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INHERITANCE AND LINKAGE RELATIONS OF REACTION TO *XANTHOMONAS PHASEOLI* (E. F. SMITH) DOWSON (COMMON BLIGHT), STAGE OF PLANT DEVELOPMENT AND PLANT HABIT IN *PHASEOLUS VULGARIS* L.[1]

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SUMMARY

The inheritance of the reaction to *Xanthomonas phaseoli* (E. F. SMITH) DOWSON Nebraska isolate Xp-816, cause of common blight disease of beans *Phaseolus vulgaris* L. was studied in crosses between the late flowering, indeterminate, blight tolerant dry bean PI 207262 (Colombia) and susceptible cvs. GN 1140, an early flowering and indeterminate dry bean; Dark Red Kidney, a late flowering and determinate dry bean; and Gallatin 50, an early and determinate green bean. The tolerant disease reaction was dominant in the F_1. A continuous distribution of disease reaction ratings, skewed in the direction of dominance, occurred in the F_2 derived from the first 2 crosses while a slight bimodal distribution was observed in the F_2 of the last cross. A low narrow sense heritability estimate of 14% was calculated by the regression of F_3 progeny means on individual F_2 plants, in the cross GN 1140 × PI 207262. The occurrence of a small number of nonsegregating families in a low number of F_3 families indicates that a small number of major genes were involved in controlling the disease reaction. Linkage did not appear to be involved between genes controlling early flowering (early maturity) and common blight tolerance. Coupling linkage occurred between genes controlling determinate plant habit and early flowering. A crossover value of 8.4% was estimated. Recombinants for early maturity, determinate habit, and blight tolerance were obtained. Transgressive segregation for early flowering and common blight susceptibility occurred in progeny derived from the cross of the two late-flowering blight tolerant lines, PI 207262 and GN Nebraska 1, sel. 27, indicating that the parents possessed different genes controlling these traits.

INTRODUCTION

Common blight, caused by *Xanthomonas phaseoli* (E. F. SMITH) DOWSON and the variant *X. phaseoli* var. *fuscans* (BURK.) STARR and BURK., is a serious disease of *Phaseolus vulgaris* dry bean types. The importance and distribution of this disease is discussed in reviews by ZAUMEYER & THOMAS (1957) and by LEAKEY (1973). SAETTLER (1972) was not successful in controlling the disease by chemicals. Recommended procedures to reduce the incidence of the disease in the United States are rotation and use of certified blight-free seed produced under irrigation in arid areas of Idaho and California where climatic conditions are generally unfavorable for the development and spread of the disease. SCHUSTER (1967) observed that the bacteria survive over

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winter in infected debris on the soil surface and can cause infection of the next bean crop.

The use of tolerant commercial dry bean cultivars should provide an additional control measure in a protection system to reduce disease losses. However, few tolerant cultivars have been introduced as yet. COYNE & SCHUSTER (1969, 1970) in Nebraska, USA, introduced the blight tolerant Great Northern cvs. Tara and Jules, and Dr. Luis CAMACHO, ICA, Colombia, released cv. Guali (personal correspondence). New breeding programs to develop common blight tolerant dry bean cultivars have been initiated at Michigan State University and Cornell University, USA, and also in Uganda and Malawi (personal correspondence and/or visits) and new tolerant varieties will be available in the future.

New sources of tolerance to *X. phaseoli* have been identified by COYNE et al. (1963, 1973) and numerous sources of tolerance have been reviewed by *Leakey* (1973). Recently SCHUSTER et al. (1973) found that *P. vulgaris* PI 207262 (Colombia) dry bean had high tolerance to virulent strains from Uganda, Colombia, and the United States, while Great Northern (GN) Nebraska 1, sel. 27, highly tolerant to all tested isolates in the United States, was moderately susceptible to former strains. PI 207262 should be a useful source of tolerance to develop blight tolerant cultivars in Uganda and Colombia and also to broaden the genetic base for tolerance to strains present in the USA. The inheritance of the disease reaction to *X. phaseoli* has been reported by several workers. HONMA (1956), COYNE (1965, 1973) and POMPEU (1972) found the disease reaction quantitatively inherited and COYNE et al. (1973) reported linkage between genes controlling late maturity, a delayed flowering response under long photoperiod $\times$ high temperature, and high blight tolerance. This presented a problem in developing adapted early blight tolerant cultivars until COYNE et al. (1973) recently succeeded in breaking the linkage.

This paper reports on the inheritance of disease reaction to *X. phaseoli* Nebraska isolate in crosses between PI 207262 and susceptible cultivars and linkage relations with the traits, maturity and plant habit. The relationship of genes controlling the tolerant reaction to the Nebraska isolate and time of flowering in the common blight tolerant lines PI 207262 and GN Nebraska 1, sel. 27 is also reported.

MATERIAL AND METHODS

Crosses were made between the mottled brown pea bean shaped, late maturing, indeterminate, common blight tolerant PI 207262 (Colombia) and the susceptible cvs. Great Northern (GN) 1140, an early and indeterminate white seeded dry bean; Dark Red Kidney, a late and determinate dry bean; and Gallatin 50, an early and determinate green bean. In addition, PI 207262 was crossed with another late maturing indeterminate common blight tolerant dry bean GN Nebraska 1, sel. 27. The F_1 plants of all crosses were grown in the greenhouse to produce F_2 seed.

The leaf water soaking method of inoculation, developed by SCHUSTER (1955), was used in all experiments. Two-day-old cultures of *Xanthomonas phaseoli* Nebraska isolate Xp-816 were used to prepare bacterial suspensions. The bacterial colonies were washed off the plates with water and diluted until the concentration of cells was approximately 1.64×10^7 cells/ml. The plants in all experiments were inoculated when

early cv. GN 1140 was in flower. The suspension was sprayed on each plant at about 120 p.s.i to induce water soaking of some leaves. The disease reaction was recorded for each plant in all populations and a numerical scale used as described in the footnote to Table 1. The plant habit, determinate or indeterminate, and stage of plant development, vegetative, flowering, flat pod, filled pod, or ripe pod were also recorded at this time.

The date of opening of the first flower on each plant in all populations was recorded and the number of days from planting to flowering was calculated.

The seed of all populations was spaced about 30.5 to 45.7 cm apart in rows 50.8 cm apart to facilitate ease of examination of each plant. The number of plants in each population is recorded in the Tables. Two to four rows, 4.57 to 15.24 m long of each of the tolerant and susceptible parents were planted at intervals in the plot as disease checks. The check cultivars were highly uniform for tolerance or susceptibility in all plots in each year.

In 1972 the parents, and F_2 generations of the crosses GN 1140 $\times$ PI 207262 and PI 207262 $\times$ GN Nebraska 1, sel. 27 were planted at Lincoln, Nebraska, on May 30. The F_1 of the former cross was also planted. The plants were inoculated on July 17 and disease reactions recorded August 1. Plants were randomly selected in the F_2 GN 1140 $\times$ PI 207262 to grow F_3 progeny in 1973, while in the other F_2 population white seeded early maturing common blight tolerant segregates were selected.

In 1973 the parents, F_2 and F_3 populations (selected as described above) of the following crosses were planted at Lincoln on May 15; Gallatin 50 $\times$ PI 207262, PI 207262 $\times$ GN Nebraska 1, sel. 27. The F_1 of the latter cross was also planted. In addition, the parents, F_1 and F_2 generation of the cross PI 207262 $\times$ Dark Red Kidney were planted. The plants were inoculated on June 25 and rated for disease reaction on July 25 and 26.

Heritability of the disease reaction was estimated by using the regression of F_3 progeny means on individual F_2 plants. Linkage strength was estimated from the product ratio using Tables prepared by STEVENS (1939).

RESULTS

Severe disease symptoms developed on all plants of the susceptible cvs. GN 1140, Dark Red Kidney and Gallatin 50 in all tests (Table 1). The 2 tolerant lines, GN Nebr. 1, sel. 27 and PI 207262, showed no disease symptoms before flowering and only slight disease symptoms after flowering (Table 1). The former line had slightly higher tolerance than the latter. Dominance for the tolerant reaction was observed in the F_1 PI 207262 $\times$ GN 1140, and PI 207262 $\times$ Dark Red Kidney. A continuous distribution of disease ratings, skewed in the direction of dominance, occurred in these F_2 populations. Plants in all F_2 populations had disease reaction ratings ranging from high tolerance to high susceptibility. A slight bimodal distribution was observed in the F_2 Gallatin 50 $\times$ PI 207262 suggesting that major genes may be involved in controlling the disease reaction. Modifying genes and environmental effects may also contribute to the observed variation. One nonsegregating family for high tolerance and one for susceptibility, occurred in 35 F_3 families in the cross PI 207262 $\times$ GN 1140. Out of 19 F_3 families in the cross PI 207262 $\times$ Gallatin 50, one nonsegregating family for

Table 1. Frequency distribution in number of plants for common blight disease reaction ratings, maturity, and/or plant habit in the parents, F_1 and F_2 generations derived from the crosses of tolerant PI 207262 and 3 susceptible cultivars.

Year	Generation	Maturity and/or plant habit	Disease reaction ratings[1]					Plant habit		Maturity[2]		Expected ratio	χ^2	P
			1	2	3	4	5	indet.	det.	late	early			
			number of plants											
1972	GN 1140	early – indet.	–	–	–	–	143							
	PI 207262	late – indet.	–	139	–	–	–							
	F_1 GN 1140 × PI 207262	early – indet.	–	5	–	–	–							
	F_2 GN 1140 × PI 207262	early	–	15	7	3	3							
	F_2 GN 1140 × PI 207262	late	–	7	3	2	9							
Column totals			–	22	10	5	12			15	34	1:3	0.79	>0.30
1973	Dark Red Kidney	late – det.	–	–	–	26	–							
	PI 207262	late – indet.	–	13	–	–	–							
	F_1 PI 207262 × Dark Red Kidney	late – indet.	–	25	–	–	–							
	F_2 PI 207262 × Dark Red Kidney	det.	–	2	4	2	–							
	F_2 PI 207262 × Dark Red Kidney	indet.	–	16	9	6	–							
Column totals			–	18	13	8	–	31	8			3:1	1.96	>0.50
1973	Gallatin 50	early – det.	–	–	–	21	–							
	F_2 Gallatin 50 × PI 207262	early – det.	–	2	1	31	3							
	F_2 Gallatin 50 × PI 207262	early – indet.	–	1	1	6	–							
	F_2 Gallatin 50 × PI 207262	late – det.	–	–	1	5	–							
	F_2 Gallatin 50 × PI 207262	late – indet.	–	66	33	15	1							
Column totals			–	69	36	57	4	123	43			3:1	0.08	>0.70
										121	45	3:1	0.38	>0.50

[1] Disease rating classes: 1, no visible symptoms; 2, slight, small lesions on about 1–5% of leaves; 3, moderate lesions of various sizes, some leaves chlorotic; 4, severe, many large lesions on most leaves, pronounced chlorosis and necrosis; 5, very severe, plants chlorotic, necrotic, and largely defoliated.
[2] Maturity: Late, plants which started flowering in 70–89 days from date of planting. These were vegetative or starting to flower at date of recording disease reaction; early, plants which started flowering in 30–49 days from date of planting. These had well filled pods at the time of recording the disease reaction.

high tolerance and three for susceptibility were observed (Tables 2 and 3). This indicated that only a small number of major genes were involved in determining the disease reaction.

A narrow sense heritability estimate of 14% was calculated. This low value is due to the large environmental effects on disease reaction, variation in the amount of in-

Table 2. Frequency distribution in number of plants in disease reaction classes in the F_3 families derived from the cross PI 207262 × GN 1140 and the disease reaction of each F_2 parent plant.

Reaction rating F_2 parent plant	F_3 Code	Disease ratings[1]					Number of plants	F_3 mean
		1	2	3	4	5		
		Number of plants						
2	3	–	1	6	14	6	27	3.9
2	4	–	8	3	1	–	12	2.4
5	5	–	–	4	4	2	10	3.8
3	6	–	6	–	1	–	7	2.3
5	7	–	4	4	10	3	21	3.6
4	8	–	1	7	4	3	15	3.6
3	9	–	5	–	–	–	5	2.0
5	10	–	1	5	18	2	26	3.8
5	11	–	3	1	2	1	7	3.1
5	12	–	2	8	2	–	12	3.0
2	13	–	6	1	–	–	7	2.1
5	15	–	11	2	1	–	14	2.3
3	16	–	8	5	1	–	14	2.5
3	17	–	1	2	4	–	7	3.4
5	18	–	2	2	–	–	4	2.5
5	19	–	–	–	15	–	15	4.0
5	20	–	3	3	2	2	10	3.3
2	23	–	4	11	3	–	18	2.9
3	22	–	1	5	2	–	8	3.1
2	26	–	10	6	–	–	16	2.4
2	27	–	13	7	3	–	23	2.6
2	28	–	6	10	3	1	20	3.0
2	29	–	2	1	–	–	3	2.3
2	30	–	2	10	2	–	14	3.0
2	31	–	3	3	–	–	6	2.5
2	32	–	4	7	6	1	18	3.2
2	33	–	2	3	5	–	10	3.3
2	36	–	2	9	–	–	11	2.8
2	37	–	2	1	1	–	4	2.8
2	39	–	–	8	2	–	10	3.2
2	40	–	–	1	8	1	10	4.0
2	41	–	2	3	–	–	5	2.6
3	42	–	3	13	10	–	26	3.3
4	43	–	6	1	1	–	8	2.4
2	44	–	11	3	–	–	14	2.2
GN 1140 (sus.)		–	–	–	–	102		
PI 207262 (tol.)		–	55					

[1] Disease rating scale: see footnote in Table 1.

Table 3. Frequency distribution in number of plants in disease reaction classes in F_3 families derived from the cross PI 207262 × Gallatin 50.

F_3 family	Disease ratings[1]					Number of plants	F_3 mean
	1	2	3	4	5		
	Number of plants						
1	–	7	4	6	–	17	2.9
2	–	4	–	1	1	6	2.8
3	–	–	–	8	–	8	4.0
4	–	5	2	–	–	7	2.3
5	–	–	–	6	–	6	4.0
6	–	5	1	3	–	9	2.8
7	–	5	3	7	–	15	3.1
8	–	–	–	3	–	3	4.0
9	–	3	4	4	1	12	3.3
10	–	3	–	1	–	4	2.5
11	–	–	–	6	–	6	4.0
12	–	2	11	–	–	13	2.9
13	–	5	4	2	–	11	2.7
14	–	1	4	3	–	8	3.3
15	–	5	2	2	–	9	2.7
16	–	6	–	–	–	6	2.0
17	–	1	–	1	1	3	3.7
18	–	2	1	3	–	6	3.2
19	–	6	–	1	–	7	2.3
Checks							
Gallatin 50 (sus.)	–	–	–	15	6		
PI 207262 (tol.)	–	55	–	–	–		

[1] Disease rating scale: see footnote in Table 1.

oculum sprayed on each plant, and the difficulty of classifying plants which had intermediate disease reaction ratings on the scale of 1 to 5.

Early flowering (early maturity) was controlled by a single dominant gene in the cross F_2 GN 1140 × PI 207262, while a recessive gene was involved in controlling this trait in the cross Gallatin 50 × PI 207262 (Table 1). A recombination of early maturity and high blight tolerance, was observed in all F_2 and F_3 populations. Plant habit, indeterminate versus determinate, was under monogenic control with the indeterminate habit dominant in the crosses PI 207262 × Dark Red Kidney and Gallatin 50 × PI 207262. Coupling linkage was detected between the genes controlling determinate plant habit and early maturity (Table 4) in the cross Gallatin 50 × PI 207262. A crossover value of 8.4% was estimated.

In both 1972 and 1973, transgressive segregation for early flowering and maturity was observed in the F_2 generation of the cross between the two late flowering and late maturing common blight tolerant lines PI 207262 and GN Nebraska 1, sel. 27 (Table 5). There was a much greater range in date of flowering of the plants in 1972 than in 1973. The date of first bloom of the parents was earlier in 1972 than in 1973. The F_1 was similar to the parents in number of days to flowering. Some transgressive segregation for common blight susceptibility was observed but none for increased

Table 4. Segregation for maturity (late, early) and plant habit (indeterminate, determinate) in the F_2 Gallatin 50 × PI 207262.

	Parental types		Recombination types		χ^2	P
	late, indet.	early, det	early, indet.	late, det.		
Observed	115	37	8	6		
Expected	93.6	10.4	31.2	31.2	110.4	<0.001

Linkage $\chi^2 = 110.4 - 0.08 - 0.38 = 109.94$; P ($\chi^2 \geq 109.94$) <0.001

Table 5. Frequency distribution in number of plants for disease reaction and number of days to first bloom in the cross between the two late-flowering common blight tolerant lines PI 207262 and GN Nebr. 1, sel. 27.

Year	Generation	Disease reaction rating[1]	Days to first bloom									
			30 39	40 49	50 59	60 69	70 79	80 89	90 99	100 109	110 119	120 129
			Number of plants									
1972	PI 207262	2			17	10	10	53	18	19	10	
	GN Nebr. 1, sel. 27	2			68	40	10	1				
	F_2 GN Nebr. 1, sel. 27	2	14	78	26	25	46	42	9	58	41	8
	F_2 GN Nebr. 1, sel. 27	3	2	4	2		5			4	2	
	F_2 GN Nebr. 1, sel. 27	4	1							1		
	F_2 GN Nebr. 1, sel. 27	5		1								
Column totals			17	83	28	25	51	42	9	63	43	8
1973	PI 207262	2						31				
	GN Nebr. 1, sel. 27	2					23	6				
	F_1 PI207262 × GN Nebr. 1, sel. 27	2						36				
	F_2 PI207262 × GN Nebr. 1, sel. 27	–		2	4	1	3	6				

[1] Disease rating scale: see footnote in Table 1.

Table 6. Segregation of common blight disease reaction ratings in F_3 families derived from the cross PI 207262 × GN Nebr. 1, sel. 27.

F_3 breeding behavior	Number of families
Nonsegregating for early flowering and high common blight tolerant reaction[1]	4
Nonsegregating for early flowering and segregating for disease reaction	5
Segregating for early flowering and disease reaction	9

[1] Plants flowering less than 60 days were classified as early flowering. PI 207262 bloomed in 80–89 days and GN Nebr. 1, sel. 27 bloomed in 70 to 89 days.

tolerance (Table 5). Out of 18 F_3 families derived from this cross, ranging in plant number from 7 to 26, 4 were nonsegregating for both early maturity and a high common blight tolerance (Table 6). This indicated that lines possessing different genes controlling a common blight tolerant reaction and early flowering can be recombined.

DISCUSSION

The difficulty of recombining earliness and high common blight tolerance, when using GN Nebraska 1, sel. 27 as a source of tolerance, due to fairly tight linkage was previously reported by COYNE et al. (1973). This problem can be overcome by using PI 207262 (Colombia) as a source of tolerance since earliness and blight tolerance were recombined in progeny derived from crosses reported here. We found that PI 207262 possesses different genes for tolerance to *X. phaseoli* Nebraska isolate than GN Nebraska 1, sel. 27 indicating that it would be desirable to utilize this new germplasm in breeding programs in the USA. In addition, PI 207262 has high tolerance to isolates of *X. phaseoli* from Colombia and Uganda (SCHUSTER et al., 1973) and should be useful germplasm for bean breeders in those countries.

COYNE et al. (1965) previously reported a low narrow sense heritability of 13% and the estimate obtained here agrees closely with that estimate. POMPEU (1972) obtained a narrow sense heritability of 45% in genetic studies conducted in growth chambers. The difference in values may be due to the more uniform environment in the growth chambers and probably the greater reliability of rating the disease reaction on a small part of a leaf using the multiple needle inoculation method in comparison with rating the disease reaction on a whole plant basis in the field. Considerable variation in the amount of water soaking of leaves between plants during inoculation occurred in the field and this may have contributed to the disease variation between plants. We studied the disease reaction in mature plants while POMPEAU (1972) used seedlings. COYNE et al. (1973) reported that the stage of plant development affects the disease reaction and that tolerance decreases with age. This factor may also have contributed to the different results.

COYNE (1966, 1970) found that the delayed flowering response in beans under long photoperiods and high temperature resulting in late maturity was under genetic control. GN 1140 possessed a major dominant gene which controlled early flowering response under long days and high temperature (COYNE, 1970). This gene can be readily transferred by backcrossing, and recombined readily, as shown here, with tolerance to *X. phaseoli*. In other crosses with PI 207262 the delayed flowering response was controlled by a major dominant gene. The results reported here show that PI 207262 and GN Nebraska 1, sel. 27 have different genes controlling the delayed flowering response, and blight tolerant transgressive early maturing segregates were obtained from the cross of these 2 parents. These recombinants should be useful as they possess genes controlling early flowering along with different genes controlling a tolerant reaction to *X. phaseoli* Nebraska strain.

ALLARD & ZAUMEYER (1944) reported that the bush (determinate) beans they tested were day neutral. Our results indicate that this is due to the linkage of the recessive genes controlling determinate plant habit and early flowering. RUDORF (1958) reported that the gene controlling the determinate plant habit was completely epistatic to the gene controlling the delayed flowering response under long days. If this was a general effect, then all determinate beans would be day neutral. This is not the case since COYNE (1966) has reported previously on the occurrence of photoperiodic sensitive determinate bean lines. We also found determinate late flowering segregates in the present crosses indicating that an epistatic effect of the gene for determinate plant

habit was not involved.

GN Nebraska 1, sel. 27 and PI 207262 possess a high level of tolerance to *X. phaseoli*. However, COYNE et al. (1973) were able to isolate considerable bacterial populations from infected plants. This has serious implications for the breeders and seed producers of tolerant varieties. WELLHAUSEN (1973) and LINCOLN (1940) found that the virulence of a bacterial population increased through mutation and selection during passage through a tolerant host. Thus, in order to reduce the possibility of breakdown of tolerance due to the emergence of more virulent strains and races, seed of tolerant varieties should be saved from plants which are free of bacteria.

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