AN ABSTRACT OF THE THESIS OF

Lorraine Luo Hong for the M.S.
(Name) (Degree)

in Genetics presented on May 9, 1968
(Major) (Date)

Title: Inheritance of Resistance to Halo Blight, Pseudomonas phaseolicola (Burk.) in Phaseolus vulgaris L.

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Inheritance of resistance to halo blight, Pseudomonas phaseolicola (Burk.), in the OSU 10183 was studied, preliminary to initiation of a breeding program to transfer resistance to commercially desirable plant types.

OSU 58 and OSU 10183 were used as susceptible and resistant parents, respectively. The former, a bush bean approaching pod quality of Blue Lake pole bean, combines good bush growth habit with high quality; it is a bush green podded, white flowered, white seeded line, while OSU 10183 lacks several good horticultural characteristics, and has colored flowers and black seeds.

Behavior of the F_1 plants showed resistance to be highly dominant, but not completely so. Although data showed a single gene largely conditioning ultimate death of the plants, many of the F_2 plants so classified were much slower in dying than plants of the susceptible parent. The behavior of backcross progeny

confirmed that additional genes are in play in the interaction of host and pathogen.

Blossom color was conditioned by a single gene, with color dominant. Chi-square value of 5.75 shows a good fit to a 9:3:3:1 ratio involving flower color and halo blight reaction. The characters of flower color and halo blight resistance are not linked; this is confirmed by a percentage of recombination of 46.5 ± 2.5, using the product method.

Transfer of halo blight resistance to a high pod quality, white seeded bean out of the OSU 10183 x 58 cross appears feasible; yet rigorous testing for resistance, selection for horticultural characters, followed by back crossing to OSU 58 will be required.

Inheritance of Resistance to Halo Blight,
Pseudomonas phaseolicola (Burk.) in
Phaseolus vulgaris L.

by

Lorraine Luo Hong

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1968

APPROVED:

Professor of Horticulture

in charge of major

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Date thesis is presented May 9, 1968

Typed by Betty Hostetter for Lorraine Luo Hong

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Dr. William A. Frazier, major professor in charge of this investigation, who introduced me to this area of research and through his genuine interest provided a constructive source of advice and encouragement.

I am also deeply grateful to Mrs. William A. Frazier, for her literary versatility in polishing this entire paper.

Appreciation is given to Dr. Harry J. Mack for his invaluable advice and constructive criticism.

Special gratitude is given to my dear parents and brother in Taiwan, China, for their constant inspiration; particularly to my beloved late father, without whose encouragement and affection I could not have progressed to this extent.

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INHERITANCE OF RESISTANCE TO HALO BLIGHT, PSEUDOMONAS PHASEOLICOLA (BURK.) IN PHASEOLUS VULGARIS L.

INTRODUCTION

The snap bean, *Phaseolus vulgaris* L., is widely distributed and is one of the most important food crops of the world. It is grown commercially to some extent in almost every state in the United States. At the present time, Oregon is the leading state in production and in total value of snap beans produced for processing in the United States.

One of the most widespread and consistent in occurrence among the diseases affecting beans is halo blight -- a seed-born disease caused by the bacterium *Pseudomonas phaseolicola* (Burk.). It has been prevalent in all states east of the Rocky Mountains as well as in Colorado, Utah, Wyoming, and Montana. It was present in western Washington and in the Willamette Valley of Oregon in 1964 and 1965. This disease has been reported from Australia, Germany, the Netherlands, Brazil, Tasmania, New Zealand, France, and Switzerland (20).

A cool and moist climate is favorable for the development of halo blight. Infected plants may have water-soaked or necrotic spots on leaves, stems, and pods. Severe infection renders the pods unfit for commercial use. Lesions on leaves are often surrounded by a yellow halo. At the point of attachment of a branch or a petiole with the main stem, water-soaking in spots may be particularly apparent. A systemic toxin may cause general plant yellowing as the disease progresses. Symptoms of halo blight may vary from complete killing of infected susceptible plants to very indistinct pin-point, necrotic symptoms, not easily found, in resistant plants.

In recent years, halo blight has occurred in severe outbreaks in many areas. The disease has not only created heavy economic losses in the United States, but has raised production problems in other countries which have imported United States seed.

Presently, all commercially desirable bush beans are highly susceptible to this disease. The purpose of this study has been to determine the inheritance of resistance to halo blight in beans and to initiate a breeding program to transfer resistance from available resistant breeding lines to commercially desirable plant types.

REVIEW OF LITERATURE

Causal Organism

Halo Blight, *Pseudomonas phaseolicola* (Burk.), of beans was first described by Burkholder in 1926 (1). In the meantime, Hedges (6) was studying a bacterial disease of the kudzu. In 1927 she named and described the causal organism as *Bacterium puerariae* Hedges. Later she (7) compared the kudzu and the halo blight organism and as a result of cross-inoculation studies discovered that the two organisms produced identical symptoms on both bean and kudzu. Since Burkholder's description had been published first, *B. puerariae* became a synonym.

Environmental Factors and Resistance

Burkholder (2) considered halo blight a low-temperature disease. He described two types of spots, the halo spots which he found to occur during cool weather, and small, numerous angular lesions without a definite halo which he observed to occur late in the season, during hot weather. Higgins (8) considered moisture to be essential for infection with halo blight, and pointed out that infection is very materially reduced if the plants are allowed to dry to the wilting point. Goss (5) presented his experimental data and indicated that at temperature of 24°C to 28°C, the symptoms of halo blight appear in six to ten days. The typical halo symptoms are noted chiefly at 20°C and below.

Jensen and Goss (9) reported the varieties Red Mexican and Schwert No. 27 possessed true physiologic resistance to halo blight. These varieties developed small, inconspicuous, necrotic lesions on leaves when inoculated with halo blight instead of the large chlorotic spots that developed on susceptible varieties. Three major factors were shown to influence the symptoms of beans infected with halo blight: temperature, physiologic resistance, and various isolates of the organism (10).

Schuster (15) stated susceptible variety U.S. No. 5 Refugee possessed a homozygous dominant gene SS for susceptibility while variety Asgrow Stringless possessed two dominant factor pairs, $S_1S_1S_2S_2$, for susceptibility. Walker and Patel (19) found that resistance to race 1 in Red Mexican U.I. 3 was inherited as a monogenic dominant character. When resistant parent P.I. 150414 was crossed with the susceptible variety, Tenderwhite, resistance was recessive (13). Coyne and Schuster (3) suggested a single major dominant gene primarily determined resistance; also, many modifying genes affected the degree of expression of resistance. Pryke (14) stated that resistance to race 1 was governed by a series of interacting loci. He suggested a three factor model with one gene controlling the local reaction and two complementary genes controlling systemic behavior. Dickson and Natti (4) reported varieties P.I. 150414 and OSU 2065 contained a single gene for resistance whereas P.I. 181954 possessed one or two recessive genes for resistance. Patel and Walker (12) found that in inoculated, susceptible, systemically chlorotic leaves there was an increase in ornithine, histidine, methionine, asparagine-glutamine, β-alanine and lysine, compared with healthy plants. In resistant plants there was little difference between healthy and infected plants in amino acid content. Stahmann (18) studied proteins and enzymatic activity of halo blight-infected leaves. He suggested that resistant varieties respond to infection with a greater increase in peroxidase activity than do susceptible varieties; and that highly virulent isolates of the pathogen produced more catalase than do less virulent isolates. He believed that the extent and speed of the inhibition of the peroxidase of the host by the catalase of the parasite may determine whether the bean plant is resistant or susceptible.

Several plant characters, flower color, pod type-stringy or stringless--and growth habit -- indeterminate or determinate -- were studied for possible linkage with halo blight reaction by Schuster (15). He concluded that the inheritance of halo blight reaction and these three characteristics were independently inherited.

MATERIALS AND METHODS

Parents

1. OSU 58 (P_1): OSU bush green pod, white flower, white seeded line 58 combines good growth habit with high quality. The 58 pod, when processed, can be considered as a close approach to the Blue Lake pod. The combinations are not only of value commercially, but form a valuable base for further improvement in the bush round pod bean. It is highly susceptible to halo blight: plants are killed by the organism at cool temperature and high humidity.

2. OSU 10183 (P_2): Bush green pod, colored flower, black seeded OSU breeding line 10183 has high physiologic tolerance to halo blight. For this study, OSU 803, a selection from 10183, was used as the resistant parent, in contrast to susceptible parent OSU 58.

Hybridization and Back Crosses

The two lines, OSU 58 and OSU 10183 were hybridized in spring, 1967, in the greenhouse; the F_2 seed and F_1's backcrossed to resistant and susceptible parents were secured in the field in the summer. In October, 1967, the parental, F_1, F_2, BC to P_1, BC to P_2 materials were planted and tested in the greenhouse.

Inoculum Source

The inoculum, prepared from fresh tissues of infected bean leaves, stems, and pods was known to contain race 2 and most likely additional races of the organism.

Inoculation Methods

The plants were inoculated by spraying with a bacterial suspension when the first trifoliate leaf was fully expanded. Three weeks after the first inoculation, plants were inoculated again to insure heavy infection of stems and leaves of susceptible plants. When the plants were inoculated, they were covered immediately with plastic bags for 24 hours to maintain high humidity. Plants were grown in the greenhouse at day temperature of 24°C and night temperature of 15°C.

Resistance Rating

A rating scale of 0 to 9 was used for determining the degree of susceptibility and resistance:

Early to late death:

0 -- Early death

1 -- Medium to early death

2 -- Severe stem infection, medium to late death.

Intermediate resistance:

3 -- medium stem infection

4 -- medium to slight stem infection

5 -- slight stem infection, severe leaf infection

6 -- slight stem infection, moderate to slight leaf infection.

High resistance:

7 -- occasional small, necrotic spot on stem and leaves

8 -- no stem infection, a few small, necrotic spots on leaves only

9 -- no necrosis of any type on stem or leaf.

Time of Reading

Seeds were planted October 19, 1967, inoculations made November 4 and November 25. The first reading was made December 15, 20 days after the second inoculation; a second reading was made January 1, 17 days after the first; a third reading was made January 9, 8 days after the second; and a fourth reading was made January 15, 6 days after the third.

Number of Plants Inoculated and Observed

Generation and Cross	No. of Plants
P_1 (OSU 58, Susceptible Parent)	25
P_2 (OSU 10183, Resistant Parent)	19
F_1: $P_1 \times P_2$ (4 crosses)	14
$P_2 \times P_1$ (3 crosses)	9
F_2: $P_1 \times P_2$ (12 crosses)	687
$P_2 \times P_1$ (6 crosses)	185
BC to P_1: $P_1 \times F_1$ (20 crosses)	61
$F_1 \times P_1$ (14 crosses)	45
BC to P_2: $P_2 \times F_1$ (2 crosses)	7
$F_1 \times P_2$ (28 crosses)	89

Total plants observed: 1141

Twenty-four plants showed severe genetic abberation and were eliminated from the population.

RESULTS

Preliminary Investigations

Plants of OSU 58 (P_1) were all killed at an early date while all plants of OSU 10183 (P_2) were highly resistant, showing only occasional small necrotic spots. A photograph of infection of the two parents and their progenies is shown in Figure 1. The relation of time with death rate in F_2 plants is shown in Figure 2. The fourth reading remained much the same as the third. Data here are reported on the basis of the third reading, when pods were fully mature, and when it was possible to determine with reasonable accuracy those plants killed as a result of systemic infection by the organism and those highly or intermediately resistant. Intermediates were placed in the resistant (surviving) groups. Histograms of relative frequency of resistance ratings are shown on Figures 3 - 8.

Data on resistance rating and flower color for each plant are shown on Table 1.

Mean ratings for disease resistance for both colored and white flower types and for each of eighteen F_2 crosses of the F_2 generation are shown in Table 2. Data were analyzed by analysis of variance.

The F test showed no significant differences for resistance

Figure 1. Halo Blight Infection of P_1(OSU 58), P_2(OSU 10183), and their Progeny.

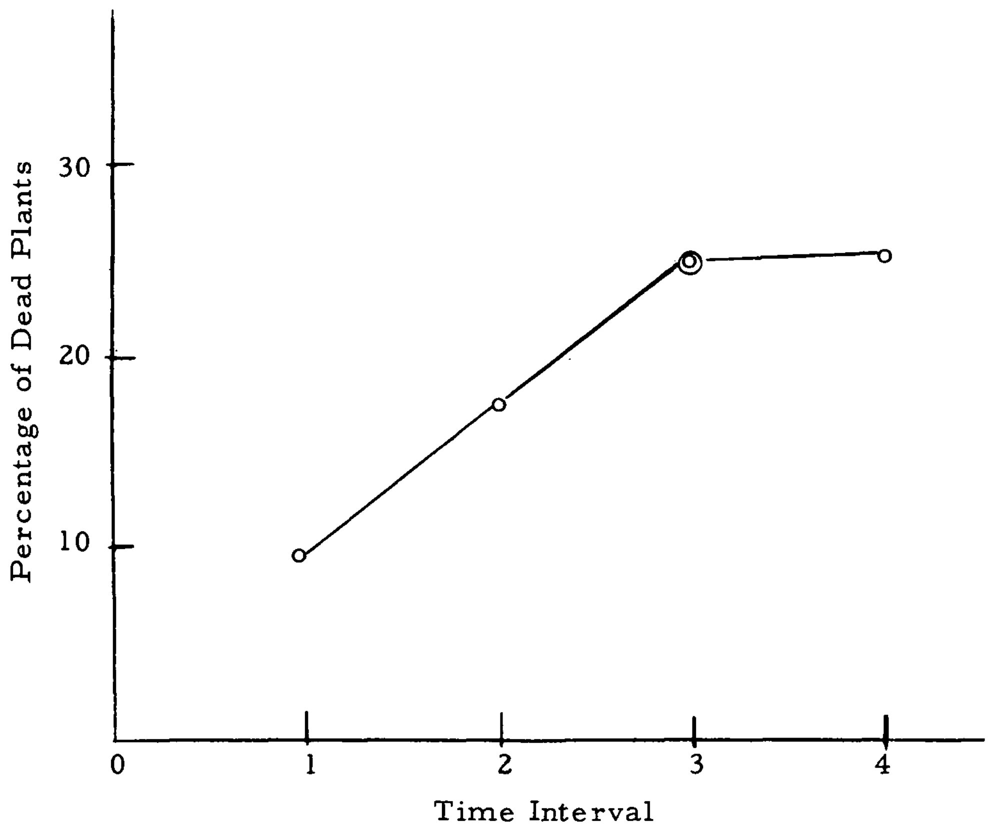

Figure 2. Effect of Time on Percentage of Dead Plants in F_2 Progeny

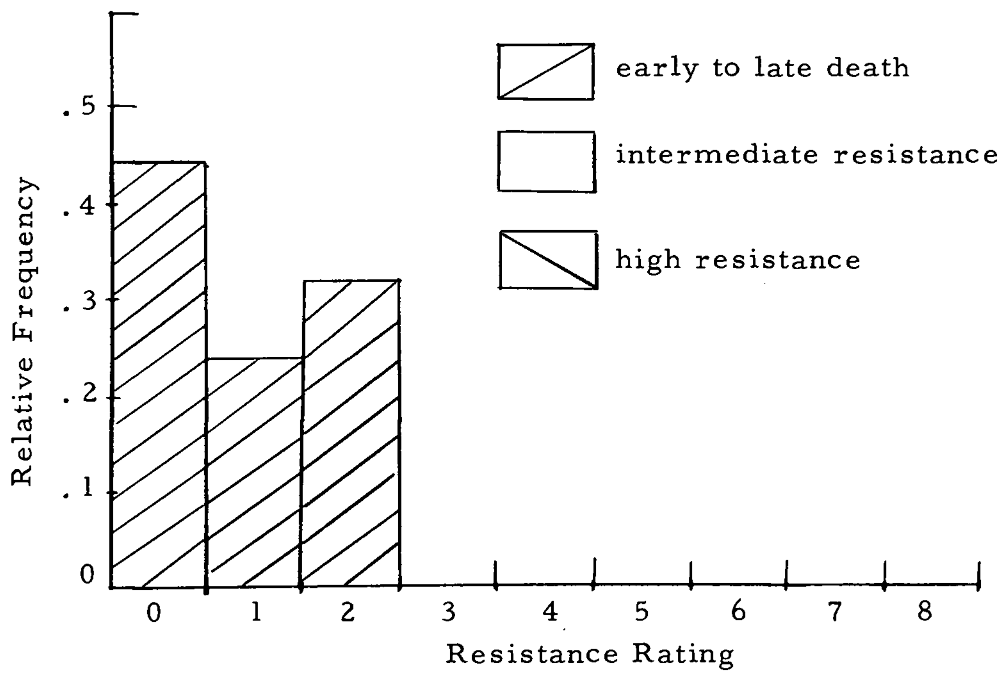

Figure 3. Histogram of Relative Frequency of Resistance Ratings in P_1 (OSU 58)

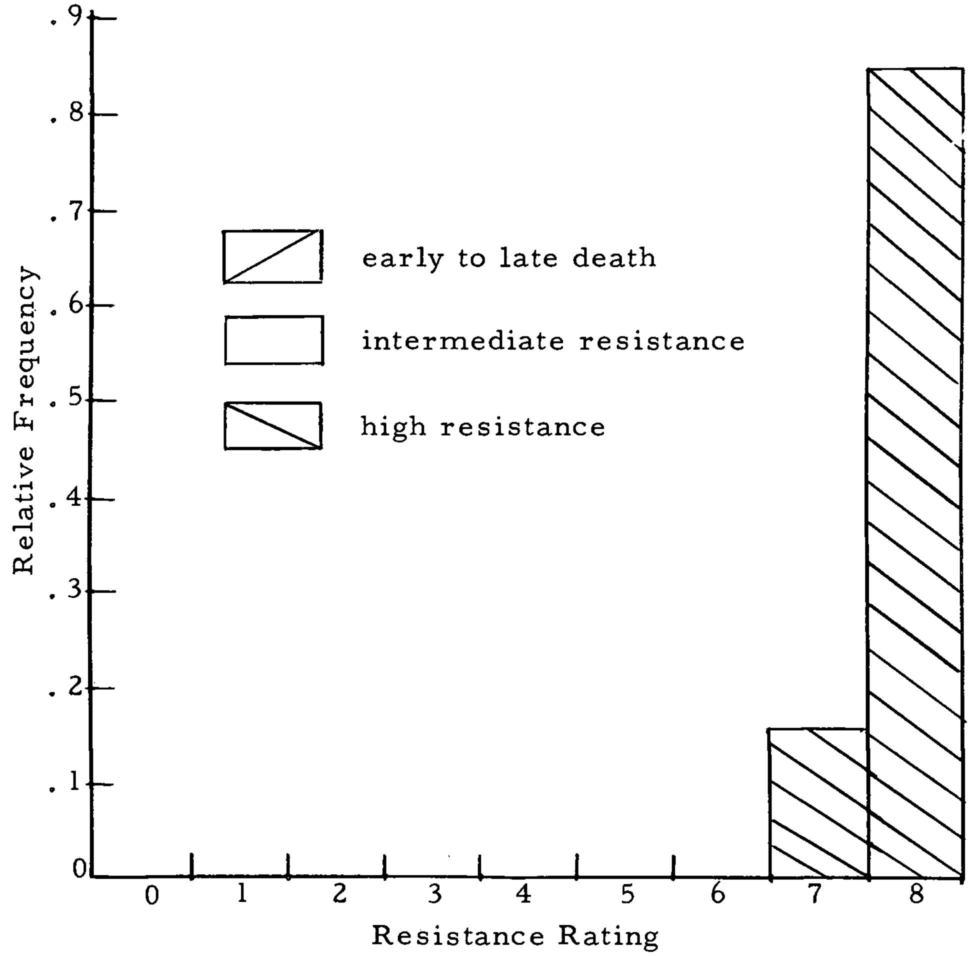

Figure 4. Histogram of Relative Frequency of Resistance Ratings in P_2 (OSU 10183)

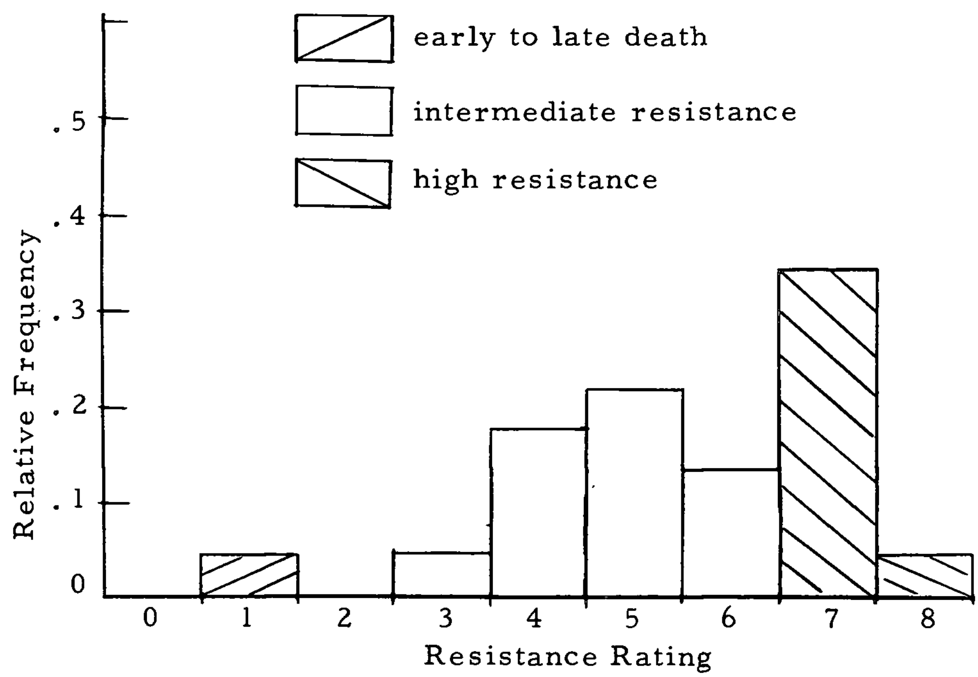

Figure 5. Histogram of Relative Frequency of Resistance Ratings in F_1 Generation

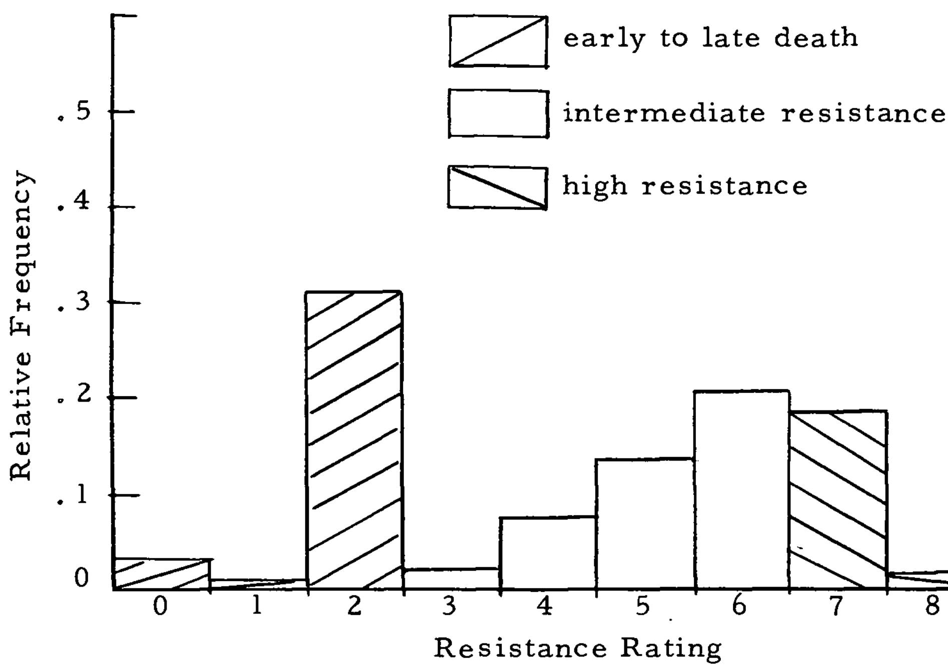

Figure 6. Histogram of Relative Frequency of Resistance Ratings in F_2 Generation

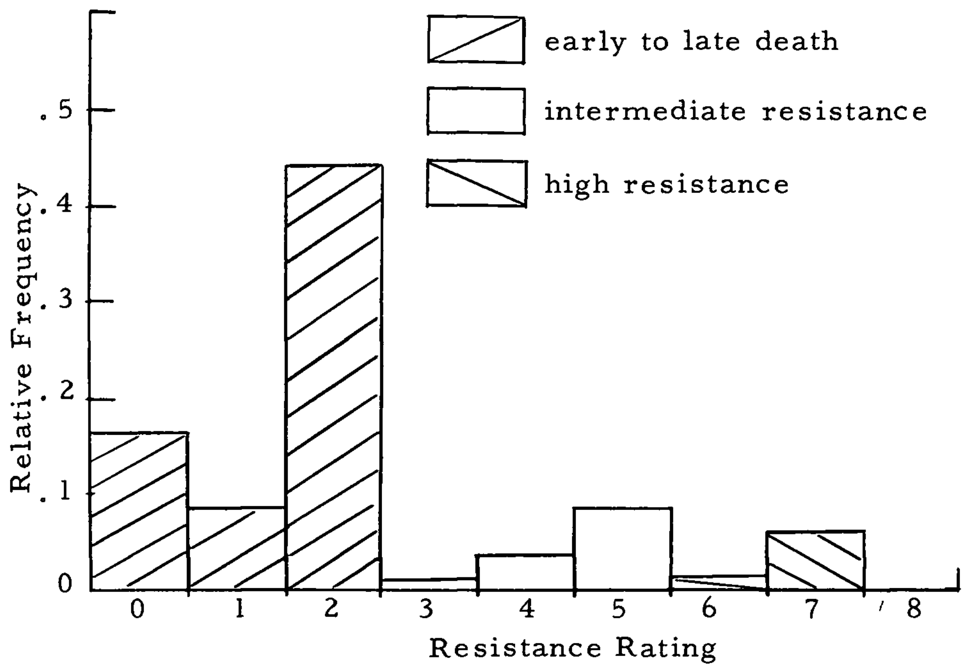

Figure 7. Histogram of Relative Frequency of Resistance Ratings in BC to P_1

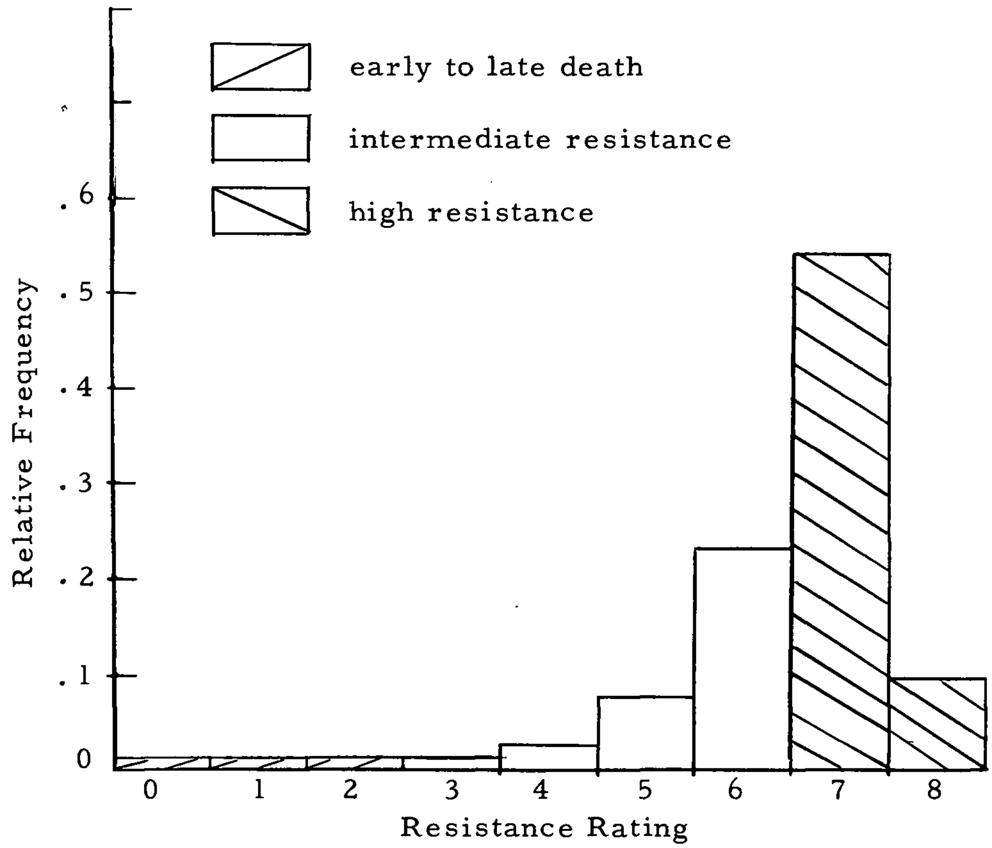

Figure 8. Histogram of Relative Frequency of Resistance Ratings in BC to P_2

Table 1. Segregation for Flower Color and Resistance in Parents, F_1, F_2, and Backcrosses.*

Resistance Rating:	0		1		2		3		4		5		6		7		8		Total	
Source	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W	C	W
P_1 (OSU58)		11		6		8														25
P_2 (OSU10183)															3		16		19	
F_1			1				1		4		5		3		8		1		23	
BC to P_1	6	11	2	7	26	21	1	0	3	1	2	7	7	5	4	3			51	55
BC to P_2	1		1		1		1		2		7		22		52		9		96	
F_2: B2979	1				3		1		3	2	4	3	4	3	2	3		1	17	12
B2980	1	1			4	1					3		9	2	4	2			21	6
B2981		2			5	1				1	3		4	1	9	2			21	7
B2982		1	1		14	2			2	1	2		8	2	8	2			35	8
B2984	1		1		8	4	1	1	1		4	1	16	7	8			1	40	14
B2985	1	1			8	3	2		6	2	4	2	12	2	11	3			44	13
B2986	1	1			4	2	2	1			6		5	5	16	4	5	1	39	14
B2987					8	3		1	3		8	2	14	2	12	1	1	1	46	10
B2997	1		1		6	2		1	2		7	1	13	1	20	4			50	9
B2998	2			1	4	2			1	1	7	2	4	1	3	1			21	8
B2999	2	1			15	3			2		4	1	9	3	11	6			43	14
B3004	2				2	1	3	1	2		2		7	2	5	1			23	5
B3005	3				9	3			1	1	1	3	14	2	14	2	1	1	43	12
B3006			1		13	3			2		7		11	1	12	3	2		48	7
B3007	1	1			9	4	3		8		9		15	2	4				49	7
B3009	3	1	1		6	4	1		5	2	12	2	9	4	4	3			41	16
B3010	1	1		1	14	2	1		6	1	8		11		9	3	2		52	8
B3011			2	1	8	4			9	2	5	7	12	4	10	5			46	23
Total	20	10	7	3	140	44	14	5	52	13	96	24	177	44	162	45	11	5	679	193

*C = colored; W = white

Table 2. Mean Rating of Resistance in Two Flower Color Types

	Mean Rating		No. of Plants		Total
Source	Colored	White	Colored	White	Mean
P_1(OSU58)		0.88		25	0.88
P_2(OSU10183)	7.84		19		7.84
F_1	5.52		23		5.52
BC to P_1	2.92	2.53	51	55	2.72
BC to P_2	6.45			96	6.45
F_2: B2979	4.41	5.83	17	12	5.00
B2980	5.00	4.67	21	6	4.93
B2981	5.33	3.71	21	7	4.93
B2982	4.31	4.30	35	8	4.31
B2984	4.90	4.71	40	14	4.85
B2985	4.89	4.38	44	13	4.77
B2986	5.79	5.21	39	14	5.64
B2987	5.30	4.60	46	10	5.18
B2997	5.48	5.11	50	9	5.42
B2998	4.38	4.00	21	8	4.28
B2999	4.40	5.07	43	14	4.56
B3004	4.70	4.80	23	5	4.72
B3005	5.05	4.92	43	12	5.02
B3006	4.92	4.71	48	7	4.89
B3007	4.53	3.33	49	7	4.38
B3009	4.34	4.44	41	16	4.37
B3010	4.62	3.75	52	8	4.50
B3011	4.80	4.83	46	23	4.81

ratings between colored-flower and white, nor between the eighteen F_2 crosses (see Table 3). Consequently, all the eighteen crosses could be added together to represent the F_2 generation.

Table 3. Analysis of Variance

Source	d. f.	SS	MS	F
Total	35	10.00		
Block (cross)	17	3.80	0.224	0.69 (F 17/17 d.f. = 2.31)*
Treatment (flower color)	1	0.64	0.64	1.99 (F 1/17 d.f. = 4.45)*
Error	17	5.56	0.327	

Conclusion: There was no significant difference within blocks and treatments.

* Significant at the .005 level of probability

Table 4 shows plant distribution on a 0 - 9 scale for resistance.

Table 5 shows segregation for halo blight resistance and flower color. Analysis of the F_2 data shows a single gene pair conditioning halo blight reaction with resistance dominant. The Chi-square value of 0.26 indicated a good fit to a 3:1 ratio.

Flower color was studied for possible linkage with halo blight resistance and as a criterion in determining absence or presence of selfs. A good fit to a 3:1 ratio of colored to white plants was obtained in the F_2 and a 1:1 ratio in the testcross. The results showed that a single gene pair governed flower color.

Table 4. Resistance Distribution for Combined Data.*

Resistance Rating: Source	0	1	2	3	4	5	6	7	8	Total
P_1 (OSU58)	11	6	8							25
P_2 (OSU10183)								3	16	19
F_1		1		1	4	5	3	8	1	23
F_2	30	10	184	19	65	120	221	207	16	872
BC to P_1	17	9	47	1	4	9	12	7		106
BC to P_2	1	1	1	1	2	7	22	52	9	96

*Since there was no linkage between flower color and halo blight resistance, and no significant differences between F_2 progeny of various crosses, data were combined

Table 5. Segregation for Resistance and Susceptibility to Halo Blight and Flower Color in the Cross OSU 58 and OSU 10183.

Generation	Susceptible (Dead)	Resistant (Surviving)	White	Colored	Total No.
P_1 (OSU58)	25		25		25
P_2 (OSU10183)		19		19	19
F_1	1	22		23	23
F_2	224	648	193	679	872
BC to P_1	73	33	55	51	106
BC to P_2	3	93		96	96

Calculation of Chi-square Test

χ^2 test for resistance in the F_2 generation:

3:1 ratio

Observed	Calculated	O-C	$(O-C)^2/C$
224	218	6	0.165
648	654	6	0.055
		χ^2 =	0.220

The correction for continuity:

$$\chi_c^2 = (X_1 - m_1 - 0.5)^2 \left(\frac{1}{m_1} + \frac{1}{m_2}\right)$$

$$= 0.2584$$

(m: calculated value, X: observed value)

With 1 d.f. for P = 0.05 (odds 19:1) is 3.84.

With 1 d.f. for P = 0.01 (odds 99:1) is 6.64.

χ^2 test to a 3:1 ratio for flower color of the F_2 generation:

Observed	Calculated	O-C	$(O-C)^2/C$
193	218	-25	2.867
679	654	25	0.956

χ^2 = 3.823, χ_c^2 = 3.671

χ^2 test to a 1:1 ratio for flower color of the test cross:

Observed	Calculated	O-C	$(O-C)^2/C$
51	53	-2	0.0755
55	53	2	0.0755

χ^2 = 0.151, χ_c^2 = 0.085

Test of Independence

1. 2 x 2 contingency table

B \ A	1	2	Total
1	X_{11}	X_{12}	$X_{1.}$
2	X_{21}	X_{22}	$X_{2.}$
Total	$X_{.1}$	$X_{.2}$	$X_{..}=N$

Here, $X_{1.}$ represents Colored

$X_{2.}$ represents White

$X_{.1}$ represents Resistant

$X_{.2}$ represents Susceptible

Therefore, $X_{11}= 512$, $X_{12} = 167$, $X_{21} = 136$, $X_{22} = 57$

$X_{1.} = 679$, $X_{2.} = 193$, $X_{.1} = 648$, $X_{.2}= 224$,

$X_{..} = 872$

$$\chi^2 = \frac{\left\{ \left|X_{11}X_{22}-X_{12}X_{21}\right| \frac{N}{2} \right\}^2 N}{(X_{1.})(X_{2.})(X_{.1})(X_{.2})} = 1.666 < \chi^2 \left({}^{1\ \text{d.f.}}_{p=0.05} \right) = 3.841$$

Chi-square value of 1.666 shows that disease reaction and flower color are independently inherited.

2. A 9:3:3:1 ratio involving flower color and halo blight reaction.

$$\chi^2 = \frac{16(X_1^2+3X_2^2+3X_3^2+9X_4^2}{9N} - N$$

Calculated value for Chi-square is $5.75 < \chi^2$ (3 d.f. $p = 0.05$)

$= 7.81$.

The characters of flower color and halo blight reaction, each being governed primarily by a single gene, are not linked. Inheritance of the two characters shows independent assortment.

<u>Calculation of the Percentage Recombination by Product Method</u>

cross	$\frac{a}{(AB)}$	$\frac{b}{(Ab)}$	$\frac{c}{(aB)}$	$\frac{d}{(ab)}$	Total
phenotype	C-R	C-S	W-R	W-S	
	512	167	136	57	872

Cross was made from coupling, the ratio of products = $\frac{bc}{ad}$.

$$\frac{bc}{ad} = \frac{167 \times 136}{512 \times 57} = 0.7782$$

From Immer and Henderson's table, recombination fraction = 0.465,

$$S.E. = \frac{0.7246}{\sqrt{872}} = 0.025$$

$\therefore$ percentage of recombination = 46.5 ± 2.5

Again, the percentage recombination indicates independent assortment.

DISCUSSION AND CONCLUSIONS

Although behavior of the F_1 plants showed resistance to halo blight to be dominant, none of the F_1 plants were as highly resistant as the resistant parent. Our results do not agree with those of Pryke (14) who found that resistance was completely dominant.

While the data showed a single gene largely conditioning ultimate death of the plants, many of the F_2 plants so classified were much slower in dying than plants of the susceptible parent. Time acted as a factor affecting death rate. Susceptibility of a bean plant depended on the date recorded and on the definition of "susceptible." Also, only a relatively few plants considered resistant (surviving) were as resistant as the resistant parent. Obviously, additional genes are in play and this is confirmed by the behavior of the backcross progeny. These results indicate the danger in forming conclusions, with respect to disease reaction, without using a back cross test. Interplay of variation within the bacterium with host plant variation must also be recognized. Use of F_3 generation families, not possible in this study, should yield useful information in clarifying the genetic nature of the disease reaction.

Reciprocal crosses were made in case there should be cytoplasmic inheritance. Statistical analysis demonstrated no maternal effect in the reaction to halo blight.

Chi-square values of 3.671 and 0.085 indicate a good fit to a 3:1 ratio of colored to white flower in the F_2 and a 1:1 ratio in the testcross, respectively. These results conform with those of Johannsen (11) who found that one factor governed flower color. Shaw (16) and Shaw and Norton (17) reported that blossom color was due to a single gene. Schuster (15) stated that a single gene pair governed flower color.

Since the cross was made from coupling, 44 percent to 49 percent of recombination was obtained by using the product method. Again, a Chi-square value of 5.75 shows a good fit to a 9:3:3:1 ratio involving flower color and halo blight reaction. The characters of flower color and halo blight resistance, each being controlled by a single gene, are not linked. The inheritance of these two characters shows independent assortment.

Transfer of halo blight resistance to a high pod quality, white flower, white seeded bean out of the OSU 10183 x OSU 58 cross appears feasible, yet rigorous testing for resistance, selection for horticultural characters, followed by back crossing to OSU 58 will be required.

SUMMARY

Inheritance of resistance to halo blight, Pseudomonas phaseolicola (Burk.), in the OSU 10183 was studied, preliminary to initiation of a breeding program to transfer resistance to commercially desirable plant types.

OSU 58 and OSU 10183 were used as susceptible and resistant parents, respectively. The former, a bush bean approaching pod quality of Blue Lake pole bean, combines good bush growth habit with high quality; it is a bush green podded, white flowered, white seeded line, while OSU 10183 lacks several good horticultural characteristics, and has colored flowers and black seeds.

The two lines were hybridized in the greenhouse. The F_2 seed and seed of F_1's backcrossed to resistant and susceptible parents were secured in the field. The two parents, the F_1, F_2, and backcrosses were planted and tested in the greenhouse.

Plants were inoculated by spraying with a bacterial suspension when the first trifoliate leaf was fully expanded. Inoculation was made twice to insure heavy infection of susceptible plants. A rating scale of 0 to 9 was used in determining the degree of susceptibility and resistance, with 0 highly susceptible and 9 immune.

Behavior of the F_1 plants showed resistance to be highly dominant, but not completely so. Although data showed a single

gene largely conditioning ultimate death of the plants, many of the F_2 plants so classified were much slower in dying than plants of the susceptible parents. The behavior of backcross progeny confirmed the additional genes are in play in the interaction of host and pathogen.

Blossom color was conditioned by a single gene, with color dominant. Chi-square value of 5.75 shows a good fit to a 9:3:3:1 ratio involving flower color and halo blight reaction. The characters of flower color and halo blight resistance are not linked; this is confirmed by a percentage of recombination of 46.5 ± 2.5, using the product method.

Transfer of halo blight resistance to a high pod quality, white seeded bean out of the OSU 10183 x 58 cross appears feasible; yet rigorous testing for resistance, selection for horticultural characters, followed by back crossing to OSU 58 will be required.

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