Allelism Tests of Three Dominant Genes for Hypersensitive Resistance to Bacterial Spot of Pepper

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Florida Agricultural Experiment Stations Journal Series 7540.
Accepted for publication 5 February 1987.

ABSTRACT

Hibberd, A. M., Bassett, M. J., and Stall, R. E. 1987. Allelism tests of three dominant genes for hypersensitive resistance to bacterial spot of pepper. Phytopathology 77:1304-1307.

Three previously reported genes, *Bs*1, *Bs*2, and *Bs*3, for hypersensitive resistance to races of *Xanthomonas campestris* pv. *vesicatoria* were tested for allelism in four pepper (*Capsicum annuum*) crosses involving the parents 271-4, Delray Bell, Florida XVR 3-25, Early Calwonder, and Early Calwonder 10 R. Breeding line 271-4, which is resistant to both races 1 and 2, was a selection from PI 271322, and Early Calwonder 10 R is near-isogenic with Early Calwonder but carries resistance gene *Bs*1. Bacterial suspensions of 5×10^8 cfu/ml of races 1 and 2 were infiltrated into leaf mesophyll. Hypersensitive resistance was assessed 24 hr after infiltration. Segregation in progenies from four crosses, 271-4 × Delray Bell, 271-4 × Florida XVR 3-25, 271-4 × Early Calwonder, and 10 R × XVR 3-25, indicated that the dominant genes *Bs*1, *Bs*2, and *Bs*3 are independent. It was also indicated that *Bs*2 controls hypersensitive resistance to both races 1 and 2 and that the resistance genotype of 271-4 was *Bs*1 *bs*2 *Bs*3. The resistance genotypes were confirmed to be *Bs*1 *Bs*2 *bs*3 for Florida XVR 3-25 and *Bs*1 *bs*2 *bs*3 for both Delray Bell and 10 R.

Bacterial leaf spot, incited by *Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye (*X. c.* pv. *vesicatoria*), is difficult to control on bell pepper (*Capsicum annuum* L.) in warm, humid environments where the bacterium is endemic (12,15,16). Sanitation has not been sufficient to eliminate the need for chemical and genetic control of *X. c.* pv. *vesicatoria*. Chemical control relies on frequent sprays with mixed copper and mancozeb (14) or copper and zineb (1). Even the most efficient spray regime is not highly effective during periods of high disease pressure. Also, genetic resistance is the more energy-efficient and cost-effective method of disease control.

Three dominant genes, designated *Bs*1, *Bs*2, and *Bs*3, were reported to control hypersensitive reactions (HR) and were in pepper introductions PI 163192 (5), PI 260435 (3,4), and PI 271322 (9), respectively. The gene symbols were given in the order of discovery (9,13), but it is not known whether any of the genes are allelic to each other.

Pathogenic variation within *X. c.* pv. *vesicatoria* has been demonstrated by inoculating pure cultures into plants carrying the appropriate genes for resistance. The gene *Bs*1 controls HR to race 2 of the pathogen (5,6), and genes *Bs*2 and *Bs*3 each control HR to race 1 (4,9). Thus, races 1 and 2 were differentiated by reaction to pepper plants with *Bs*1 (6). Races 1 and 2 are common in Florida, but race 1 predominates in other pepper production areas of the world (7,9).

We observed that some plants of PI 271322, the source of *Bs*3, were hypersensitive to strains of *both* races 1 and 2, and we hypothesized that these plants may carry two genes for HR. Similarly, Florida XVR 3-25 is known to carry *Bs*1 and *Bs*2 (2), but it is not known whether *Bs*2 is allelic with either *Bs*1 or *Bs*3. This paper reports the results of inheritance studies involving the resistance genes found in PI 271322 and Florida XVR 3-25.

MATERIALS AND METHODS

Host material. Seed for test plants of PI 271322 was obtained from the South Atlantic Regional Plant Introduction Station, Experiment, GA. Seed was on hand for the homozygous lines Early Calwonder (ECW), its near-isogenic line Early Calwonder 10 R (10 R) with gene *Bs*1 (8), Delray Bell (DB) with gene *Bs*1 (A. A. Cook, *personal communication*), and Florida XVR 3-25 (XVR 3-25) with genes *Bs*1 and *Bs*2 (2). Plants were grown in steamed peat-vermiculite mix in 10-cm-diameter pots arranged in rows of eight plants on a greenhouse bench (temperature range 20–35 C). Plants were watered as required and treated four times during the experiments with about 0.4 g/pot of soluble 20:20:20 fertilizer.

Inoculum preparation. The *X. c.* pv. *vesicatoria* strains used in these studies were all isolated from plants grown in Florida and stored in water cultures. After recovery from these water cultures, they were tested for pathogenicity and stored frozen in 15% glycerol or in refrigerated, sterilized water. Inocula were prepared from 24-hr nutrient broth shake cultures. After centrifugation, bacterial pellets were resuspended in sterile tap water and standardized photometrically to 0.3 *A* at 600 nm wavelength to approximate a density of 5×10^8 cfu/ml. This inoculum density was used for detecting HR (11). Inoculation was accomplished by hypodermic infiltration of intercostal leaf tissues (10). Races were identified by the presence or absence of HR in ECW and 10 R (6).

Heterogeneity of resistance in PI 271322. Variability in resistance of PI 271322 to races 1 and 2 was initially estimated from 15 plants. Plants of ECW and 10 R were used as controls. All plants of PI 271322, ECW, and 10 R were observed for HR 24 hr after inoculating two fully expanded leaves on each plant with each of three strains: XV 0623 and XV 82-8 (both race 1) and XV 82-7 (race 2). Each leaf was inoculated with all three strains. All the plants inoculated had developed to the stage just before bloom.

The reactions to four strains of race 1 (XV 0623, XV 71-21, XV 80-5, and XV 82-8) and eight strains of race 2 (XV 61-38, XV 65-1, XV 70-7, XV 80-6, XV 81-23, XV 82-7, XV 83-3, and XV E3) were tested in an additional population of 166 plants of PI 271322 as described.

Allelism tests for genes *Bs*1 and *Bs*3. A single plant of PI 271322, designated 271-4, was selected for HR to both races 1 and 2. A single inbred progeny plant of 271-4 was crossed with single plants of DB (*Bs*1) and ECW (*bs*1). Single F_1 plants of both crosses were self-pollinated to yield F_2 seed and cross-pollinated with additional plants of respective parents to give backcross progenies.

The first experiment involved progenies of 271-4 and DB. Population sizes were 12 plants of the parents, DB and 271-4, 20 of F_1, 241 of F_2, 20–40 of the two backcrosses, and 5 each of control

lines ECW and 10 R. Reactions to strains XV 82-8, representative of race 1, and XV 82-7 (race 2) were observed 24 hr after inoculating segments of a fully expanded leaf on each plant. The leaf was infiltrated with both strains in nonoverlapping areas. There is no cross-protection between these strains (A. A. Cook and R. E. Stall, *unpublished*). The tests were repeated on the same plants several days later. All the plants were initially inoculated at the first bloom stage.

A second experiment involved progenies of 271-4 and ECW. Two separate plantings of the following seven populations were made: parents 271-4 and ECW, F_1, F_2, backcrosses, and control line 10 R. Line 10 R carries the *Bs*1 gene and permits the differential reaction of races 1 and 2 to be demonstrated. Population sizes varied in the two plantings. Using plants at the initial bloom stage, we inoculated fully expanded leaves with strains XV 82-8 of race 1 and XV 82-7 of race 2 to observe HR as described before. A single plant (BC 31-4) heterozygous for the genes *Bs*1 and *Bs*3 was selected from the first backcross to ECW; i.e., this plant showed HR to both races. This plant was both self-pollinated and backcrossed again to ECW. Inbred backcross and second backcross populations were grown and observed for HR to the same strains of *X. c.* pv. *vesicatoria*, i.e., selected for *Bs*1 and *Bs*3. All ratios of genetic segregation were compared by the χ^2 test against those expected for independent segregation of two dominant genes.

Allelism tests for gene *Bs*2 with genes *Bs*1 and *Bs*3. Single plants of 271-4 and 10 R were cross-pollinated with one of XVR 3-25. Single F_1 plants of both crosses were cross-pollinated with one of ECW to produce test-cross progeny.

In the first experiment, data were recorded for the segregation of genes *Bs*2 and *Bs*3 in 414 progeny of the test cross (271-4 × XVR 3-25) F_1 × ECW. Other populations included in this experiment were 30–40 plants each of 271-4, XVR 3-25, ECW and (271-4 × XVR 3-25) F_1, and eight of line 10 R. The presence of hypersensitivity to each race was observed in a repeated test of each plant. The first, second, seventh, and eighth leaves above the cotyledons were inoculated with strains XV 80-5 (race 1) and XV E3 (race 2), using plants at the initial bloom stage of development. Where necessary, plants were tested three or four times to be sure of their response.

In the second experiment, data were recorded for segregation of genes *Bs*1 and *Bs*2 in progenies derived from the test cross (10 R × XVR 3-25) F_1 × ECW. Populations of 39 of these test-cross plants and five each of ECW and 10 R were tested. Observations were made for the presence of hypersensitivity to each race after inoculating the first and second leaves above the cotyledons with strains XV 71-21 (race 1) and XV 81-23 (race 2), using plants at the initial bloom stage. Two test-cross progeny plants were selected. One of these plants, designated plant A, was hypersensitive to race 2 only, and the other, designated plant B, was hypersensitive to both races 1 and 2. These plants were self-pollinated, and their progenies were tested for reaction to each race. Population sizes were 150 plants of population A (Table 1) derived from selfing plant A, 399 plants of population B derived from selfing plant B, and 15 plants each of 10 R, XVR 3-25, and ECW. The first and second leaves above the cotyledons were inoculated with strain XV 7-21 (race 1) and XV 81-23 (race 2), using plants at the initial bloom stage of development.

RESULTS AND DISCUSSION

Heterogeneity of resistances in PI 271322. Hypersensitive necrosis to strain XV 82-7 of race 2 developed within 24 hr after inoculating plants of 10 R. A susceptible reaction occurred in leaves of 10 R inoculated with race 1 and in ECW with both races. The susceptible reaction was characterized by host tissue becoming soft and water-soaked 24–36 hr after inoculation and necrotic within 2.5–3 days.

Heterogeneity for HR to both races 1 and 2 occurred among plants of PI 271322. Fourteen of 15 plants showed HR to strains XV 0623 and XV 82-8 of race 1, and four plants showed HR to strain XV 82-7 of race 2. One plant was without HR to any strain. The plant 271-4 of PI 271322 was selected for HR to strains XV 0623 and XV 82-8 of race 1 and XV 82-7 of race 2. Inbred progeny of 271-4 were homogeneous for their reactions to these same strains.

In a larger planting of PI 271322 (Table 2), all four strains of race 1 induced typical HR in 123 (or 74.1%) plants. All eight strains of race 2 induced HR in 65 (or 39.2%) plants. The frequencies of typical HR to strains of races 1 and 2 were independent of each other (Table 2).

The HR to the strains of race 1 was hypothesized to represent the effect of gene *Bs*3, which was designated by Kim and Hartmann (9) but not known to be at a different locus from *Bs*2. The locus controlling HR to race 2 in PI 271322 is postulated to be *Bs*1, which controls HR to race 2 in DB and 10 R.

Allelism tests for genes *Bs*1 and *Bs*3. All plants of parents 271-4 and DB, and their F_1, F_2, and backcross progenies, and line 10 R, but none of ECW, were hypersensitive to strain XV 82-7 of race 2 (Table 3). This is consistent with the hypothesis that gene *Bs*1 is present in homozygous condition in both parents, 271-4 and DB.

All plants of 271-4, the F_1, and one backcross (F_1 × 271-4) but no plants of DB, 10 R, and ECW were hypersensitive to strain XV 82-8 of race 1 (Table 3). The segregation observed in the F_2 (271-4 × DB) and backcross (F_1 × DB) populations was consistent with a ratio in the F_2 of 3:1 (HR to non-HR) and a ratio in the backcross of 1:1 (HR to non-HR). These ratios indicate that

TABLE 1. Segregation for hypersensitive reactions in pepper test-cross and inbred test-cross populations inoculated with races 1 and 2 of *Xanthomonas campestris* pv. *vesicatoria*

		Reaction[a]			
		Race 1 (strain XV 71-21)		Race 2 (strain XV 81-23)	
Host population	Genotype	HR[b]	non-HR	HR	non-HR
10 R[c]	*Bs*1 *bs*2 *bs*3	0[d]	15	15	0
XVR 3-25[c]	*Bs*1 *Bs*2 *bs*3	15	0	15	0
Early Calwonder[c]	*bs*1 *bs*2 *bs*3	0	15	0	15
F_1 × Early Calwonder[e]		16	23	39	0
Inbred test crosses[f]					
Population A		0	150	110	40
Population B		287	112	363	36

[a] Inoculum concentration about 5×10^8 cfu/ml.
[b] HR = hypersensitive reaction.
[c] Data were combined from tests of two sets of plants.
[d] Number of plants.
[e] For the ratio 16:23 from F_1 × Early Calwonder, the χ^2 (1:1) = 1.26 ($P = 0.25$).
[f] Populations A and B were selfed progenies of test-cross plants; A was hypersensitive to race 2 only and B was hypersensitive to races 1 and 2. The postulated genotypes of the selfed parents were *Bs*1/*bs*1, *bs*2/*bs*2 for A and *Bs*1/*bs*1, *Bs*2/*bs*2 for B. For the ratio 110:40 (population A, race 2), the χ^2 (3:1) = 0.22 ($P = 0.85$). For the ratios 287:112 and 363:36 (population B), the χ^2 (3:1) = 2.01 ($P = 0.15$) and χ^2 (15:1) = 5.23 ($P = 0.075$), respectively.

TABLE 2. Hypersensitivity in plants of PI 271322 to inoculation with four strains of race 1 and eight strains of race 2 of *Xanthomonas campestris* pv. *vesicatoria*

Hypersensitivity[a]		
Race 1	Race 2	Frequency[b]
Present	Present	47
Present	Absent	76
Absent	Present	18
Absent	Absent	25
Total		166

[a] Hypersensitivity to four strains of race 1 and eight strains of race 2.
[b] Number of plants.

resistance to race 1 in 271-4 is controlled by *Bs*3 and that *Bs*3 is neither allelic with nor linked to *Bs*1. These results also indicate that DB carries the recessive allele at the *bs*3 locus.

Independent segregation of *Bs*1 and *Bs*3 occurred in F_1, F_2, and backcross progenies of 271-4 × ECW (Table 4). The F_1 progeny were hypersensitive to races 1 and 2. Four combinations of HR to races 1 and 2 occurred in F_2 populations (Table 4). In the first planting, segregation was consistent with the ratio of 9:3:3:1 (HR to races 1 and 2:HR to race 1 only:HR to race 2 only:lacking HR). In the second planting, the data marginally fit this ratio (Table 4); i.e., values below $P = 0.05$ usually indicate that the hypothesis should be rejected. The marginal fit resulted from unexpectedly few plants hypersensitive to strain XV 82-7 of race 2. Independent segregation of *Bs*1 and *Bs*3 was supported by data from backcross progenies in both plantings. All plants of the backcross (F_1 × 271-4) were hypersensitive to both races 1 and 2, whereas segregation in the backcross (F_1 × ECW) was consistent with equal frequencies of plants in the four combinations of HR to races 1 and 2 (Table 4).

Segregation ratios observed in the inbred backcross and second backcross populations adequately fit those expected for independent assortment of both genes in all populations (Table 4). It is clear that 271-4 carries a second resistance gene, *Bs*1, which segregates independently from *Bs*3.

Allelism tests for genes *Bs*2 and *Bs*3. All plants of the parents 271-4 and XVR 3-25, their F_1 and test-cross progeny (F_1 × ECW), and check line 10 R, but none of susceptible check cultivar ECW, were hypersensitive to strain XV E3 of race 2 in each of two separate tests (Table 5). These data are consistent with a model in which one allelic dominant gene is present in homozygous condition in both parents 271-4 and XVR 3-25. The dominant gene *Bs*1, for HR to race 2, has already been established to be present in 271-4 (Table 3). Cook (2) reported that XVR 3-25 also carries *Bs*1 derived by backcrossing to cultivar Florida VR-2.

All plants of both parents 271-4 and XVR 3-25 and their F_1 progeny, but none of check lines 10 R and ECW, were hypersensitive to strain XV 80-5 of race 1 (Table 5). The test-cross progeny (F_1 × ECW) segregated 318:96 (hypersensitive:nonhypersensitive), which is consistent with a 3:1 ratio ($\chi^2 = 0.72$, $P = 0.40$) expected with two independently segregating dominant genes, one present in homozygous condition in 271-4 and the other in XVR 3-25. The *Bs*2 gene in XVR 3-25 must be the second gene, which also confers resistance to race 1. If *Bs*2 were really an allele at the *Bs*3 locus, there would have been no segregation for HR to race 1 in the test-cross progeny. It is also clear that XVR 3-25 carries the recessive allele at the *bs*3 locus and 271-4 carries the recessive allele at the *bs*2 locus.

Allelism tests for genes *Bs*1 and *Bs*2. All plants of the parents 10 R and XVR 3-25, and the test-cross progeny (10 R × XVR 3-25) F_1 × ECW, but none of ECW, were hypersensitive to strain XV 81-23 of race 2 (Table 1). These data are consistent with one allelic dominant gene present in homozygous condition in both parents 10 R and XVR 3-25. The dominant gene *Bs*1 has already been

TABLE 3. Segregation for hypersensitivity in progenies of peppers 271-4 and Delray Bell inoculated with races 1 and 2 of *Xanthomonas campestris* pv. *vesicatoria*

	Numbers of plants[a]					
	Race 2 strain XV 82-7		Race 1 strain XV 82-8		XV 82-8	
Generation	HR[b]	non-HR	HR	non-HR	Expected ratio	χ^2 (*P*)
271-4	12	0	12	0	...	...
Delray Bell (*Bs*1)	12	0	0	12	...	...
F_1 (271-4 × Delray Bell)	20	0	20	0	...	...
F_2	241	0	173	68	3:1	1.33 ($P = 0.25$)
F_1 × 271-4	18	0	18	0	...	
F_1 × Delray Bell	35	0	15	20	1:1	0.71 ($P = 0.40$)
Controls						
Early Calwonder	0	5	0	5	...	...
10 R	5	0	0	5	...	...

[a] Inoculum concentration about 5×10^8 cfu/ml.
[b] HR = hypersensitive reaction.

TABLE 4. Segregation for hypersensitivity in progenies of pepper cross 271-4 × Early Calwonder (ECW) inoculated with races 1 and 2 of *Xanthomonas campestris* pv. *vesicatoria*

	Number of plants with each of the four possible genotypes[a]					
Generation	*Bs*1 *Bs*3	*bs*1 *Bs*3	*Bs*1 *bs*3	*bs*1 *bs*3	Expected ratio[b]	χ^2 (*P*)
271-4	46[c]	0	0	0	...	...
	54	0	0	0	...	...
ECW	0	0	0	49	...	...
	0	0	0	42	...	...
F_1 (271-4 × ECW)	51	0	0	0	1:0:0:0	...
	36	0	0	0		...
F_2	60	22	23	10	9:3:3:1	1.53 ($P = 0.68$)
	138	54	35	23		7.62 ($P = 0.05$)
F_1 × 271-4	60	0	0	0	1:0:0:0	...
	63	0	0	0		
F_1 × ECW	20	9	15	19	1:1:1:1	4.75 ($P = 0.19$)
	29	25	25	18		2.59 ($P = 0.46$)
Second backcross (BC) (BC 31-4)[d] × ECW	15	12	17	14	1:1:1:1	0.90 ($P = 0.83$)
Inbred BC (BC 31-4) selfed	62	20	14	4	9:3:3:1	2.68 ($P = 0.44$)

[a] Race 1 strain XV 82-8 and race 2 strain XV 82-7 at inoculum concentration 5×10^8 cfu/ml were used to determine genotype.
[b] Ratio expected for independent segregation of two dominant genes, *Bs*1 and *Bs*3.
[c] Upper value from first planting; lower value from second planting.
[d] Female parent refers to a single plant selection from first backcross.

TABLE 5. Segregation for hypersensitive reactions in a pepper test-cross population inoculated with races 1 and 2 of *Xanthomonas campestris* pv. *vesicatoria*

Host population	Genotype	Reaction[a]			
		Race 1 (strain XV 80-5)		Race 2 (strain XV E3)	
		HR[b]	non-HR	HR	non-HR
271-4	*Bs1 Bs3*	30	0	30	0
XVR 3-25	*Bs1 Bs2*	35	0	35	0
F_1 (271-4 × XVR 3-25)		40	0	40	0
F_1 × Early Calwonder[c]		318	96	414	0
Early Calwonder	*bs1 bs2 bs3*	0	40	0	40
10 R	*Bs1 bs2 bs3*	0	8	8	0

[a] Inoculum concentration about 5×10^8 cfu/ml.
[b] HR = hypersensitive reaction.
[c] For the ratio 318:96 from F_1 × ECW, the χ^2 (3:1) = 0.72 ($P = 0.40$).

established to be present in XVR 3-25 (Table 5) and was reported to be in 10 R (8).

All plants of parent XVR 3-25, but none of 10 R and ECW, were hypersensitive to strain XV 71-21 of race 1 (Table 1). The test-cross progeny segregated 16:23 (hypersensitive:nonhypersensitive), which is consistent with a 1:1 ratio ($\chi^2 = 1.26$, $P = 0.25$) expected for a single dominant gene present only in parent XVR 3-25. This must be the dominant gene *Bs2* that already has been established to be present in XVR 3-25 (Table 5).

All plants of XVR 3-25 and 10 R, but none of ECW, were hypersensitive to strain XV 81-23 of race 2 (Table 1). Plants of population A (Table 1), which was derived by selfing test-cross plant A, segregated 110:40 (hypersensitive:nonhypersensitive). This is consistent with a 3:1 ratio ($\chi^2 = 0.22$, $P = 0.85$) expected for a single dominant gene in heterozygous condition in parent plant A. In contrast, plants of population B (Table 1), which was derived by selfing test-cross plant B, segregated 363:36 (hypersensitive: nonhypersensitive). This is consistent with the ratio 15:1 ($\chi^2 = 5.23$, $P = 0.075$) expected for two independently segregating dominant genes, each controlling hypersensitivity to race 2 and both present in heterozygous condition in the parental plant B. The *Bs2* gene, derived from XVR 3-25, must be the second gene. It is also clear that 10 R carries the recessive allele at the *bs2* locus.

All plants of the parent XVR 3-25, but none of parents 10 R and ECW, were hypersensitive to strain XV 71-21 of race 1 (Table 1). No plant of population A was hypersensitive to this strain. This is consistent with the presence of only the recessive allele of gene *bs2* in plant A of the test cross. Plants of population B segregated 287:112 (hypersensitive:nonhypersensitive), which is consistent with the 3:1 ratio ($\chi^2 = 2.01$, $P = 0.15$) expected for a single dominant gene in heterozygous condition in plant B of the test cross. All 287 plants hypersensitive to race 1 were also hypersensitive to race 2. The combined segregation ratios are consistent with the gene *Bs1* controlling resistance to race 2 only and *Bs2* controlling resistance to both races 1 and 2.

Taking all the data into consideration, the genes *Bs1*, *Bs2*, and *Bs3* must be independent. The resistance genotype of 271-4 must be *Bs1 bs2 Bs3*, XVR 3-25 must be *Bs1 Bs2 bs3*, and DB must be *Bs1 bs2 bs3*.

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