Copper Tolerance and Zinc Sensitivity of Mexican Strains of *Xanthomonas campestris* pv. *vesicatoria*, Causal Agent of Bacterial Spot of Pepper

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ABSTRACT

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Copper-sensitive strains of *Xanthomonas campestris* pv. *vesicatoria* were isolated from infected pepper plants from two locations in Arizona where there is limited use of copper bactericides. Three copper-tolerant strains of the bacterium also were isolated from diseased plants from the west coast and central Mexico, where copper bactericides have been used for more than 30 yr. The Arizona strains were sensitive to various copper formulations (copper hydroxide, copper sulfate, copper ammonium carbonate, and basic copper sulfate) with and without the addition of mancozeb as determined by the presence of inhibition zones in disk assays. The Mexican strains were tolerant to all copper formulations but were slightly sensitive to copper-mancozeb combinations. Both strains were sensitive to zinc compounds (zinc sulfate and zineb) in similar assays. In dilution tests using copper sulfate and zinc sulfate with bacterial concentrations of 5×10^7 cfu/ml, the Arizona strains were sensitive to copper at concentrations higher than 28 mg a.i./L, whereas some colonies of the Mexican strains still grew at copper concentrations of 1,800 mg a.i./L. Strains that were sensitive or tolerant to copper were sensitive to zinc concentrations higher than 56 mg a.i./L. However, a strain initially insensitive to copper and sensitive to zinc developed tolerance to zinc after repeated exposures. In the greenhouse, several copper formulations prevented infection of Cal Wonder 300 pepper plants (*Capsicum annuum*) by the Arizona strains but not by the Mexican strains of *X. campestris* pv. *vesicatoria*. Zineb sprays prevented infection by both strains.

One of the major agricultural areas of North America is located in Sinaloa, Mexico, where about 6,000 ha of winter peppers (*Capsicum annuum* L. and *C. frutescens* L.) are grown each year. The major disease of peppers in this subtropical area (25° north latitude) is bacterial spot, caused by *Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye (6). The warm maritime climate of this coastal region of Mexico, combined with winter rains and coastal fogs, provides an ideal environment for infection of the leaves, petioles, stems, and fruit. The disease results in both reduced yield and reduced quality of pepper fruits (6).

Standard recommendations for controlling bacterial spot disease of peppers have been copper bactericides or copper formulations in combination with mancozeb or streptomycin (3,5,10,11). Low toxicity and the relatively low cost of these compounds have made their use widespread in agricultural areas to control foliar bacterial diseases. In the last few years, however, these compounds have failed to give adequate control of bacterial spot of pepper on the west coast of Mexico (R. B. Hine, *personal observation*).

X. campestris pv. *vesicatoria* is a heterogeneous bacterium in its physiology and pathogenicity (1,5). Strains of *X. campestris* pv. *vesicatoria* isolated in Florida vary in their sensitivity to copper-containing compounds (10). The objective of this research was to determine if a similar situation existed in Mexico and to find, if possible, an alternate method of chemical control of bacterial spot of pepper.

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MATERIALS AND METHODS

Isolation, identification, and pathogenicity tests of strains. Strains of *X. campestris* pv. *vesicatoria* were isolated from typically infected leaves of pepper plants from two locations in southeastern Arizona (Elfrida and Willcox) and from two locations in Mexico (Sacramento, Coahuila, and Culican, Sinaloa). Arizona strains were collected in 1979 by S. M. Alcorn, University of Arizona, and in 1984, by R. B. Hine. Mexican strains were collected by R. B. Hine in 1984. The 1979 isolates had been maintained on glucose-yeast-carbonate agar at 10 C and transferred periodically before this study. Since 1984, all strains were grown on nutrient agar (NA) and Gram stains (9) were conducted for each of the strains isolated.

Flagellation was determined by scanning electron microscopy (SEM). For this, cultures were smeared on aluminum foil and frozen in nitrogen slush. The foil was placed on a copper block cooled to liquid nitrogen temperatures, then block and foil were exposed to vacuum (10^{-7} torr) and allowed to warm to room temperature for 24 hr before observations were made.

Inoculum was prepared for each strain by suspending 48-hr cultures grown on NA in sterile deionized water (SDW) at pH 7.0. A Bausch & Lomb Spectronic 20 spectrophotometer set at 540 nm was used to adjust the inoculum concentration (8). A bacterial suspension with a transmittance reading of 70% was found to contain 1×10^8 colony-forming units (cfu) per milliliter as determined by dilution plating. Bacterial suspensions containing 1×10^8 cfu/ml were hand-sprayed to runoff on 7-wk-old Cal Wonder 300 peppers (Petoseed Co. Inc., Saticoy, CA) in 10-cm-diameter pots (12). The plants were then placed on a greenhouse bench and misted with water automatically for 5 sec every 40 min. After 48 hr, the plants were transferred to dry benches and watered as needed without wetting the foliage. Greenhouse temperatures during the experiment ranged between 32 and 35 C during the day and between 24 and 27 C at night (temperatures that were considered optimal) (4,12). Symptoms of the disease were observed after 2 wk. Pathogenic strains were reisolated and maintained as stock cultures in SDW at room temperature (25 C) throughout the study.

Screening of strains for sensitivity to copper and zinc. Bacterial strains were screened for sensitivity to several formulations of copper, copper-mancozeb combinations, and zinc by in vitro disk assays. Chemical concentrations initially tested were based on dosages recommended by the respective manufacturers for use in the field and involved the following: copper hydroxide (Kocide 101), 50% metallic copper equivalent (MCE), 0.36 g/100 ml of SDW equaling 1,800 mg/L of copper; basic copper sulfate (Tri-Basic Copper Sulfate), 53% MCE, 0.479 g/100 ml of SDW equaling 2,539 mg/L of copper; copper ammonium carbonate (COPPER-COUNT-N), 8% MCE, 2.30 ml/100 ml of SDW equaling 1,800 mg/L of copper; copper sulfate (crystals, analytical grade), 25% MCE, 0.72 g/100 ml of SDW equaling 1,800 mg/L of copper; mancozeb (Manzate 200), 80% a.i., 0.18 g/100 ml of SDW equaling 1,440 mg a.i./L; zineb, 17.7% metallic zinc equivalent (MZE), 1.02

g/100 ml of SDW equaling 1,805 mg/L of zinc; and zinc sulfate (analytical grade) 40% MZE, 0.44 g/100 ml of SDW equaling 1,760 mg/L of zinc. In several tests, 0.18 g of mancozeb was also combined with 0.479 g of basic copper sulfate, 2.25 g of copper ammonium carbonate, 3.68 g of copper hydroxide, or 0.72 g of copper sulfate in 100 ml of SDW. Stocks were diluted for lower concentrations for subsequent tests. Analytical paper disks (Schleicher and Schuell Inc., Keene, NH) 1.27 cm in diameter were infiltrated with 100 µl of single or mixed chemicals just before use. Suspensions of the strains of *X. campestris* pv. *vesicatoria* were prepared as described for the pathogenicity studies. One hundred microliters of each bacterial suspension was spread evenly over NA plates with sterile glass rods and allowed to dry. Three treated paper disks were placed on the medium and tapped lightly to ensure even contact. All plates were incubated at 27 C for 48 hr. Zones of inhibition were recorded (measured from the outer edge of the disk). Each treatment contained three replicates and the experiment was repeated twice.

Copper hydroxide, copper sulfate (analytical grade), zineb, and zinc sulfate (analytical grade) also were assayed using a modification of Thompson's direct dilution method (10,11). Stock solutions of each salt or suspensions of each commercial formulation, at a 3,600-mg a.i./L concentration, were prepared as described. The preparations of each chemical were mechanically shaken overnight at room temperature and sterilized by filtration through a sterile 0.1-µm Millipore filter. Serial dilutions of each chemical were made by the sequential 1:1 addition of either a suspension of a strain of the bacterium (prepared as described in the pathogenicity test) or with SDW. The final concentrations of active ingredients of the zinc and copper ranged from 0 to 1,800 mg/L, and the final bacterial concentrations were 5×10^7 cfu/ml when mixed with the chemicals. Two strains of the bacterium were tested, XV 84-5 (copper-tolerant) and XV 84-4 (copper-sensitive). After 2 hr of incubation at room temperature, the viability of the strains exposed to each chemical concentration was determined by plating 100 µl of the bacterial-chemical mixtures onto NA. The number of colonies per plate was determined after 48 hr of incubation at 27 C. Assay disks also were prepared from the check dilutions and used to compare the sensitivity of agar assays with the dilution series method. The concentrations of copper and zinc in the serial dilutions with the bacteria were confirmed by atomic absorption spectrophotometry (10). The dilution tests were repeated twice, each with two replicates.

Development of tolerance of zinc. A colony tolerant to copper and surviving the highest concentration of zinc in the first dilution experiment was used in a second dilution series. Again, a colony surviving the greatest concentration of zinc was used in a third dilution series. Each dilution was replicated twice.

Control of bacterial spot with copper and zinc compounds. The effectiveness of the chemicals in protecting plants of the pepper cultivar Cal Wonder 300 against infection by two strains, XV 84-4 and XV 84-5, of *X. campestris* pv. *vesicatoria* was determined in greenhouse tests. Plants were grown from seed in a peat-sand-loam mix (1:1:2 ratio) and ranged in age from 6 to 7 wk. Temperatures were between 32 and 35 C during the day and between 24 and 27 C at night. Plants were first sprayed with the chemical compounds at manufacturer-recommended rates plus 1.24 ml/L of Nu-Film 17 Sticker, allowed to dry (1–2 hr), and then sprayed to runoff with a suspension containing about 1×10^8 cells of the desired strain of *X. campestris* pv. *vesicatoria* and treated as described in the pathogenicity studies. The sticker also was tested alone at the rate previously mentioned. All treatments were randomized on the greenhouse bench. Disease incidence was evaluated 3 wk after inoculation using a disease index (DI), where 0 = no leaves infected, 1 = 1–3 leaves infected, 2 = 4–6 leaves infected, 3 = 7–9 leaves infected, and 4 = 10 or more leaves infected. Leaves infected had one or more lesions per leaf. Treatments were replicated five times and the experiment was conducted twice.

RESULTS

Identification and pathogenicity tests. All strains produced uniform circular,

Table 1. Differential sensitivity of *Xanthomonas campestris* pv. *vesicatoria* strains from Arizona and Mexico to copper and zinc compounds determined by the disk method

Chemical	Formulation	Concentration[a] (mg/L)	Inhibition zones[b]				
			Arizona		Mexico		
			XV 79-2[c]	XV 84-4	XV 84-1	XV 84-3	XV 84-5
Copper sulfate	$CuSO_4 \cdot 5H_2O$	1,800	5	6	0	0	0
		1,200	3	4	0	0	0
		600	2	2	0	0	0
Copper hydroxide	$Cu(OH)_2$	1,800	6	5	0	0	0
		1,200	5	3	0	0	0
		600	3	2	0	0	0
Basic copper sulfate (BCS)	$CuSO_4 \cdot 3Cu(OH)_2 \cdot H_2O$	2,400	3	3	0	0	0
		1,200	2	2	0	0	0
Copper ammonium carbonate	Copper ammonium carbonate	1,800	7	6	0	0	0
		1,200	6	5	0	0	0
		600	3	2	0	0	0
Mancozeb (M)	Coordination product of Mn-Zn ethylene bisdithiocarbamate	1,400	1	2	1	1	2
M + BCS		1,400 + 2,400	6	5	3	2	3
		1,400 + 1,200	5	4	2	1	2
Zinc sulfate	$ZnSO_4$	1,800	9	8	7	6	6
		900	5	5	3	2	3
Zineb	Zinc ethylene bisdithiocarbamate	1,800	4	4	6	5	4
		900	2	2	5	3	2
Control disk		0	0	0	0	0	0

[a] Concentrations tested were based on field recommendations calibrated for 900 L of H_2O per hectare.
[b] Inhibition zones were measured as the radius of the zone of inhibition from the outer edge of the disk. Values represent the average of three replicates in two experiments.
[c] Bacterial strains: XV 79-2, Elfrida, AZ; XV 84-4, Willcox, AZ; XV 84-1 and XV 84-5, Sacramento, Mexico; and XV 84-3, Culican, Mexico, isolated from pepper leaves.

yellow colonies on NA after 48 hr and were gram-negative. Rod-shaped bacteria about 0.5–0.8 × 1–2 μm with monotrichous flagella were found in SEM observations. All strains were pathogenic and induced typical symptoms of the disease (10,13).

Screening of strains for sensitivity to copper and zinc. The Arizona strains, XV 79-2 and XV 84-4, were sensitive to copper and zinc (Table 1). No apparent differences in inhibition were noted between analytical and agricultural grades of copper sulfate or zinc sulfate. The Mexican strains, XV 84-1, XV 84-3, and XV 84-5, however, had a high level of tolerance to copper at the concentrations of the copper formulations. However, when the strains were tested against mancozeb plus basic copper sulfate, a common recommendation for bacterial spot control (3,10), or mancozeb plus the other copper formulations, inhibition zones developed. When mancozeb alone was tested, inhibition zones also occurred, although smaller than when mancozeb was used in combination with the copper-containing chemicals.

Because zinc is a heavy-metal ion and an ingredient of the mancozeb formulation, the inhibitory effects of zinc as zinc sulfate and zineb were tested against the Mexican isolates. Both produced zones of inhibition. These results were similar to those obtained for the Arizona strains. However, occasional colonies of *X. campestris* pv. *vesicatoria* developed within the zones of inhibition.

The concentration at which each bacterial strain was sensitive to the copper or the zinc ions was determined from the dilution series of copper sulfate and zinc sulfate (Table 2). The Arizona strain did not grow after exposures to copper and zinc concentrations higher than 56 mg/L. However, the Mexican strain was not sensitive to any of the concentrations of copper but was sensitive to 112 mg/L or more of zinc. Assay disks prepared from the check dilution series and used in the disk method produced 1-mm inhibition zones at concentrations of 14–28 ppm of copper sulfate or 28–56 ppm of zinc sulfate. Dilutions yielding these concentrations of Cu^{2+} and Zn^{2+} would have contained 50–200 cfu of the bacteria.

The Arizona and Mexican strains survived the exposure to all concentrations of copper hydroxide and zineb with the direct dilution method. However, atomic absorption spectrophotometric determination indicated low levels (between 0 and 20 mg/L) of copper and zinc ions from the low to high dilutions of each formulation.

Bacterial colonies of XV 84-5 that grew at the highest zinc concentrations (56 mg/L) in the modified Thompson's test were reexposed to zinc in the dilution series experiment. Surviving bacterial colonies were used in a repeat of the dilution experiment. Again there were survivors. Thus, after just three exposures to zinc, the copper-tolerant strain of the *X. campestris* pv. *vesicatoria* from Mexico became tolerant to zinc at 900 mg/L.

Control of bacterial spot with copper and zinc compounds. Results of the greenhouse tests to determine if foliage applications of several copper compounds, a copper-mancozeb mixture, and zineb could prevent bacterial spot on peppers are presented in Table 3. Spotting occurred randomly on the surface of mature leaves of control plants within 14 days but never exceeded 25% of the leaf surface. Spotting also occurred on stems and petioles. Chlorotic halos developed around the necrotic lesions, general chlorosis followed, and some of the infected leaves abscised within 3 wk. None of the copper formulations or the copper-mancozeb mixtures controlled the Mexican strain (Table 3). In contrast, foliage applications of copper prevented the copper-sensitive Arizona strain from causing disease. Tested plants appeared similar in all respects to the uninoculated checks. Although plants treated with copper-mancozeb mixtures developed disease, the incidence was not extensive. Results in the repeat experiment were similar to those reported in Table 3.

Because several strains of *X. campestris* pv. *vesicatoria* from Arizona and Mexico were sensitive to zinc in vitro, tests were conducted in the greenhouse to determine if zinc-containing chemicals could be used as foliar protectants against this pathogen. The techniques used were the same as those used for the copper evaluations.

Bacterial strains, XV 84-1 and XV 84-5, from two locations in Sacramento, Mexico, were used in the greenhouse studies of zinc to control bacterial spot. Previously, both isolates were determined in the laboratory to be tolerant to copper (1,800 mg/L of Cu^{2+}) and sensitive to zinc (112 mg/L of Zn^{2+}). Zineb (17.7% a.i. zinc) and zinc sulfate (agricultural grade

Table 2. Differential sensitivity of two strains of *Xanthomonas campestris* pv. *vesicatoria* to copper and zinc ions in solution

Concentration[a] (mg a.i./L)	Number of surviving cfu[b]			
	XV 84-4[c]		XV 84-5[c]	
	Cu	Zn	Cu	Zn
0	>500	>500	>500	>500
3.5	>500	>500	>500	>500
7	410	420	>500	>500
14	175	182	>500	>500
28	58	50	>500	54
56	0	0	>500	2
112	0	0	>500	0
225	0	0	>500	0
450	0	0	>500	0
900	0	0	490	0
1,800	0	0	300	0

[a] Concentration for each solution containing either Cu^{2+} ($CuSO_4$, analytical grade) or Zn^{2+} ($ZnSO_4$, analytical grade) ions.
[b] Number of surviving colony-forming units (cfu) per 100 μl of dilution. Average of two replicates.
[c] Bacterial strains: XV 84-5, Sacramento, Mexico; and XV 84-4, Willcox, AZ, isolated from pepper leaves.

Table 3. Effect of foliage applications of copper, copper-mancozeb mixtures, and a zinc compound on the incidence of bacterial spot of peppers caused by strains of *Xanthomonas campestris* pv. *vesicatoria* from Arizona and Mexico

Treatment	Concentration[w]	Disease index[x]	
		XV 84-4[y]	XV 84-5
Copper hydroxide	1,800	0.0 a[z]	1.4 b
Basic copper sulfate (BCS)	2,470	0.0 a	2.6 cd
Copper ammonium carbonate	1,800	0.0 a	1.8 bc
Mancozeb (M)	1,440	2.2 c	2.6 cd
M + BCS	1,440 + 2,470	0.8 b	3.4 d
Zineb	1,800	0.0 a	0.0 a
Sticker	1.24	2.0 c	2.8 d
Inoculated checks	0	2.8 d	2.6 cd
Uninoculated checks	0	0.0 a	0.0 a

[w] Chemicals were applied at the highest field recommendation rate. Sprays also contained Nu-Film 17 sticker at the rate of 1.24 ml/L.
[x] Disease index scale: 0 = 0 leaves infected, 1 = 1–3 leaves infected (one or more lesions per leaf), 2 = 2–4 leaves infected, 3 = 7–9 leaves infected, and 4 = 10 or more leaves infected. Values are based on five replicates from one experiment.
[y] Bacterial strains obtained from leaf lesions on peppers, XV 84-4 from Willcox, AZ, and XV 84-5 from Sacramento, Mexico.
[z] Values followed by different letters in the same column differ significantly according to Duncan's multiple range test ($P = 0.05$).

36% Zn^{2+}) were used as the zinc sources. Zineb at the rate of 1,800 mg a.i./L of zinc (about 2 kg of 50% zineb per hectare in 900 L of H_2O) gave complete protection (Table 3), whereas plants treated with zinc sulfate at the same concentration developed only minor levels of disease (DI = 1.1). Unsprayed, inoculated checks had a DI of 2.6 with 1–25% of the leaf area infected. However, when the zinc-tolerant strain of *X. campestris* pv. *vesicatoria* was used as inoculum for zineb-sprayed plants, disease incidence increased (DI = 1.5) compared with the zinc-sensitive wild type (DI = 0.0).

In the greenhouse, plants received about 25 mm of simulated rainfall during the 48-hr misting cycle. In this system, adequate control was obtained with the described materials. However, if the misting regime was extended to 96 hr, an equivalent of 50 mm of simulated rainfall, none of the techniques tested controlled bacterial spot.

DISCUSSION

Copper-sensitive strains of *X. campestris* pv. *vesicatoria* were isolated from two locations in Arizona (Elfrida and Wilcox). Arizona has a very limited pepper acreage and the use of copper bactericides is not a common practice. The copper-tolerant strains were isolated from Sinaloa, Mexico, a major production area of peppers and tomatoes in North America where copper bactericides and copper-mancozeb combinations have been applied for control of bacterial spot for more than 30 yr.

Copper-tolerant strains of *X. campestris* pv. *vesicatoria* have been reported from Florida (10). Since the presence of a plasmid has been cited by Stall et al (14) to relate to the tolerance to copper, the high levels of insensitivity of the Mexican strains determined in our studies could possibly be due to multiple plasmids with genes for copper tolerance occurring in the bacterial cell.

Both copper-tolerant and copper-sensitive strains of *X. campestris* pv. *vesicatoria* were sensitive to copper-mancozeb combinations in the disk assay. Previous workers demonstrated in dilution studies that copper solubility is increased by mancozeb and that this increase of copper in solution was probably responsible for the activity of the copper-mancozeb combination (10). However, on the basis of chemical bioassays, including in vitro disk assays, dilution tests, and greenhouse studies using two formulations of zinc compounds, we have demonstrated that zinc is involved in the observed control of bacterial spot caused by the Arizona copper-sensitive and the Mexican copper-tolerant strains of *X. campestris* pv. *vesicatoria*. Furthermore, reports from several other countries have indicated the use of zineb as a seed treatment for control of bacterial spot (2,7).

The differential sensitivity of *X. campestris* pv. *vesicatoria* to copper and zinc detected in the disk assay was confirmed in the greenhouse. Zineb was more effective than zinc sulfate sprays for disease control. Perhaps the commercial formulation enhanced the adhesion of the zinc, preventing its removal from the plant. Zineb, a registered material on pepper for other disease problems, may be used as a protectant against copper-tolerant strains of *X. campestris* pv. *vesicatoria*. However, since zinc tolerance was rapidly induced in the in vitro studies, we suggest that field strains of *X. campestris* pv. *vesicatoria* are likely to develop tolerance to zinc if zinc compounds are used frequently.

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