Two Resistant Responses in Cowpea Induced by Different Strains of *Xanthomonas campestris* pv. *vignicola*

R. D. GITAITIS, Department of Plant Pathology, University of Georgia, Coastal Plain Experiment Station, Tifton 31793

ABSTRACT

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Twenty-eight cowpea cultivars and plant introductions were identified as resistant to bacterial blight and canker. Two types of resistant responses were observed and characterized. The first response was a rapid confluent necrosis, typical of a normal hypersensitive response, and was expressed against incompatible fluorescent pseudomonads and most strains of *Xanthomonas campestris* pv. *vignicola*. The second response was represented by a brown-red discoloration without complete collapse of the tissue. The brown-red reaction was expressed against two strains of *X. campestris* pv. *vignicola* as well as all other pathovars of *X. campestris* that had been isolated from a variety of hosts other than cowpea.

Additional key words: *Vigna unguiculata*

Foliar leaf spot and stem canker caused by *Xanthomonas campestris* pv. *vignicola* (Burkholder) Dye is an important disease of cowpea (*Vigna unguiculata* (L.) Walp) in most areas where cowpea is cultivated (1,11,18). Two strains of the bacterium are responsible for two separate disease syndromes (11). The first is cowpea bacterial blight and canker (CBB), which appears as large, irregularly shaped, necrotic areas on the foliage, similar to those of common blight of bean (22). Stem cankers are often associated with CBB and can severely afflict certain cultivars, causing wilt or plant lodging (1). The second disease syndrome is bacterial pustule (CBP). Initial symptoms are small, raised, water-soaked pustules on the undersides of leaves, and the pustules remain circular throughout their development (11,16). At present, CBP is restricted to areas in Africa, whereas CBB has a worldwide distribution.

All major cowpea cultivars cultivated for processing in Georgia are either moderately or highly susceptible to CBB (9). The primary source of inoculum in this area is infested seed (7), for which control measures are limited and often ineffective. Consequently, economic control measures such as the use of resistant cultivars are needed.

Several techniques have been used by various workers to identify resistance (5,12). Researchers may choose a certain technique because of individual preference or because of the type of resistance one is trying to identify (4,8). A simplistic approach often used is to classify two types of resistance. One type of resistance, expressed to varying degrees but generally the same to all strains of the pathogen, has been referred to as nonspecific (6) or horizontal resistance (23). A second type of resistance, highly effective against some races of the pathogen but not against others, has been called specific (6) or vertical resistance (23). The hypersensitive reaction has been described as a form of specific or vertical resistance (4). This paper reports on the evaluation of cowpea germ plasm for identification of hypersensitivity to the CBB pathogen.

The typical hypersensitive reaction in a plant leaf to phytopathogenic bacteria is a zone of confluent necrosis within 24 hr of inoculation with inocula of 10^8 cfu/ml, whereas under the same conditions, a susceptible reaction requires 3–5 days or more (14,21). Production of an atypical response in cowpea leaves by certain strains of *X. campestris* pv. *vignicola*, which was unlike either a susceptible or hypersensitive reaction, prompted the evaluation and characterization of the hypersensitive, susceptible, and atypical reactions observed.

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MATERIALS AND METHODS

Strains of *X. campestris* pv. *vignicola* causing CBB were isolated from the foliage of diseased cowpeas in southern Georgia or were recovered from a bioassay (7) of seed lots of cowpea from diverse sources (Table 1). Inoculum was prepared by centrifugation of 24-hr nutrient broth shake cultures at 2,000 *g* for 10 min. Pellets were resuspended in sterile water and adjusted photometrically until inoculum density was 10^8 cfu/ml (21). Strain XVG 80-4 was used for initial screening of cowpea germ plasm. Intercellular spaces of primary leaves of 14-day-old seedlings were infiltrated with a bacterial suspension (10^8 cfu/ml), using a syringe fitted with a 27-gauge needle. Plants were maintained in the greenhouse (18–28 C) and examined daily for 10 days and their responses recorded. Four or more pots with three plants per pot of 112 cultivars or plant introductions were planted for evaluation.

The following cultivars and plant introductions (PI) of cowpea were evaluated for resistance to bacterial blight and canker: Acre (PI 292870), Big Boy, Blackeye × Iron (PI 194202-194205), Blue Goose, Brabham (PI 293466), Brabham K 892, Browneye Cream (PI 293470), Browneye Purplehull, Cabbage Pea (PI 293474), Calhoun, Calico, California Blackeye No. 3, California Blackeye No. 5, Canide (PI 352772), Champion, Chinese Red (PI 293482), Chinese Red × Iron (PI 194206-194215), Colossus, Coronet, Cream White (PI 293498), Dixie Lee, Egyptian (PI 339571), Groit (PI 293514), Iran Grey (PI 339601), Iron (PI 293520), Iron K 329 (PI 293521), Jackson Ala (PI 293522), Jackson Bunch (PI 293523), Jackson Bunch Purplehull (PI 293524), Jackson Purplehull (PI 293525), Knucklehull Purplehull, Lobra (PI 165486), Mississippi Purple, Mississippi Silver, New Era (PI 186386, PI 293537, PI 300171, PI 339602, PI 352835, PI 352836, PI 352892), Pinkeye Purplehull, Purplehull 49, Pusa Phalgun (PI 269667), Queene Anne, Red Ripper, Running Acre, S A Dandy, Sekgald (PI 339572), Speckled Purplehull, Suwannee, Tennessee White Crowder, Texas Cream 8, Texas Cream 12, Texas Cream 40, Texas Purplehull, Victor (PI 293581), Whipperwill, White Acre, White Crowder, Yori Muni (PI 312202), Zippercream, Zwonka Yellow (PI 292906), PI 124609, PI 197057, PI 211753, PI 292871, PI 292899, PI 292914, PI 298051, PI 325775, PI 339565, PI 339593, PI 346339, PI 352838, PI 352880, PI 352997, PI 353000, PI 353057, PI 353089, PI 353094, PI 353110, PI 353161, PI 353365, PI 353383, PI 354494, PI 354667, PI 354678, PI 354693, PI 354724, PI 354821, PI 354857, PI 382106, PI 382114, PI 382118, PI 382124, PI 406289, PI 406290, PI 406292, and PI 406293.

Plants that showed an apparent hypersensitive reaction were inoculated with additional CBB strains (Table 1) to ascertain whether other pathogenic races were a significant component of the population. Populations of bacteria in the susceptible, hypersensitive, and atypical reactions in cowpea were determined by the dilution-plate method. Disks 1 cm in diameter were sampled from leaves 5 days after inoculation and triturated in 1 ml of 0.85% saline. Serial dilutions (0.1:0.9) were made with 0.1 ml of the suspension spread onto plates of nutrient agar. Population counts were made from three replicates after 4–5 days of incubation at 30 C.

Increase of the conductance of water over time is indicative of electrolyte leakage and is a way to characterize hypersensitivity (3). Conductance was measured for the three types of reactions. Fifteen 1-cm-diameter disks were suspended in 15 ml of sterile distilled water and subjected to vacuum (−90 kPa) for 3 min. Samples then were agitated on a reciprocal shaker (120 cycles/min) for 1 hr. Conductivity was measured before and after shaking with a conductivity bridge (YSI Model 31, Yellow Springs, OH 45387) and a conductivity cell with a cell constant of K = 0.1. The differences between the two readings were considered as the amount of electrolytes lost due to the treatment. All values were calculated as a mean of three replicates.

Leaves of cowpea cultivar Brabham K 892 were infiltrated with various concentrations (10^6, 10^7, 10^8, and 10^9 cfu/ml) of XVG 80-4 and XVG 81-30 to determine the effects of inoculum concentration on the induction of the hypersensitive and atypical reactions. In addition, responses of cowpea cultivars were observed after infiltration of other pathovars of phytopathogenic bacteria (Table 1). These latter pathovars had been adjusted to a concentration of 10^8 cfu/ml.

Table 1. Origin of phytopathogenic bacteria used to analyze resistance in cowpea cultivars and plant introductions

Bacterial strain	Host	Scientist/state
Xanthomonas campestris		
pv. *vignicola*[a]		
XVG 80-4	Cowpea (Mississippi Silver-f)	Gitaitis/Georgia
XVG 80-6	Cowpea (SA Dandy-f)	Gitaitis/Georgia
XVG 80-8	Cowpea (Dixie Lee-f)	Gitaitis/Georgia
XVG 81-30	Cowpea (California Blackeye no. 5-f)	Gitaitis/Georgia
XVG 82-36	Cowpea (Coronet-f)	Gitaitis/Georgia
XVG 82-37	Cowpea (White Acre-f)	Gitaitis/Georgia
MIC-1	Cowpea (Mixed Iron and Clay-s)	Gitaitis/Georgia
CB5-1	Cowpea (California Blackeye no. 5-s)	Gitaitis/Georgia
C-1	Cowpea (Colossus-s)	Gitaitis/Georgia
TC-1	Cowpea (Texas Cream 40-s)	Gitaitis/Georgia
Z-1	Cowpea (Zippercream-s)	Gitaitis/Georgia
SA-1	Cowpea (SA Dandy-s)	Gitaitis/Georgia
X. campestris		
pv. *phaseoli*		
XP11	Bean	Saettler/Michigan
XPa	Bean	Saettler/Michigan
XBP	Bean	Gitaitis/Georgia
X. campestris		
pv. *malvacearum*		
XM race 1	Cotton	Essenberg/Oklahoma
XM race 18	Cotton	Essenberg/Oklahoma
X. campestris		
pv. *cannae*		
086 1097	Canna lily	Miller/Florida
X. campestris		
pv. *pruni*		
XPR 82-1	Peach	Gitaitis/Georgia
X. campestris		
pv. *translucens*		
110	Wheat	Cunfer/Georgia
X. campestris		
pv. *vesicatoria*		
XV 81-11	Pepper	Gitaitis/Georgia
XV 82-14	Tomato	Gitaitis/Georgia
XV 82-15	Tomato	Gitaitis/Georgia
X. campestris		
pv. *campestris*		
XC 81-4	Cauliflower	Gitaitis/Georgia
XC 81-5	Cabbage	Gitaitis/Georgia
XC 81-6	Cabbage	Gitaitis/Georgia
XC 82-13	Cabbage	Gitaitis/Georgia
XC 82-14	Broccoli	Gitaitis/Georgia
XC 82-15	Cauliflower	Gitaitis/Georgia
Pseudomonas syringae		
pv. *tomato*		
PT 81-17	Tomato	Gitaitis/Georgia
P. fluorescens		
PF 80-1	Tomato	Gitaitis/Georgia

[a] *X. campestris* pv. *vignicola* strains were either isolated from diseased foliage (f) or recovered from seeds (s).

RESULTS

Twenty-eight of 112 (25%) cultivars or plant introductions of cowpea displayed a hypersensitive response when challenged with strain XVG 80-4 of *X. campestris* pv. *vignicola* (Table 2). At least 14 of these 28 lines, including Brabham, Brabham K 892, nine samples of Chinese Red × Iron, Iron K 329, and Victor, have a pedigree traced to the cultivar Iron; however, all sources of Blackeye × Iron were susceptible. Sources of New Era were varied in their response; many were susceptible but hypersensitive reactions occurred with the greatest frequency in PI 186386, which is a source of New Era from Uruguay (Table 2).

A second pathogenic race capable of overcoming resistance was not detected among 12 strains of *X. campestris* pv. *vignicola* obtained from various sources. Two strains (XVG 81-30 and CB5-1), however, caused neither a susceptible reaction nor a typical hypersensitive response on all lines that were hypersensitive to XVG 80-4. Both strains originated from California Blackeye No. 5. Strain XVG 81-30 was isolated from diseased cowpea foliage in Georgia, whereas CB5-1 was recovered from infested seed produced in California. The atypical reaction induced by these strains was characterized by only a brown-red discoloration without complete collapse of the tissue. There was no colonization of the leaf because the discoloration was confined to the inoculated area, even after 10–14 days of incubation. The atypical reaction developed slower than the normal HR but occurred within 24–48 hr, which is more rapid than a susceptible reaction of 3–5 days.

Population trends of XVG 81-30 and

CB5-1 in leaves of four different cultivars that showed brown-red discoloration were representative of resistance and not of a susceptible reaction due to a new race. Populations of bacteria in leaves inoculated with 10^8 cfu/ml and sampled immediately upon inoculation were 5.5 $\times 10^5$ to 1×10^6 cfu/ml/1-cm-diameter disk of leaf tissue. In a susceptible reaction, bacterial populations increased after 5 days to 5.2×10^9 cfu/ml per disk, which represented extensive bacterial growth and colonization of plant tissues (Table 3). In plants showing either a normal hypersensitive reaction or brown-red discoloration, there was a bacteriostatic effect with no significant increase in the bacterial population after 5 days of incubation.

As expected, there was not an increase in electrolyte losses in the first 24 hr after inoculation for the susceptible reaction (Table 4); however, an increase in electrolyte leakage was detected in Brabham K 892 only 6 hr after inoculation with XVG 80-4 and reached a maximum within 24 hr. Electrolyte patterns such as this are consistent with the hypersensitive response (3). The atypical reaction in Brabham K 892 induced by XVG 81-30 was characterized by a modest increase in electrolyte leakage, which was scarcely detectable after 6 hr. After a 24-hr exposure to the inoculum, only 33% of the electrolytes were lost in the atypical reaction compared with the amount lost in the typical hypersensitive response (Table 4).

Injections of Brabham K 892 with various inoculum densities resulted in no unexpected effects on the quality of the two resistant reactions. The typical hypersensitive response appeared normal at inoculum densities of 10^7 cfu/ml and greater but failed to produce confluent necrosis at a concentration of 10^6 cfu/ml. The response at the low level of inoculum, however, did not resemble the atypical reaction. The atypical response also was not affected by inoculum density. Responses to inoculum levels as high as 10^9 cfu/ml of XVG 81-30 were still characteristic of a brown-red discoloration and not confluent necrosis.

Inoculations of cowpea with various pathovars of *X. campestris* that are pathogenic to host plants other than cowpea produced reactions comparable to the brown-red discolorations induced by XVG 81-30 and CB5-1, but injections with *Pseudomonas syringae* pv. *tomato* (a fluorescent pseudomonad) resulted in a normal hypersensitive response with confluent necrosis. Exposures to the saprophytic *P. fluorescens* resulted in no detectable reactions other than a slight chlorosis after prolonged incubation (14–21 days).

DISCUSSION

Several sources of cowpea resistant to CBB were identified and characterized as eliciting a hypersensitive response when inoculated with strains of *X. campestris* pv. *vignicola*. Many of these lines already possess horticulturally acceptable characteristics and should be valuable additions to programs where plant breeders are incorporating disease resistance into cowpea. Hoffmaster (10), Preston (17), and Sherwin and Lefebvre (19) have previously reported Brabham, New Era, and Iron cowpea lines as having moderate to high levels of resistance or being immune to CBB. Their data, however, represented an average response for a population and their studies were done prior to the understanding of the

Table 2. Cultivars or plant introductions (PI) of cowpea that showed a hypersensitive response to strain XVG 80-4 of *Xanthomonas campestris* pv. *vignicola*

Cowpea cultivar	PI no.	Origin	Plants displaying HR (%)
Acre	292870	Israel	44
Brabham	293466	United States	100
Brabham K 892	293467	United States	100
Browneye Cream	293470	United States	100
Chinese Red × Iron	194206	United States	100
Chinese Red × Iron	194207	United States	100
Chinese Red × Iron	194208	United States	100
Chinese Red × Iron	194209	United States	100
Chinese Red × Iron	194210	United States	100
Chinese Red × Iron	194211	United States	100
Chinese Red × Iron	194212	United States	100
Chinese Red × Iron	194214	United States	100
Chinese Red × Iron	194215	United States	50
Iron	293520	United States	100
Iron K 329	293521	United States	100
Jackson Bunch	293523	United States	67
Jackson Bunch Purplehull	293524	United States	100
New Era	186386	Uruguay	80
New Era	352892	India	57
New Era	339602	South Africa	14
Sekgald	339572	Uganda	100
Suwanee	293571	United States	100
Victor	293581	United States	100
IC10227	353057	India	75
PLL17A	353089	India	100
P1120	354667	India	50
P1335	354821	India	100
...[a]	382118	Nigeria	100

[a] No cultivar name.

Table 3. Populations of *Xanthomonas campestris* pv. *vignicola* 5 days after leaves of various cultivars were infiltrated with suspensions of 10^8 cfu/ml of strains XVG 80-4, XVG 81-30, and CB5-1

Bacterial strain	Cowpea cultivar	Reaction[a]	Population[b] (cfu/ml/disk)
XVG 80-4	California Blackeye No. 5	S	4.0×10^8
XVG 81-30	California Blackeye No. 5	S	1.1×10^9
CB5-1	California Blackeye No. 5	S	8.6×10^8
XVG 80-4	Mississippi Silver	S	5.1×10^8
XVG 81-30	Mississippi Silver	S	5.2×10^9
CB5-1	Mississippi Silver	S	1.8×10^9
XVG 80-4	Brabham K892	HR	6.0×10^6
XVG 81-30	Brabham K892	BHR	5.4×10^6
CB5-1	Brabham K892	BHR	2.8×10^6
XVG 80-4	Acre	HR	3.6×10^6
XVG 81-30	Acre	BHR	1.2×10^6
XVG 80-4	Chinese Red × Iron	HR	4.4×10^6
XVG 81-30	Chinese Red × Iron	BHR	7.0×10^5
XVG 81-30	Sekgald	HR	5.6×10^5
XVG 81-30	Sekgald	BHR	1.3×10^6

[a] Reaction types: S = susceptible; HR = hypersensitive response characterized by confluent necrosis; and BHR = brown hypersensitive response, atypical resistant reaction characterized by brown-red discoloration.
[b] Populations reported as a mean of three replicates. Values determined from 1-cm-diameter disk of leaf tissue triturated in 1 ml of saline. Initial population in the leaf at time 0 was 5.5×10^5 to 1×10^6 cfu/ml/disk.

Table 4. Average electrolyte losses over time in cowpea with a susceptible (Mississippi Silver) and a resistant cultivar (Brabham K 892) after being inoculated with strains of *Xanthomonas campestris* pv. *vignicola* that induce a normal hypersensitive response (XVG 80-4) and brown-red discoloration (XVG 81-30)

Strain	Cultivar	Reaction[a]	Conductivity (umhos)			
			4 Hr	6 Hr	8 Hr	24 Hr
80-4	Mississippi Silver	S	32.3[b]	31.3	23.3	29.8
81-30	Mississippi Silver	S	29.6	32.6	20.6	25.6
80-4	Brabham K 892	HR	23.0	60.6	92.3	296.3
81-30	Brabham K 892	BHR	34.6	43.3	52.0	107.3

[a] Reaction types: S = susceptible, HR = hypersensitive response characterized by rapid confluent necrosis, and BHR = brown hypersensitive response, atypical resistant reaction characterized by brown-red discoloration.
[b] Electrolyte losses reported as a mean of three replicates.

hypersensitive response to phytopathogenic bacteria (13).

In this study, some cowpea cultivars such as New Era were heterogenous in the expression of hypersensitivity, which reflected not only different sources of the germ plasm but also differences within a population from a single source. Consequently, if population averages were used, cultivars such as Brabham and Iron would have appeared slightly more resistant than New Era, and PI 186386 of New Era would have appeared more resistant than other sources of that cultivar. This is the most probable explanation of differences among these cultivars in previous evaluations of their resistance to CBB. In a somewhat different situation, Vakili et al (22) reported intermediate but low levels of disease on cowpeas inoculated with strains of *X. campestris* pv. *phaseoli*. It is possible that the low levels referred to as intermediate were representative of the brown-red discoloration type of immune reaction. The three strains of *X. campestris* pv. *phaseoli* used in this study all induced the brown-red discoloration type reaction.

In some plants, the hypersensitive response characterized by sudden and rapid tissue collapse (within 6–24 hr) has been reported as the general response to incompatible phytopathogenic bacteria (13,14,21). Muller (15) described the hypersensitive reaction as the premature dying of infected tissue, which results in inactivation and localization of the infectious agent. It was apparent, however, that a resistant response to incompatible bacteria occurred in cowpea that did not involve premature dying of tissue with its sudden collapse. During the screening of germ plasm, if one is searching only for the general hypersensitive response, it is possible to miss significant sources of resistance of the atypical response described.

Although not widely reported, various types of hypersensitive responses have been noted previously with bacterial pathogens. Cook (2) described differences in the quality of hypersensitive responses in pepper induced by the tomato and pepper strains of *X. campestris* pv. *vesicatoria*. At least two types of resistant reactions induced by incompatible cereal pathotypes and other incompatible phytopathogenic bacteria have been reported to occur in oats (20). Development of a brown discoloration classified as brown-red hypersensitive response by Patel (16), as well as a normal hypersensitive response, have previously been reported to occur in cowpea in response to different strains of the CBP pathogen. Patel (16) used the differences to form a set of differentials to identify pathotypes of the CBP strain of *X. campestris* pv. *vignicola*. There was no evidence in this study, however, that the different reactions observed were related to pathotype of the CBB pathogen. All cowpea lines responding with a normal hypersensitive response to XVG 80-4 were also resistant to strains XVG 81-30 and CB5-1. Conversely, all susceptible lines were susceptible to all strains of the pathogen that were tested.

Patel (16) did not report on cowpea responses to phytopathogenic bacteria other than to *X. campestris* pv. *vignicola*. In this study, a normal hypersensitive response occurred in cowpea when it was inoculated with *P. syringae* pv. *tomato*; however, the brown-red hypersensitive type reaction was exhibited uniformly against incompatible pathotypes of *X. campestris* that were from hosts other than cowpea. These responses, as well as the population trends in the brown-red hypersensitive reaction, are evidence that brown-red hypersensitive reaction is a form of resistance in cowpea. The responses reported here and elsewhere (16,20) are types of specific resistance characterized by bacteriostatic effects and localization of the pathogen without the rapid premature death of tissues.

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