most commonly encountered were:

W	produces color; ww produces white
Iv	produces non-ivory; iviv produces ivory
Y	produces non-yellow; yy produces yellow
B	produces purple or magenta; bb produces blue
P	produces purple or magenta; pp produces pinks, roses, or reds
Dil	produces intense color; dil dil produces dilute color

The genes were named for their recessive phenotype and in some species the dominance was reversed or the genes were incompletely dominant in effect. No ivory (Iv), yellow (Y), or blue (B) colors were encountered in this study, but the presence of W, P, and Dil genes was probable.

In 1964 Hendrychova-Tomkova (7) investigated flower color inheritance in *S. splendens*. She found that four genes controlled the parental colors white (*S. splendens* forma *alba*), purple (f. *violacea*), red (f. *rubra*), rose (f. *rosea*), and salmon (f. *carnea*). The pigment, P, gene controlled colored (P_) versus white (pp) flowers. Watts (18) also made reference to this gene for white color in his

1980 text on plant breeding. This gene is analogous to the W gene previously mentioned.

Another common gene is the purple versus nonpurple type, and indeed Hendrychova-Tomkova (7) found a single gene for purple color (V_) versus red color (vv). She noted its incompletely dominant nature but did not quantify the heterozygous (Vv) class separately from the VV purples. Both the purple (V) and white (P) genes were epistatic to the other genes and partly epistatic to each other. A cross of white and purple segregated some ppV_ individuals that she called white but counted separately from the ppvv whites, indicating some color difference due to the V gene. In that cross (and white backcross) disproportionately low numbers of red and ppV_ white recombinants indicated a strong linkage relationship between the P and V genes.

Hendrychova-Tomkova (7) also did a pigment analysis of the parental colors. White contained no anthocyanins, and purple was due primarily to violet and purple derivatives of delphinidin and cyanidin with small amounts of pelargonidin. The red group (red, rose, and salmon) was composed largely of salvianin, a pelargonidin derivative, with small amounts of purple cyanidin. Red, rose, and salmon differed from each other in the concentration and localization of the pigment which was found to be governed by two genes working in complementary fashion. She called these genes Int, intensity, and L, limited localization. Red resulted when the dominant alleles of both loci were present (Int_L_). A weaker concentration of the intense red color produced rose (int int L_). Salmon (Int_ll) was also a dilution of red color, but in this case, the pigment was largely confined to the outer corolla epidermis, the inner epidermis being nearly white. Crosses of red with rose or salmon produced monogenic ratios of 3:1. Rose and salmon crossed together produced red F_1 plants which segregated in a dihybrid ratio of 9 red: 3 rose: 3 salmon: 1 pink with light rose or pink as the double recessive (int int ll). Crosses of purple with rose and salmon segregated two different shades of light violet (V_int int L_ and V_Int_ll) with the expected colors of purple, red, and rose or salmon.

In addition to the above mentioned colors, orange and burgundy colors were also included in this study.

Orange color in many flower species is the result of yellow and red copigmentation (10,6), but the orange in this study is actually closer to a very deep shade of salmon than to the vivid orange color the word implies. This indicated that the orange color may be the result of a diluter gene or multiple allele system of the red color. A diluter gene like the type mentioned by Paris et al. (12) would dilute all colors, such as, in stocks where Schnack et al. (13,14) found the gene P diluted purple to light purple, wine to pale wine, and light red to rose. Similarly, Mehlquist and Geissman (10) working on flower color in carnation found a gene M that altered the sugar portion of the pigment molecule. The result was diluted shades of the colors that carried the dominant allele. Another possibility for orange color was a multiple allele system, such as Müntzing (11) found in _Galeopsis_ where the locus R had four alleles that differentiated red R, light red R_1, faintly red R_2, and white r.

The burgundy color in salvia is a relatively new development. It could even be described as variegated since the body is burgundy colored while the upper lip is scarlet red. Hendrychova-Tomkova (7) found that the red color contains small amounts of cyanidin. Genes that regulate cyanidin to pelargonidin are known. Lawrence, Scott-Moncrieff, and Sturgess (8) found that cyanidin (magenta/rose) versus pelargonidin (pink/salmon) pigment was monogenically controlled in _Streptocarpus_. Very similar results were reported by Mehlquist and Geissman (10) who found a single gene distinguished cyanidin (magenta/crimson) from pelargonidin (rose/scarlet). A magenta colored mutant of _Salvia coccinea_ was found in a red population. D'Cruz and Jadhav (4) made crosses with magenta and concluded it was monogenically inherited. The pigments, however, were not analyzed.

MATERIALS AND METHODS

All the plants used in this investigation were grown at the Plant Science Greenhouses at Michigan State University. Dwarf, early flowering and primarily day-neutral cultivars were used, therefore, no supplemental lighting or black cloth was necessary. The plants were grown under normal conditions recommended for salvia culture. The parent and F_1 plants were grown in 6 or 8 inch pots and fertilized at regular intervals.

Salvia plants have long flower stalks with the individual tubular flowers whorled about the inflorescence. The flowers expand from the bottom of the inflorescence upward, with each flower lasting a single day. The stamens are curved back within the flower bud. By inserting tweezers into the side of the bud, the stamens become wrapped around the tweezer points and can be pulled outward with minimal damage to the style and stigma. Bud emasculations were done daily on flowers to be pollinated the next morning. The pollinated flower usually yielded 2 to 3 seeds with a maximum of 4 possible. A whole spike would be labeled and pollinated repeatedly, until the amount of seed needed was accumulated.

Once fertilization was achieved, the seed grew quickly with seed harvest following 2 to 3 weeks later. It was necessary for the seed to be completely dried before planting, otherwise, germination was severely delayed. Optimally, seed germination requires 12 to 15 days at 21° C. A fungicide drench was applied at the time of planting and again after transplanting. The F_2 generations were grown in flats of 48 plants each, while the backcrosses were grown in either 48 or 32 insert flats. Flowering in the flat occurred approximately 8 weeks after transplanting.

Color evaluations were made using both volumes of the Horticultural Colour Chart, H.C.C. (3). As a British publication the H.C.C. color names do not correspond to the names used in the United States. To avoid confusion, the color class names are those currently used in the horticultural trade and only the H.C.C. number is listed.

Colors were evaluated in the greenhouse on overcast days when the colors were most intense, and light quality was bright but diffuse. This was necessary since some color shades are indistinguishable under bright direct light. All evaluations were made on newly opened flowers. The main body of the flower differs in color intensity from the upper lip, but, in most cases it differed by only one color gradation. The white color class is a pure bright white and therefore does not have an H.C.C. number. The parent lines with their respective color class, seed source, and H.C.C. numbers are listed in Table 1.

Table 1. Salvia Parents Used in This Study

Color Class	Parent	Source	H.C.C. Vol.#	Number Color #
White	Carabiniere White	Pan American	-	----
White	Cleopatra Mix	Royal Sluis	-	----
Pink	F_2 Selection from Pixie	---	1	21/2 *
Rose	Cleopatra Mix	Royal Sluis	2	.20/1
Rose	Carabiniere Cherry	Pan American	2	.20/1
Rose	F_2 Selection from Pixie	---	2	.20/1
Salmon	Cleopatra Mix	Royal Sluis	2	620/1
Salmon	Champagne	Harris	2	620/1
Salmon	F_2 Selection from Pixie	---	2	620/1
Red	Pixie	Harris	1	18/0
Red	Tally Ho	Harris	1	18/0
Red	Cleopatra Mix	Royal Sluis	1	18/0
Orange	Carabiniere Orange	Pan American	2	619/0
Burgundy	Burgundy	Harris	2	824/3
Purple	Cleopatra Mix	Royal Sluis	2	931/2
Purple	Purple Blaze	Sluis & Grut	2	931/2

* The two or three digit number represents the flower color while the number after the slash indicates the degree of intensity.

In order to cross each color class with every other color, it was necessary to self-pollinate the parent lines to determine if they were true-breeding for flower color. All parents proved true except Pixie, which was known to be an F_1 hybrid from rose and salmon parents (5). Therefore, the self seed would segregate as the F_2 generation. A true-breeding plant may carry inhibitor or epistatic genes that hide the effects of other genes. Those other loci may or may not be homozygous. Consequently, F_1 plants were not interpollinated and seed was collected separately from each plant.

In most cases 10 to 20 F_1 plants from each cross were used to evaluate color uniformity. The F_1 plants were self-pollinated for the F_2 generation and backcrossed to each parent. Backcross populations numbered at least 20, while the F_2 generation contained 200 to 300 plants. F_2 and backcross segregations were quantitatively analyzed using the Chi Square statistic. Sometimes it was necessary to combine color classes of an incompletely dominant gene (i.e. BbrrLL and BBrrLL where the B gene is incompletely dominant), when the colors were not significantly different. By comparing segregations, it was possible to develop genotypes for the phenotypes. From there, line drawings were made to demonstrate the interaction of all seven genes for flower color. Calyx color was not evaluated quantitatively, but there seems to be a strong linkage between calyx and flower color genes. As new colors arose in the study, they were matched with the Horticultural Colour Chart and their H.C.C. numbers appear in the line drawings.

RESULTS

Parents of the same color class were crossed together when parents from different sources were available. The intercrossing of whites produced white F_1s and all white F_2 progeny. Likewise, crosses within the color classes salmon, red, and purple also produced self-colored progeny. Only the cross rose (Cleo) X rose (CA Cherry) exhibited complementary genes for the single color phenotype. The F_1 was red and the F_2 segregated 9 red: 7 rose/cherry (Table 4), demonstrating complementary epistasis. The two genotypes for rose color are designated hereafter as rose (R gene) and cherry (Int gene). The colors of the F_1 plants are presented in Table 2.

The genes discovered by Hendrychova-Tomkova (7) retain their original designations. Only the R, E, and B genes are new to this study. The R and E genes are named for the recessive phenotype, while the B gene name represents the dominant phenotype. The practice of naming genes for the biosynthetic pathway they control or effect is a good one, but this aspect was not studied, and therefore, it was necessary to use phenotypic designations. The gene names with their recessive and dominant phenotypes are presented in Table 3. The gene action is also noted.

Table 2. Color of the F_1 Plants

Color	White	Pink	Salmon	Rose	Cherry	Red	Orange	Burgundy	Purple
White	White	Red	Red	Red	Red	Red	Light Red	Red Burgundy	Rose Purple
Pink		Pink	Salmon	Rose	Red	Red	Light Red	Red Burgundy	Rose Purple
Salmon			Salmon	Red	Red	Red	Light Red	Red Burgundy	Rose Purple
Rose				Rose	Red	Red	Light Red	Red Burgundy	Rose Purple
Cherry					Cherry	Red	Light Red	Red Burgundy	Rose Purple
Red						Red	Light Red	Red Burgundy	Rose Purple
Orange							Orange	Lt. Red Burgundy	Lt. Rose Purple
Burgundy								Burgundy	Rose Purple
Purple									Purple

Table 3. Description of the Salvia Flower Color Genes

Gene	Color Source	Phenotype Recessive	Phenotype Dominant	Gene Action
P (Pigment)	White	White	Colored	Complete Dominance
R (Rose)	Rose	Rose with L Pink with l	Red with L	Complete Dominance
L (Limited Localization)	Salmon	Salmon with R Pink with r	Red with R	Complete Dominance
Int (Intense)	Cherry	Rose with R & L	Red with R & L	Complete Dominance
V (Violet)	Purple	Red with R, L & Int	Purple VV Rose Purple Vv	Incomplete Dominance
B (Burgundy)	Burgundy	Red with R, L & Int	Burgundy BB Red Burgundy Bb	Incomplete Dominance
E (Enhance)	Orange	Intense Colors	Dilute Colors	Incomplete Dominance

The R and L genes control the colors red R_L_, rose rrL_, salmon R_ll, and pink rrll (Table 4). Aside from these colors, dominant R and L genes are found in all other parent colors.

The Int gene was discovered from the parent cultivar Carabiniere Cherry. Rose and cherry are the same color but they are designated separately due to different genotypes. The cherry genotype results when recessive int int is combined with dominant R and L genes. A cross of cherry X salmon segregated the color ratio 9 red: 3 cherry: 3 salmon: 1 pink (Table 4). The pink color from cherry X salmon is indistinguishable from the pink color by rose X salmon. Thus, rose and pink colors can be formed in two ways. Rose color is Int_rrL_ or int int R_L_ while pink color is Int_rrll or int int R_ll. Recessive int int with recessive rr produces a shriveled flower stalk. The color is either rose or pink depending upon the status of the L gene. The shriveled condition is characterized by reduced and distorted flower buds which tend to fall off before opening. Those that do open have pollen but fail to set seed when pollinated.

The P gene controls colored (P_) versus white (pp) flowers. Recessive pp is totally epistatic to the R, L, Int, and E genes and partially epistatic to the V and B genes (Table 5). Recessive epistasis with two genes produces a 9:3:4 ratio where 4/16 would be white. White crossed with purple separates the white portion into 1 pure white (vvpp)

Table 4. Segregation Data for the R, L, and Int Genes

Color	Genotype	Ratio	Obs.	Exp.
Cherry X Rose F_2				
Red	R_ Int_	9	129	133.9
Rose/Cherry	rr Int_ & R_ int int	6	94	89.2
Rose Shriveled	rr int int	1	15	14.9
		16	238	238.0
$D^2/e = .438$	$P > .80$			
Rose X Salmon F_2				
Red	R_ L_	9	132	135.6
Rose	rr L_	3	39	45.2
Salmon	R_ ll	3	54	45.2
Pink	rr ll	1	16	15.0
		16	241	241.0
$D^2/e = 2.724$	$P > .30$			
Cherry X Salmon F_2				
Red	L_ Int_	9	135	133.31
Cherry	L_ int int	3	44	44.44
Salmon	ll Int_	3	45	44.44
Pink	ll int int	1	13	14.81
		16	237	237.00
$D^2/e = .253$	$P > .95$			
Pink X Cherry F_2				
Red	R_ L_ Int_	27	44	54
Rose/Cherry	rr L_ Int_ & R_ L_ int int	18	35	36
Salmon	R_ ll Int_	9	27	18
Pink	rr ll Int_ & R_ ll int int	6	15	12
Rose Shriveled	rr L_ int int	3	4	6
Pink Shriveled	rr ll int int	1	3	2
		64	128	128
$D^2/e = 8.294$	$P > .10$			

Table 5. Segregation Data for the P Gene

Color	Genotype	Ratio	Obs.	Exp.
Pink X White F_2				
Red	P_ R_ L_	27	159	144
White	pp -- --	16	77	85
Rose	P_ rr L_	9	43	48
Salmon	P_ R_ ll	9	48	48
Pink	P_ rr ll	3	14	16
		64	341	341
$D^2/e = 3.084$	$P > .50$			
White X Purple F_2				
Rose Purple	P_ Vv	6	113	110.6
Purple	P_ VV	3	62	55.3
Red	P_ vv	3	67	55.3
Purple-White	pp V_	3	42	55.3
White	pp vv	1	11	18.5
		16	295	295.0
$D^2/e = 9.576$	$P > .01$			
White X Burgundy F_2				
Red Burgundy	P_ Bb	6	77	79.0
Red	P_ bb	3	48	39.6
Burgundy	P_ BB	3	37	39.6
Pink-White	pp B_	3	31	39.6
White	pp bb	1	18	13.2
		16	211	211.0
$D^2/e = 5.613$	$P > .20$			

to 3 purple-tinged whites (Vvpp). Likewise, white X burgundy segregated pure whites and pink-tinged whites (Table 5).

The E gene dilutes the color produced by the other genes. The only source of the E gene was the parent color orange which was found to be a dilution of red. Since E is incompletely dominant, there are three shades of every color: intense color ee; light shades Ee; and dilute shades EE (Table 6). For example, rose X orange (Cross # 24) segregated red, light red, and orange, plus rose, light rose, and dilute rose. The E gene also dilutes the purple and burgundy colors, but, since they are incompletely dominant as well, the ratios are greatly expanded. In the case of orange X purple (Cross # 34), the diluted forms of VV and Vv were identical in color so they were combined into a single class called dilute purple. Similarly, diluted BB and Bb were combined into one color class (Cross # 33).

The incompletely dominant V gene controls purple versus red color. Homozygous dominant VV with dominant L and Int genes produces purple color while VvL_Int_ is rose purple color. Salmon X purple and purple X pink crosses segregated a new light violet color with the genotype V_llInt_ indicating ll dilutes V in some way (Table 7). The Int gene also effects purple color. Cherry X purple segregated dusty purple, VVR_L_int int, and dusty rose purple, VvR_L_int int (Table 7). The color in both cases was greyed and the flower stalk was somewhat reduced but not shriveled. The R

Table 6. Orange X Pink F_2 Segregation

Color	Genotype	Ratio	Obs.	Exp.
Orange X Pink F_2				
Light Red	Ee R_ L_	18	65	67.50
Red	ee R_ L_	9	40	33.75
Orange	EE R_ L_	9	33	33.75
Light Rose	Ee rr L_	6	22	22.50
Light Salmon	Ee R_ ll	6	21	22.50
Rose	ee rr L_	3	15	11.25
Salmon	ee R_ ll	3	11	11.25
Dilute Rose	EE rr L_	3	9	11.25
Dilute Salmon	EE R_ ll	3	12	11.25
Light Pink	Ee rr ll	2	6	7.50
Pink	ee rr ll	1	3	3.25
Dilute Pink	EE rr ll	1	3	3.25
		64	240	240.00
$D^2/e = 3.731$	$P > .975$			

Table 7. Segregation Data for the V Gene

Color	Genotype	Ratio	Obs.	Exp.
Purple X Pink F_2				
Rose Purple	Vv -- L_	24	79	90.00
Purple	VV -- L_	12	53	45.00
Light Violet	V_ -- ll	12	42	45.00
Red	vv R_ L_	9	41	33.75
Rose	vv rr L_	3	11	11.25
Salmon	vv R_ ll	3	7	11.25
Pink	vv rr ll	1	7	3.75
		64	240	240.00
$D^2/e = 8.949$	$P > .10$			
Cherry X Purple F_2				
Rose Purple	Vv Int_	6	75	72
Purple	VV Int_	3	36	36
Red	vv Int_	3	34	36
Dusty Rose Purple	Vv int int	2	22	24
Dusty Purple	VV int int	1	14	12
Cherry	vv int int	1	11	12
		16	192	192
$D^2/e = .819$	$P > .975$			

gene seems to have no effect on the V gene since the rose X purple cross showed no new segregates. The B gene also had no effect on the V gene, at least in the presence of dominant R, L, and Int genes which both parents carried.

The burgundy color is rather unique because it is actually two colors. The body is burgundy (or wine) colored while the upper lip is intense red. Burgundy body coloring is produced by the B gene with dominant R, L, and Int genes. In the hybrid condition (Bb), the body color becomes more reddish than burgundy. The R, L, and Int genes determine the basic color of the flower while the B gene lends a purple cast to the body, thus red becomes burgundy and rose becomes fuchsia (Table 8). The lip color is generally as it would appear if the B gene were recessive. The H.C.C. numbers given to the burgundy related colors represent the body color only.

By analyzing the F_2 and backcross populations, it was possible to determine the parent genotypes presented in Table 9; as they were all homozygous, only the haploid genotypes are given. A summary of crosses is presented in Table 10. For each cross, the F_2 ratio tested, the Chi Square value, and the probability is given. Table 11 gives the segregating genes for each cross. The complete F_2 and backcross segregations can be found in the appendix by using the cross number.

Table 8. Burgundy X Pink F_2 Segregation

Color	Genotype	Ratio	Obs.	Exp.
Burgundy X Pink F_2				
Red Burgundy	Bb R_ L_	18	127	112.50
Burgundy	BB R_ L_	9	51	56.25
Red	bb R_ L_	9	53	56.25
Peach-Rose	B_ R_ ll	9	41	56.25
Fuchsia	Bb rr L_	6	42	37.50
Maroon	BB rr L_	3	23	18.75
Rose-Pink	B_ rr ll	3	21	18.75
Rose	bb rr L_	3	9	18.75
Salmon	bb R_ ll	3	23	18.75
Pink	bb rr ll	1	10	6.25
		64	400	400.00
$D^2/e = 16.735$	$P > .05$			

Table 9. Parent Genotypes

Parent Color Class	Genotype						
White	p	v	b	e	R	L	Int
Purple	P	V	b	e	R	L	Int
Burgundy	P	v	B	e	R	L	Int
Orange	P	v	b	E	R	L	Int
Red	P	v	b	e	R	L	Int
Rose	P	v	b	e	r	L	Int
Salmon	P	v	b	e	R	l	Int
Pink	P	v	b	e	r	l	Int
Cherry	P	v	b	e	R	L	int

Table 10. Summary of Crosses

Cross Number	Cross	F_2 Ratio	Chi Square	P greater than
1	Pink X White *	27:16:9:9:3	3.084	.50
2	White X Salmon	9:4:3	1.111	.50
3	White X Rose	9:4:3	1.755	.30
4	White X Cherry	9:4:3	1.147	.50
5	White X Orange	6:4:3:3	.674	.80
6	White X Red	3:1	.544	.30
7	White X Burgundy *	6:3:3:3:1	5.613	.20
8	White X Purple *	6:3:3:3:1	9.576	.01
9	Pink X Salmon	3:1	1.896	.10
10	Pink X Rose	3:1	.037	.80
11	Pink X Cherry *	27:18:9:6:3:1	8.294	.10
12	Orange X Pink *	18:9:9:6:6:3:3:3:3:2:1:1	3.731	.975
13	Red X Pink	9:3:3:1	7.450	.05

* F_2 data also presented in text

Table 10 (cont'd.)

Cross Number	Cross	F_2 Ratio	Chi Square	P greater than
14	Burgundy X pink *	18:9:9:9:6:3:3:3:3:1	16.735	.05
15	Purple X Pink *	24:12:12:9:3:3:1	8.949	.10
16	Pixie self	9:3:3:1	.784	.80
17	Rose X Salmon *	9:3:3:1	2.724	.30
18	Cherry X Salmon *	9:3:3:1	.253	.95
19	Salmon X Orange	6:3:3:2:1:1	7.368	.10
20	Salmon X Red	3:1	.022	.80
21	Salmon X Burgundy	6:3:3:3:1	1.705	.70
22	Salmon X Purple	6:3:3:3:1	3.294	.50
23	Cherry X Rose *	9:6:1	.438	.80
24	Rose X Orange	6:3:3:2:1:1	7.547	.10
25	Rose X Red	3:1	.781	.30
26	Rose X Burgundy	6:3:3:2:1:1	4.185	.50

* F_2 data also presented in text

Table 10 (cont'd.)

Cross Number	Cross	F_2 Ratio	Chi Square	P greater than
27	Rose X Purple	8:4:3:1	8.299	.01
28	Orange X Cherry	6:3:3:2:1:1	3.086	.50
29	Cherry X Red	3:1	.160	.50
30	Cherry X Burgundy	6:3:3:2:1:1	4.225	.50
31	Cherry X Purple *	6:3:3:2:1:1	.819	.975
32	Orange X Red	2:1:1	.211	.80
33	Orange X Burgundy	4:3:2:2:2:1:1:1	6.944	.30
34	Orange X Purple	4:3:2:2:2:1:1:1	3.185	.80
35	Burgundy X Red	2:1:1	.209	.80
36	Purple X Red	2:1:1	.157	.90
37	Burgundy X Purple	8:4:2:1:1	1.958	.70

* F_2 data also presented in text

Table 11. Status of Genes

Cross Number	Cross	Status of Genes *						
		P	V	B	E	R	L	Int
1	Pink X White	S	r	r	r	S	S	d
2	White X Salmon	S	r	r	r	d	S	d
3	White X Rose	S	r	r	r	S	d	d
4	White X Cherry	S	r	r	r	d	d	S
5	White X Orange	S	r	r	S	d	d	d
6	White X Red	S	r	r	r	d	d	d
7	White X Burgundy	S	r	S	r	d	d	d
8	White X Purple	S	S	r	r	d	d	d
9	Pink X Salmon	d	r	r	r	S	r	d
10	Pink X Rose	d	r	r	r	r	S	d
11	Pink X Cherry	d	r	r	r	S	S	S
12	Orange X Pink	d	r	r	S	S	S	d
13	Red X Pink	d	r	r	r	S	S	d
14	Burgundy X Pink	d	r	S	r	S	S	d
15	Purple X Pink	d	S	r	r	S	S	d
16	Pixie self	d	r	r	r	S	S	d
17	Rose X Salmon	d	r	r	r	S	S	d
18	Cherry X Salmon	d	r	r	r	d	S	S
19	Salmon X Orange	d	r	r	S	d	S	d
20	Salmon X Red	d	r	r	r	d	S	d

* S -segregating gene   r -recessive in both parents

d -dominant in both parents

Table 11 (cont'd.)

Cross Number	Cross	Status of Genes *						
		P	V	B	E	R	L	Int
21	Salmon X Burgundy	d	r	S	r	d	S	d
22	Salmon X Purple	d	S	r	r	d	S	d
23	Cherry X Rose	d	r	r	r	S	d	S
24	Rose X Orange	d	r	r	S	S	d	d
25	Rose X Red	d	r	r	r	S	d	d
26	Rose X Burgundy	d	r	S	r	S	d	d
27	Rose X Purple	d	S	r	r	S	d	d
28	Orange X Cherry	d	r	r	S	d	d	S
29	Cherry X Red	d	r	r	r	d	d	S
30	Cherry X Burgundy	d	r	S	r	d	d	S
31	Cherry X Purple	d	S	r	r	d	d	S
32	Orange X Red	d	r	r	S	d	d	d
33	Orange X Burgundy	d	r	S	S	d	d	d
34	Orange X Purple	d	S	r	S	d	d	d
35	Burgundy X Red	d	r	S	r	d	d	d
36	Purple X Red	d	S	r	r	d	d	d
37	Burgundy X Purple	d	S	S	r	d	d	d

* S -segregating gene   r -recessive in both parents

d -dominant in both parents

Line charts were developed in order to clearly demonstrate the gene interactions. Figure 1 shows the interaction of the R, L, and Int genes. The genes being considered are listed horizontally across the top of the chart with the color phenotype and H.C.C. number at the far right. The chart works like a botanical key for each gene. There are either two choices if the gene is dominant, or three choices if it is incompletely dominant. To find the genotype of a color, start at the top left corner with the first gene shown. In the case of Figure 1, there is R, or moving downward recessive r. If the genotype for the pink shriveled phenotype is desired, then r would be selected. By following the lines downward and across the chart, the genotype for pink shriveled is found to be rrllint int. Only the haploid genotypes are shown on the charts, but homozygosity is assumed unless the gene is incompletely dominant, in which case, the intermediate class is also given.

Figures 2, 3, and 4 show the interaction of the E, B, and V genes with R, L, and Int. The interactions of V with B, V with E, and B with E are shown in Figure 5.

Genes			Color	H.C.C.#
R	L	Int	Red	18/0
		int	Cherry	∘ 20/1
	l	Int	Salmon	620/1
		int	Pink	21/2
r	L	Int	Rose	∘ 20/1
		int	Rose Shriveled	∘ 20/1
	l	Int	Pink	21/2
		int	Pink Shriveled	21/2

Figure 1. Interaction of the R, L, and Int Genes

Genes					Color	H.C.C.#
P	E	R	L	Int	Orange	619/0
				int	Dilute Cherry	∘621/2
			l		Dilute Salmon	520/3
		r	L		Dilute Rose	∘621/2
			l		Dilute Pink	623/3
	Ee	R	L	Int	Light Red	17/1
				int	Light Cherry	20/2
			l		Light Salmon	621/2
		r	L		Light Rose	20/2
			l		Light Pink	623/2
	e				Figure 1	
p					All White	--

Figure 2. Interaction of the P, E, R, L, and Int Genes

P	B	R	L	Int	Color	H.C.C.#
P	B	R	L	Int	Burgundy/red lip	824/3
				int	Maroon/rose lip	824/3
			l		Peach-Rose	25/2
		r	L		Maroon/rose lip	824/3
			l		Rose-Pink	27/2
	Bb	R	L	Int	Red Burgundy	820/0
				int	Fuchsia	22/1
			l		Peach-Rose	25/2
		r	L		Fuchsia	22/1
			l		Rose-Pink	27/2
	b				Figure 1	
p	B_				Pink-White	427/3
	b				White	--

Figure 3. Interaction of the P, B, R, L, and Int Genes

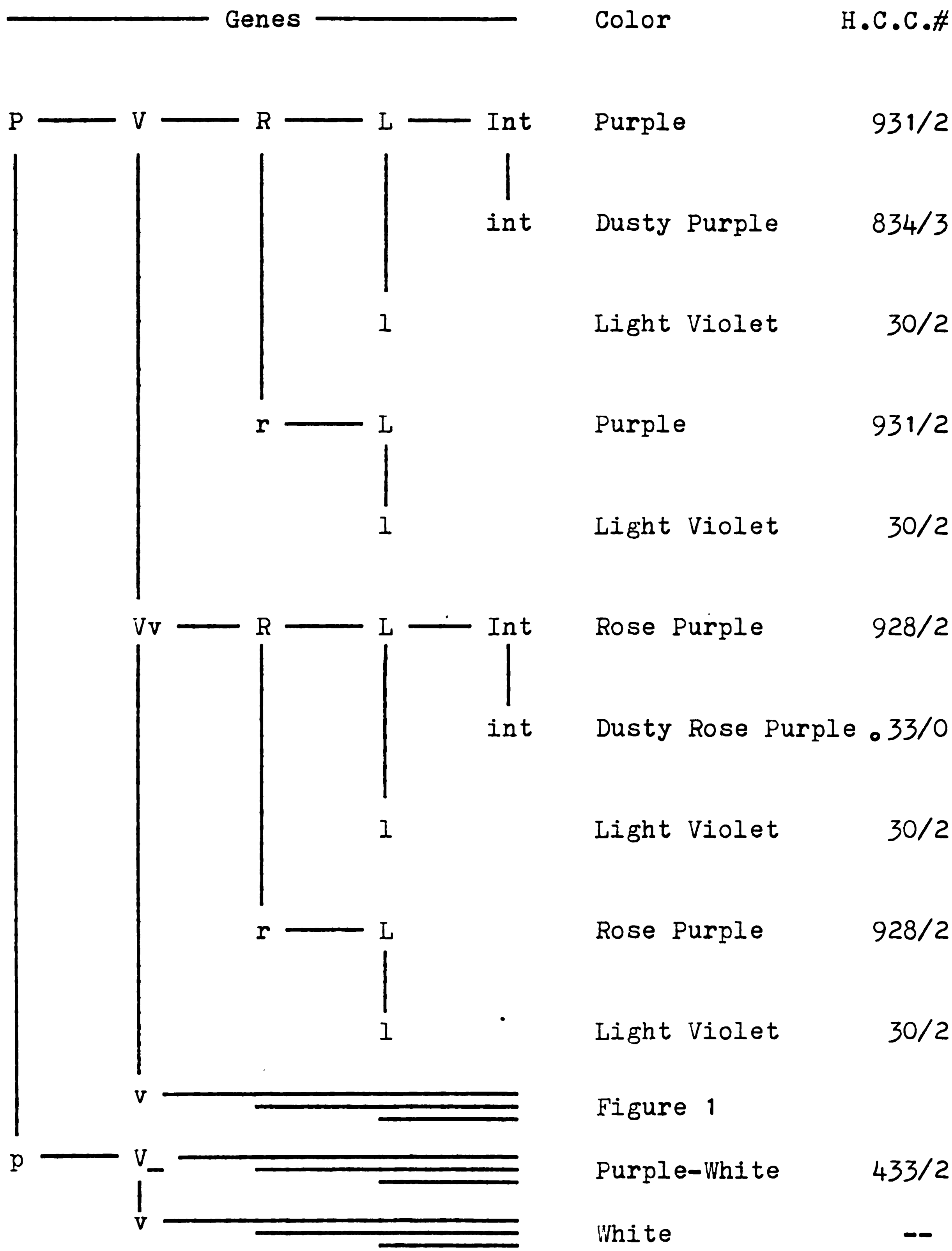

Figure 4. Interaction of the P, V, R, L, and Int Genes

Genes			Color	H.C.C.#
V	B			
	Bb			
	b	e	Purple	931/2
		Ee	Light Purple	830/1
		E	Dilute Purple	∘31/1
Vv	B			
	Bb			
	b	e	Rose Purple	928/2
		Ee	Light Rose Purple	∘31/0
		E	Dilute Purple	∘31/1
v	B	e	Burgundy	824/3
		Ee	Light Burgundy	722/0
		E	Dilute Burgundy	25/2
	Bb	e	Red Burgundy	820/0
		Ee	Light Red Burgundy	20/0
		E	Dilute Burgundy	25/2
	b	e	Red	18/0
		Ee	Light Red	17/1
		E	Orange	619/0

Figure 5. Interaction of the V, B, and E Genes

DISCUSSION

The L and Int genes were discovered by Hendrychova-Tomkova (7). Salmon (L gene) crossed with white, red, rose, and purple produced data confirming Hendrychova-Tomkova's (7) results. She also found that rose X purple segregated a light violet color. The R gene did not segregate any light violet shades when combined with V, but the Int gene did, therefore her rose color must have been due to the Int gene. Since she had no other source of rose color, she would not have discovered the R gene.

Hendrychova-Tomkova (7) also discovered the pigment, P, and violet, V, genes. She found these genes to be closely linked, but in this study, the cross white X purple showed no indication of linkage. Possibly in the twenty years since her study, the linkage between the P and V genes has been broken, at least in cultivated populations. Crosses of salmon, rose, and red with white and purple produced data substantiating her results.

The R, B, and E genes are new to this study. The R and Int genes both produce rose color and segregate identical colors when combined with the B and E genes. Only the V gene is affected differently. Recessive int int with V produces dusty purple, while recessive rr has no effect on the

V gene. The R and Int genes are deleterious when their recessive alleles are combined. The shriveled flower stalk phenotype is not lethal but effectively unreproductive.

The B gene can be considered a variegation gene since it primarily affects the body color of the flower. The lip color is the same as if the B gene were recessive. The R, L, and Int genes determine the basic color of the flower while the B gene adds a purple cast to the body. Hendrychova-Tomkova (7) did a pigment analysis and found small amounts of purple cyanidin in the red color. Theoretically, the B gene could increase the cyanidin content and cause the pelargonidin colors to be purple-tinted. Obviously, a pigment study is needed to verify this hypothesis.

The E gene dilutes the colors produced by the other genes. Since E is incompletely dominant, there are three shades of every color: intense color ee, light shades Ee, and dilute shades EE. The E gene had limited effect on the B gene. The light burgundy and light red burgundy colors were not greatly different from their intense forms. A side by side comparison was necessary to differentiate them. If the E gene acts primarily on the pelargonidin pigment and burgundy color is due to cyanidin, then this could explain the limited dilution of B by E. Another possibility is modifier genes. All of the incompletely dominant genes (V, B, and E) were somewhat variable in their coloring, particularly within the intermediate class. The colors were always within their color chart designations, but minor differences were apparent in the intensity of the colors.

All parents except rose, salmon, and pink carried dominant R and L genes, and the other five genes were each found from different colors. With this situation, only three genes could be segregating in any single cross, and consequently, all gene combinations were not recovered. For example, both purple and burgundy parents carried dominant R, L, and Int genes, and the B gene seemed to have no effect on the V gene in the cross purple X burgundy. If B, however, was combined with V and recessive ll or int int, then the effect of B might be seen. The orange (E gene) parent also carried dominant R, L, and Int genes, therefore the effect of B and/or V on the diluted colors was not seen. The potential for new colors is very high.

SUMMARY

This study was undertaken to determine the number of genes for flower color in *Salvia splendens*. The colors were divided into eight distinct classes and intercrossed. The resulting F_2 and backcross populations for each cross were grown and analyzed genetically. Seven genes were identified and line charts were developed to show their interaction.

R	produces red with L; rr produces rose with L
L	produces red with R; ll produces salmon with R
Int	produces red with R and L; int int produces rose with R and L
P	produces colored flowers; pp produces white
V	produces purple; vv produces red with L and Int
B	produces burgundy; bb produces red with R, L, and Int
E	produces dilute colors; ee produces intense colors

The R, L, Int, and P genes exhibit complete dominance while the V, B, and E genes are incompletely dominant. The R, B, and E genes were discovered in this study.

APPENDIX

APPENDIX

The data to support the conclusions in this thesis are presented here. The order of the crosses is the same as in Table 10. The F_2 and backcross segregations are included for each cross, and the non-segregating genes are also given. In some cases, it was necessary to combine classes when the color was not able to be differentiated. An * indicates the Chi Square value has been calculated using Yates' Correction for Continuity (15).

Cross 1

Pink X White

non-segregating genes - v, b, e, Int

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_R_L_	27	Red	159	144	1.562
pp----	16	White	77	85	.752
P_rrL_	9	Rose	43	48	.520
P_R_ll	9	Salmon	48	48	.000
P_rrll	3	Pink	14	16	.250
	64		341	341	3.084

df = 4 .70 > P > .50

(Pink X White) X Pink

P_RrLl	1	Red	21	17.5	.700
P_rrLl	1	Rose	17	17.5	.014
P_Rrll	1	Salmon	16	17.5	.128
P_rrll	1	Pink	16	17.5	.128
			70	70.0	.970

df = 3 .90 > P > .80

(Pink X White) X White

P_R_L_	1	Red	12	15	.416
pp----	1	White	18	15	.416
			30	30	.832 *

df = 1 .50 > P > .30

Cross 2

White X Salmon

non-segregating genes - v, b, e, R, Int

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_L_	9	Red	156	148.0	.432
pp--	4	White	63	65.7	.110
P_ll	3	Salmon	44	49.3	.569
	16		263	263.0	1.111

df = 2 $.70 > P > .50$

(White X Salmon) X Salmon

P_Ll	1	Red	37	32.5	.492
P_ll	1	Salmon	28	32.5	.492
			65	65.0	.984 *

df = 1 $.50 > P > .30$

(White X Salmon) X White

P_L_	1	Red	29	26	.240
pp--	1	White	23	26	.240
			52	52	.480 *

df = 1 $.50 > P > .30$

Cross 3

White X Rose

non-segregating genes - v, b, e, L, Int

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_R_	9	Red	211	205.9	.126
pp--	4	White	81	91.5	1.204
P_rr	3	Rose	74	68.6	.425
	16		366	366.0	1.755

df = 2 $.50 > P > .30$

(White X Rose) X Rose

P_Rr	1	Red	43	39	.314
P_rr	1	Rose	35	39	.314
			78	78	.628 *

df = 1 $.50 > P > .30$

(White X Rose) X White

P_R_	1	Red	38	32	.945
pp--	1	White	26	32	.945
			64	64	1.890 *

df = 1 $.20 > P > .10$

Cross 4

White X Cherry

non-segregating genes - v, b, e, R, L

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_Int_	9	Red	105	104.0	.009
pp--	4	White	41	46.3	.606
P_int int	3	Cherry	39	34.7	.532
	16		185	185.0	1.147

df = 2 $.70 > P > .50$

(White X Cherry) X Cherry

P_Int int	1	Red	39	32	1.320
P_int int	1	Cherry	25	32	1.320
			64	64	2.640 *

df = 1 $.20 > P > .10$

(White X Cherry) X White

P_Int_	1	Red	22	22.5	.011
pp--	1	White	23	22.5	.011
			45	45.0	.022

df = 1 $.90 > P > .80$

Cross 5

White X Orange

non-segregating genes - v, b, R, L, Int

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_Ee	6	Light Red	58	55.50	.112
pp--	4	White	35	37.00	.108
P_ee	3	Red	30	27.75	.182
P_EE	3	Orange	25	27.75	.272
	16		148	148.00	.674

df = 3 $.90 > P > .80$

(White X Orange) X Orange

P_Ee	1	Light Red	33	33.5	.007
P_EE	1	Orange	34	33.5	.007
			67	67.0	.014

df = 1 $.95 > P > .90$

(White X Orange) X White

pp--	2	White	22	23	.043
P_Ee	1	Light Red	12	11.5	.021
P_ee	1	Red	12	11.5	.021
			46	46.0	.085

df = 2 $.975 > P > .95$

Cross 6

White X Red

non-segregating genes - v, b, e, R, L, Int

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_	3	Red	100	104.25	.134
pp	1	White	39	34.75	.410
	4		139	139.00	.544 *

df = 1 $\qquad .50 > P > .30$

(White X Red) X White

Pp	1	Red	15	15	.000
pp	1	White	15	15	.000
			30	30	.000

df = 1 $\qquad P > .99$

(White X Red) X Red

P_	1	Red	30	30	--

Cross 7

White X Burgundy

non-segregating genes - v, e, R, L, Int

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_Bb	6	Red Burgundy	77	79.0	.050
P_bb	3	Red	48	39.6	1.781
P_BB	3	Burgundy	37	39.6	.170
ppB_	3	Pink-White	31	39.6	1.745
ppbb	1	White	18	13.2	1.867
	16		211	211.0	5.613

df = 4 .30 > P > .20

(White X Burgundy) X White

PpBb	1	Red Burgundy	20	17.75	.285
Ppbb	1	Red	20	17.75	.285
ppBb	1	Pink-White	15	17.75	.426
ppbb	1	White	16	17.75	.172
			71	71.00	1.168

df = 3 .80 > P > .70

(White X Burgundy) X Burgundy

P_Bb	1	Red Burgundy	31	31.5	.007
P_BB	1	Burgundy	32	31.5	.007
			63	63.0	.014

df = 1 .95 > P > .90

Cross 8

White X Purple

non-segregating genes - b, e, R, L, Int

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
P_Vv	6	Rose Purple	113	110.6	.052
P_VV	3	Purple	62	55.3	.811
P_vv	3	Red	67	55.3	2.475
ppV_	3	Purple-White	42	55.3	3.198
ppvv	1	White	11	18.5	3.040
	16		295	295.0	9.576

df = 4 $.05 > P > .01$

(White X Purple) X White

PpVv	1	Rose Purple	18	16	.250
Ppvv	1	Red	14	16	.250
ppVv	1	Purple-White	20	16	1.000
ppvv	1	White	12	16	1.000
			64	64	2.500

df = 3 $.50 > P > .30$

(White X Purple) X Purple

P_Vv	1	Rose Purple	38	31	1.362
P_VV	1	Purple	24	31	1.362
			62	62	2.724 *

df = 1 $.10 > P > .05$

Cross 9

Pink X Salmon

non-segregating genes - v, b, e, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
R_	3	Salmon	76	69.75	.474
rr	1	Pink	17	23.25	1.422
	4		93	93.00	1.896 *

df = 1 .20 > P > .10

(Pink X Salmon) X Pink

Rr	1	Salmon	15	15.5	.016
rr	1	Pink	16	15.5	.016
			31	31.0	.032

df = 1 .90 > P > .80

(Pink X Salmon) X Salmon

R_	1	Salmon	21	21	--

Cross 10

Pink X Rose

non-segregating genes - v, b, e, R, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
L_	3	Rose	149	150.7	.009
ll	1	Pink	52	50.3	.028
	4		201	201.0	.037 *

df = 1 .90 > P > .80

(Pink X Rose) X Pink

Ll	1	Rose	11	10	.025
ll	1	Pink	9	10	.025
			20	20	.050 *

df = 1 .90 > P > .80

(Pink X Rose) X Rose

L_	1	Rose	33	33	--

Cross 11

Pink X Cherry

non-segregating genes - v, b, e, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
R_L_Int_	27	Red	44	54	1.851
rrL_Int_ & R_L_int int	18	Rose/Cherry	35	36	.027
R_llInt_	9	Salmon	27	18	4.500
rrllInt_ & R_llint int	6	Pink	15	12	.750
rrL_int int	3	Rose Shriveled	4	6	.666
rrllint int	1	Pink Shriveled	3	2	.500
	64		128	128	8.294

df = 5 $.20 > P > .10$

(Pink X Cherry) X Cherry

R_L_Int int	1	Red	20	19.5	.012
R_L_int int	1	Cherry	19	19.5	.012
			39	39.0	.024

df = 1 $.90 > P > .80$

(Pink X Cherry) X Pink

RrLlInt_	1	Red	3	2.75	.022
rrLlInt_	1	Rose	3	2.75	.022
RrllInt_	1	Salmon	4	2.75	.568
rrllInt_	1	Pink	1	2.75	1.113
			11	11.00	1.725

df = 3 $.70 > P > .50$

Cross 12

Orange X Pink

non-segregating genes - v, b, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
EeR_L_	18	Light Red	65	67.50	.092
eeR_L_	9	Red	40	33.75	1.157
EER_L_	9	Orange	33	33.75	.016
EerrL_	6	Light Rose	22	22.50	.011
EeR_ll	6	Light Salmon	21	22.50	.100
eerrL_	3	Rose	15	11.25	1.250
eeR_ll	3	Salmon	11	11.25	.005
EErrL_	3	Dilute Rose	9	11.25	.450
EER_ll	3	Dilute Salmon	12	11.25	.050
Eerrll	2	Light Pink	6	7.50	.300
eerrll	1	Pink	3	3.25	.150
EErrll	1	Dilute Pink	3	3.25	.150
	64		240	240.00	3.731

df = 11 $.99 > P > .975$

(Orange X Pink) X Orange

EeR_L_	1	Light Red	17	15.5	.064
EER_L_	1	Orange	14	15.5	.064
			31	31.0	.128 *

df = 1 $.80 > P > .70$

Cross 12 (cont'd.)

(Orange X Pink) X Pink

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
EeRrLl	1	Light Red	6	5	.05
EerrLl	1	Light Rose	6	5	.05
EeRrll	1	Light Salmon	3	5	.45
Eerrll	1	Light Pink	4	5	.05
eeRrLl	1	Red	6	5	.05
eerrLl	1	Rose	6	5	.05
eeRrll	1	Salmon	5	5	.00
eerrll	1	Pink	4	5	.05
	8		40	40	.75 *

df = 7 P > .995

Cross 13

Red X Pink

non-segregating genes - v, b, e, Int, P

R_L_	9	Red	142	135	.362
rrL_	3	Rose	55	45	2.222
R_ll	3	Salmon	33	45	3.200
rrll	1	Pink	10	15	1.666
	16		240	240	7.450

df = 3 .10 > P > .05

(Red X Pink) X Red

R_L_	1	Red	72	72	--

Cross 13 (cont'd.)

(Red X Pink) X Pink

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
RrLl	1	Red	13	13	.000
rrLl	1	Rose	11	13	.307
Rrll	1	Salmon	12	13	.076
rrll	1	Pink	16	13	.692
			52	52	1.075

df = 3 .80 > P > .70

Cross 14

Burgundy X Pink

non-segregating genes - v, e, Int, P

BbR_L_	18	Red Burgundy	127	112.50	1.868
BBR_L_	9	Burgundy	51	56.25	.490
bbR_L_	9	Red	53	56.25	.187
B_R_ll	9	Peach-Rose	41	56.25	4.134
BbrrL_	6	Fuchsia	42	37.50	.540
BBrrL_	3	Maroon	23	18.75	.963
B_rrll	3	Rose-Pink	21	18.75	.270
bbrrL_	3	Rose	9	18.75	5.070
bbR_ll	3	Salmon	23	18.75	.963
bbrrll	1	Pink	10	6.25	2.250
	64		400	400.00	16.735

df = 9 .10 > P > .05

Cross 14 (cont'd.)

(Burgundy X Pink) X Pink

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
BbRrLl	1	Red Burgundy	5	5	.0
BbrrLl	1	Fuchsia	4	5	.2
BbRrll	1	Peach-Rose	7	5	.8
Bbrrll	1	Rose-Pink	3	5	.8
bbRrLl	1	Red	7	5	.8
bbrrLl	1	Rose	6	5	.2
bbRrll	1	Salmon	5	5	.0
bbrrll	1	Pink	3	5	.8
	8		40	40	3.6

df = 7 $.90 > P > .80$

(Burgundy X Pink) X Burgundy

BbR_L_	1	Red Burgundy	25	24	.0104
BBR_L_	1	Burgundy	23	24	.0104
			48	48	.0208 *

df = 1 $.90 > P > .80$

Cross 15

Purple X Pink

non-segregating genes - b, e, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
Vv--L_	24	Rose Purple	79	90	1.344
VV--L_	12	Purple	53	45	1.422
V_--ll	12	Light Violet	42	45	.200
vvR_L_	9	Red	41	33.75	1.557
vvrrL_	3	Rose	11	11.25	.005
vvR_ll	3	Salmon	7	11.25	1.605
vvrrll	1	Pink	7	3.75	2.816
	64		240	240.00	8.949

df = 6 .20 > P > .10

(Purple X Pink) X Pink

Vv--L_	2	Rose Purple	11	10.50	.023
Vv--ll	2	Light Violet	8	10.50	.595
vvRrLl	1	Red	7	5.25	.583
vvrrLl	1	Rose	8	5.25	1.440
vvRrll	1	Salmon	3	5.25	.964
vvrrll	1	Pink	5	5.25	.012
			42	42.00	3.617

df = 5 .70 > P > .50

Cross 15 (cont'd.)

(Purple X Pink) X Purple

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
VvR_L_	1	Rose Purple	23	24	.0104
VVR_L_	1	Purple	25	24	.0104
			48	48	.0208 *

df = 1 .90 > P > .80

Cross 16

Pixie self (Rose X Salmon)

non-segregating genes - v, b, e, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
R_L_	9	Red	134	129.4	.163
rrL_	3	Rose	40	43.1	.222
R_ll	3	Salmon	40	43.1	.222
rrll	1	Pink	16	14.4	.177
	16		230	230.0	.784

df = 3 .90 > P > .80

(Rose X Salmon) X Rose

RrL_	1	Red	17	16	.015
rrL_	1	Rose	15	16	.015
			32	32	.030 *

df = 1 .90 > P > .80

(Rose X Salmon) X Salmon

R_Ll	1	Red	12	11.5	.021
R_ll	1	Salmon	11	11.5	.021
			23	23.0	.042

df = 1 .90 > P > .80

Cross 17

Rose X Salmon

non-segregating genes - v, b, e, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
R_L_	9	Red	132	135.6	.095
rrL_	3	Rose	39	45.2	.850
R_ll	3	Salmon	54	45.2	1.713
rrll	1	Pink	16	15.0	.066
	16		241	241.0	2.724

df = 3 .50 > P > .30

(Rose X Salmon) X Rose

RrL_	1	Red	25	23	.097
rrL_	1	Rose	21	23	.097
			46	46	.194 *

df = 1 .70 > P > .50

(Rose X Salmon) X Salmon

R_Ll	1	Red	30	25	.810
R_ll	1	Salmon	20	25	.810
			50	50	1.620 *

df = 1 .30 > P > .20

Cross 18

Cherry X Salmon

non-segregating genes - v, b, e, R, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
L_Int_	9	Red	135	133.31	.021
L_int int	3	Cherry	44	44.44	.004
llInt_	3	Salmon	45	44.44	.007
llint int	1	Pink	13	14.81	.221
	16		237	237.00	.253

df = 3 .975 > P > .95

(Cherry X Salmon) X Salmon

LlInt_	1	Red	11	12	.020
llInt_	1	Salmon	13	12	.020
			24	24	.040 *

df = 1 .90 > P > .80

(Cherry X Salmon) X Cherry

L_Int int	1	Red	32	32.5	.007
L_int int	1	Cherry	33	32.5	.007
			65	65.0	.014

df = 1 .95 > P > .90

Cross 19

Salmon X Orange

non-segregating genes - v, b, Int, R, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
EeL_	6	Light Red	111	108	.083
eeL_	3	Red	61	54	.907
EEL_	3	Orange	58	54	.296
Eell	2	Light Salmon	35	36	.027
eell	1	Salmon	15	18	.500
EEll	1	Dilute Salmon	8	18	5.555
	16		288	288	7.368

df = 5 .20 > P > .10

(Salmon X Orange) X Salmon

EeLl	1	Light Red	14	10.5	1.166
eeLl	1	Red	10	10.5	.023
Eell	1	Light Salmon	8	10.5	.595
eell	1	Salmon	10	10.5	.023
			42	42.0	1.807

df = 3 .70 > P > .50

(Salmon X Orange) X Orange

EeL_	1	Light Red	20	19.5	.012
EEL_	1	Orange	19	19.5	.012
			39	39.0	.024

df = 1 .90 > P > .80

Cross 20

Salmon X Red

non-segregating genes - v, b, e, R, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
L_	3	Red	168	169.5	.005
ll	1	Salmon	58	56.5	.017
	4		226	226.0	.022 *

df = 1 .90 > P > .80

(Salmon X Red) X Salmon

Ll	1	Red	37	35.5	.028
ll	1	Salmon	34	35.5	.028
			71	71.0	.056 *

df = 1 .90 > P > .80

(Salmon X Red) X Red

L_	1	Red	47	47	--

Cross 21

Salmon X Burgundy

non-segregating genes - v, e, R, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
BbL_	6	Red Burgundy	68	75	.653
BBL_	3	Burgundy	41	37.5	.326
bbL_	3	Red	36	37.5	.060
B_ll	3	Peach-Rose	40	37.5	.166
bbll	1	Salmon	15	12.5	.500
	16		200	200.0	1.705

df = 4 $\quad .80 > P > .70$

(Salmon X Burgundy) X Salmon

BbLl	1	Red Burgundy	12	11	.090
bbLl	1	Red	11	11	.000
Bbll	1	Peach-Rose	10	11	.090
bbll	1	Salmon	11	11	.000
			44	44	.180

df = 3 $\quad .99 > P > .975$

(Salmon X Burgundy) X Burgundy

BbL_	1	Red Burgundy	15	14	.017
BBL_	1	Burgundy	13	14	.017
			28	28	.034 *

df = 1 $\quad .90 > P > .80$

Cross 22

Salmon X Purple

non-segregating genes - b, e, R, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
VvL_	6	Rose Purple	104	108	.148
VVL_	3	Purple	59	54	.462
V_ll	3	Light Violet	60	54	.666
vvL_	3	Red	53	54	.018
vvll	1	Salmon	12	18	2.000
	16		288	288	3.294

df = 4 .70 > P > .50

(Salmon X Purple) X Salmon

VvLl	1	Rose Purple	10	9.5	.026
Vvll	1	Light Violet	9	9.5	.026
vvLl	1	Red	10	9.5	.026
vvll	1	Salmon	9	9.5	.026
			38	38.0	.104

df = 3 .99 > P > .95

(Salmon X Purple) X Purple

VvL_	1	Rose Purple	25	22.5	.177
VVL_	1	Purple	20	22.5	.177
			45	45.0	.354 *

df = 1 .70 > P > .50

Cross 23

Cherry X Rose

non-segregating genes - v, b, e, L, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
R_Int_	9	Red	129	133.9	.179
rrInt_ & R_int int	6	Rose/Cherry	94	89.2	.258
rrint int	1	Rose Shriveled	15	14.9	.001
	16		238	238.0	.438

df = 2 .90 > P > .80

(Cherry X Rose) X Rose

RrInt_	1	Red	19	16	.390
rrInt_	1	Rose	13	16	.390
			32	32	.780 *

df = 1 .50 > P > .30

(Cherry X Rose) X Cherry

R_Int int	1	Red	36	34	.066
R_int int	1	Cherry	32	34	.066
			68	68	.132 *

df = 1 .80 > P > .70

Cross 24

Rose X Orange

non-segregating genes - v, b, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
EeR_	6	Light Red	92	98.2	.391
eeR_	3	Red	64	49.1	4.521
EER_	3	Orange	49	49.1	.0002
Eerr	2	Light Rose	32	32.8	.019
eerr	1	Rose	15	16.4	.119
EErr	1	Dilute Rose	10	16.4	2.497
	16		262	262.0	7.547

df = 5 $.20 > P > .10$

(Rose X Orange) X Rose

EeRr	1	Light Red	7	8.5	.264
eeRr	1	Red	9	8.5	.029
Eerr	1	Light Rose	8	8.5	.029
eerr	1	Rose	10	8.5	.264
			34	34.0	.586

df = 3 $.90 > P > .80$

(Rose X Orange) X Orange

EeR_	1	Light Red	21	19	.118
EER_	1	Orange	17	19	.118
			38	38	.236 *

df = 1 $.70 > P > .50$

Cross 25

Rose X Red

non-segregating genes - v, b, e, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
R_	3	Red	223	216	.195
rr	1	Rose	65	72	.586
	4		288	288	.781 *

df = 1 .50 > P > .30

(Rose X Red) X Rose

Rr	1	Red	18	18	.000
rr	1	Rose	18	18	.000
			36	36	.000

df = 1 P > .99

(Rose X Red) X Red

R_	1	Red	38	38	--

Cross 26

Rose X Burgundy

non-segregating genes - v, e, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
BbR_	6	Red Burgundy	124	112.50	1.175
BBR_	3	Burgundy	47	56.25	1.521
bbR_	3	Red	51	56.25	.490
BBrr	1	Maroon	16	18.75	.403
Bbrr	2	Fuchsia	41	37.50	.326
bbrr	1	Rose	21	18.75	.270
	16		300	300.00	4.185

df = 5 .70 > P > .50

(Rose X Burgundy) X Rose

BbRr	1	Red Burgundy	6	7	.142
bbRr	1	Red	6	7	.142
Bbrr	1	Fuchsia	10	7	1.285
bbrr	1	Rose	6	7	.142
			28	28	1.711

df = 3 .70 > P > .50

(Rose X Burgundy) X Burgundy

BbR_	1	Red Burgundy	16	16	.000
BBR_	1	Burgundy	16	16	.000
			32	32	.000

df = 1 P > .99

Cross 27

Rose X Purple

non-segregating genes - b, e, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
Vv--	8	Rose Purple	139	154.5	1.555
VV--	4	Purple	96	77.3	4.523
vvR_	3	Red	50	57.9	1.077
vvrr	1	Rose	24	19.3	1.144
	16		309	309.0	8.299

df = 3 $.05 > P > .01$

(Rose X Purple) X Rose

Vv--	2	Rose Purple	20	17.50	.357
vvRr	1	Red	5	8.75	1.607
vvrr	1	Rose	10	8.75	.178
			35	35.00	2.142

df = 2 $.50 > P > .30$

(Rose X Purple) X Purple

Vv--	1	Rose Purple	38	40	.056
VV--	1	Purple	42	40	.056
			80	80	.112 *

df = 1 $.80 > P > .70$

Cross 28

Orange X Cherry

non-segregating genes - v, b, R, L, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
EeInt_	6	Light Red	113	102.75	1.022
eeInt_	3	Red	54	51.38	.133
EEInt_	3	Orange	48	51.38	.222
Eeint int	2	Light Cherry	28	34.25	1.140
eeint int	1	Cherry	17	17.12	.568
EEint int	1	Dilute Cherry	14	17.12	.001
	16		274	274.00	3.086

df = 5 .70 > P > .50

(Orange X Cherry) X Cherry

EeInt int	1	Light Red	12	11	.090
eeInt int	1	Red	12	11	.090
Eeint int	1	Light Cherry	9	11	.363
eeint int	1	Cherry	11	11	.000
			44	44	.543

df = 3 .95 > P > .90

(Orange X Cherry) X Orange

EeInt_	1	Light Red	15	14	.017
EEInt_	1	Orange	13	14	.017
			28	28	.034 *

df = 1 .90 > P > .80

Cross 29

Cherry X Red

non-segregating genes - v, b, e, R, L, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
Int_	3	Red	185	188.25	.040
int int	1	Cherry	66	62.75	.120
	4		251	251.00	.160 *

df = 1 $.70 > P > .50$

(Cherry X Red) X Cherry

Int int	1	Red	35	31.5	.285
int int	1	Cherry	28	31.5	.285
			63	63.0	.570 *

df = 1 $.50 > P > .30$

(Cherry X Red) X Red

Int_	1	Red	54	54	--

Cross 30

Cherry X Burgundy

non-segregating genes - v, e, R, L, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
BbInt_	6	Red Burgundy	85	79.12	.436
BBInt_	3	Burgundy	35	39.56	.525
bbInt_	3	Red	38	39.56	.061
Bbint int	2	Fuchsia	33	26.38	.771
BBint int	1	Maroon	10	13.19	1.661
bbint int	1	Cherry	10	13.19	.771
	16		211	211.00	4.225

df = 5 .70 > P > .50

(Cherry X Burgundy) X Cherry

BbInt int	1	Red Burgundy	11	9	.444
Bbint int	1	Fuchsia	7	9	.444
bbInt int	1	Red	12	9	1.000
bbint int	1	Cherry	6	9	1.000
			36	36	2.888

df = 3 .50 > P > .30

(Cherry X Burgundy) X Burgundy

BbInt_	1	Red Burgundy	15	13	.173
BBInt_	1	Burgundy	11	13	.173
			26	26	.346 *

df = 1 .70 > P > .50

Cross 31

Cherry X Purple

non-segregating genes - b, e, R, L, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
VvInt_	6	Rose Purple	75	72	.125
VVInt_	3	Purple	36	36	.000
vvInt_	3	Red	34	36	.111
Vvint int	2	Dusty Rose Purple	22	24	.167
VVint int	1	Dusty Purple	14	12	.333
vvint int	1	Cherry	11	12	.083
	16		192	192	.819

df = 5 $.99 > P > .975$

(Cherry X Purple) X Cherry

VvInt int	1	Rose Purple	6	7.25	.215
Vvint int	1	Dusty Rose Purple	8	7.25	.077
vvInt int	1	Red	7	7.25	.008
vvint int	1	Cherry	8	7.25	.077
			29	29.00	.377

df = 3 $.95 > P > .90$

(Cherry X Purple) X Purple

VvInt_	1	Rose Purple	25	23.5	.042
VVInt_	1	Purple	22	23.5	.042
			47	47.0	.084 *

df = 1 $.80 > P > .70$

Cross 32

Orange X Red

non-segregating genes - v, b, R, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
Ee	2	Light Red	137	134.50	.008
ee	1	Red	68	67.25	.046
EE	1	Orange	64	67.25	.157
	4		269	269.00	.211

df = 2 $.90 > P > .80$

(Orange X Red) X Orange

Ee	1	Light Red	28	29	.008
EE	1	Orange	30	29	.008
			58	58	.016 *

df = 1 $.95 > P > .90$

(Orange X Red) X Red

Ee	1	Light Red	16	14.5	.068
ee	1	Red	13	14.5	.068
			29	29.0	.136 *

df = 1 $.80 > P > .70$

Cross 33

Orange X Burgundy

non-segregating genes - v, R, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
BbEe	4	Light Red Burgundy	73	71.0	.056
BBEe	2	Light Burgundy	25	35.3	3.005
Bbee	2	Red Burgundy	36	35.3	.013
bbEe	2	Light Red	36	35.3	.013
B_EE	3	Dilute Burgundy	59	53.0	.679
BBee	1	Burgundy	16	17.7	.163
bbee	1	Red	24	17.7	2.242
bbEE	1	Orange	14	17.7	.773
	16		283	283.0	6.944

df = 7 .50 > P > .30

(Orange X Burgundy) X Orange

BbEe	1	Light Red Burgundy	8	10	.400
BbEE	1	Dilute Burgundy	8	10	.400
bbEe	1	Light Red	14	10	1.600
bbEE	1	Orange	10	10	.000
			40	40	2.400

df = 3 .50 > P > .30

Cross 33 (cont'd.)

(Orange X Burgundy) X Burgundy

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
BbEe	1	Light Red Burgundy	14	13	.307
BBEe	1	Light Burgundy	11	13	.076
Bbee	1	Red Burgundy	15	13	.076
BBee	1	Burgundy	12	13	.307
			52	52	.766

df = 3 $.90 > P > .80$

Cross 34

Orange X Purple

non-segregating genes - b, R, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
VvEe	4	Light Rose Purple	60	55.0	.454
VVEe	2	Light Purple	30	27.5	.227
Vvee	2	Rose Purple	25	27.5	.227
vvEe	2	Light Red	22	27.5	1.100
V_EE	3	Dilute Purple	37	41.25	.437
VVee	1	Purple	16	13.75	.368
vvee	1	Red	14	13.75	.004
vvEE	1	Orange	16	13.75	.368
	16		220	220.00	3.185

df = 7 $.90 > P > .80$

Cross 34 (cont'd.)

(Orange X Purple) X Orange

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
VvEe	1	Light Rose Purple	14	12.25	.250
VvEE	1	Dilute Purple	14	12.25	.250
vvEe	1	Light Red	11	12.25	.127
vvEE	1	Orange	10	12.25	.413
			49	49.00	1.040

df = 3 .80 > P > .70

(Orange X Purple) X Purple

VvEe	1	Light Rose Purple	12	11	.090
VVEe	1	Light Purple	11	11	.000
Vvee	1	Rose Purple	11	11	.000
VVee	1	Purple	10	11	.090
			44	44	.180

df = 3 .99 > P > .975

Cross 35

Burgundy X Red

non-segregating genes - v, e, R, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
Bb	2	Red Burgundy	112	114	.035
BB	1	Burgundy	56	57	.017
bb	1	Red	60	57	.157
	4		228	228	.209

df = 2 $.90 > P > .80$

(Burgundy X Red) X Red

Bb	1	Red Burgundy	17	16	.015
bb	1	Red	15	16	.015
			32	32	.030 *

df = 1 $.90 > P > .80$

(Burgundy X Red) X Burgundy

Bb	1	Red Burgundy	12	12.5	.020
BB	1	Burgundy	13	12.5	.020
			25	25.0	.040

df = 1 $.90 > P > .80$

Cross 36

Purple X Red

non-segregating genes - b, e, R, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
Vv	2	Rose Purple	84	85.50	.026
VV	1	Purple	45	42.75	.118
vv	1	Red	42	42.75	.013
	4		171	171.00	.157

df = 2 $.95 > P > .90$

(Purple X Red) X Red

Vv	1	Rose Purple	42	40	.056
vv	1	Red	38	40	.056
			80	80	.112 *

df = 1 $.80 > P > .70$

(Purple X Red) X Purple

Vv	1	Rose Purple	21	20	.012
VV	1	Purple	19	20	.012
			40	40	.024 *

df = 1 $.90 > P > .80$

Cross 37

Burgundy X Purple

non-segregating genes - e, R, L, Int, P

Genotype	Ratio	Color	Obs.	Exp.	D^2/e
Vv--	8	Rose Purple	162	168.5	.250
VV--	4	Purple	92	84.2	.722
vvBb	2	Red Burgundy	43	42.1	.019
vvBB	1	Burgundy	23	21.1	.171
vvbb	1	Red	17	21.1	.796
	16		337	337.0	1.958

df = 4 .80 > P > .70

(Burgundy X Purple) X Burgundy

VvB_	2	Rose Purple	19	19.0	.000
vvBb	1	Red Burgundy	9	9.5	.026
vvBB	1	Burgundy	10	9.5	.026
			38	38.0	.052

df = 2 .99 > P > .95

(Burgundy X Purple) X Purple

Vv--	1	Rose Purple	18	18	.000
VV--	1	Purple	18	18	.000
			36	36	.000

df = 1 P > .99

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