Epiphytic Populations of *Xanthomonas campestris* pv. *vesicatoria* and Bacterial Spot of Tomato as Influenced by Nitrogen and Potassium Fertilization

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ABSTRACT

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Epiphytic populations of *Xanthomonas campestris* pv. *vesicatoria* were monitored weekly on tomato plants supplied through drip irrigation with combinations of two rates of NH_4NO_3 and three rates of KCl. Bacterial populations and the percentage of defoliation were then related, through a repeated measures analysis of variance, to fertilization and soil salinity and also were correlated with the mineral content of leaves. Lower epiphytic populations of the pathogen developed on plants receiving combinations of the higher rates of nitrogen and potassium; an interaction between the two fertilizers was significant ($P = 0.01$) in each of three seasons. Defoliation was more severe at the low rate of nitrogen application, but the rate of potassium application had little influence. Epiphytic populations of *X. c. vesicatoria*, but not the severity of defoliation, also were associated with increases in soil salinity that resulted from high rates of fertilization. Applications of NH_4NO_3 increased the concentration of nitrogen in leaves throughout the season, and applications of KCl similarly increased foliar concentrations of potassium. Through fruit set, however, increased application of NH_4NO_3 reduced potassium concentrations while greater applications of KCl reduced nitrogen concentrations in leaves. Although a higher rate of NH_4NO_3 also reduced the foliar concentrations of calcium and magnesium, magnesium but not calcium was affected by the rate of KCl. Early in the season, epiphytic populations of *X. c. vesicatoria* were inversely correlated with the foliar concentration of potassium; at harvest, however, populations were inversely related to magnesium content. Defoliation increased significantly with increasing concentrations of both magnesium and calcium.

Bacterial spot, caused by *Xanthomonas campestris* pv. *vesicatoria*, is one of the most destructive diseases of tomato in Florida and is a significant threat in other states as well (17). Copper compounds provide partial control, but during periods of high disease pressure these may be inadequate (1). Streptomycin is also ineffective in Florida because of the development of resistance in the pathogen population (21). Tomato cultivars resistant to *X. c. vesicatoria* have yet to be released; thus, nutritional manipulation to reduce disease losses warrants investigation.

Manipulation of mineral nutrition for the control of plant diseases has proven commercially useful in a number of crops (6).

Examples with tomato include reduced Fusarium wilt with increased calcium and boron fertilization (3) or an integrated nitrate-lime-benomyl regime (18), a lowered incidence of Botrytis gray mold with increased calcium and reduced phosphorus applications (20), and a reduced severity of bacterial wilt when tomato plants are provided with higher levels of calcium nitrate (8). Under greenhouse conditions, increased rates of potassium reduced bacterial spot on pepper, another host of *X. c. vesicatoria* (15). Increased rates of nitrogen and potassium similarly reduced this disease in a greenhouse study with tomatoes (16); however, field studies regarding the effects of increased fertilization with nitrogen and potassium have not been reported.

In west central Florida where the soils are sandy and annual rainfall averages 142 cm, nutrients may quickly leach unless rows are covered with plastic. This necessity for plastic mulch, coupled with drip irrigation, allows excellent control of fertilization. Although the climate in this part of Florida favors the production of two crops of tomatoes annually, the high rainfall and humidity, especially during the fall, provide an environment conducive for the establishment of high populations of epiphytic organisms. Bacterial plant pathogens are known to live as epiphytes, and these can serve as a reservoir of inoculum (2,9). Measuring the numbers of these epiphytes also can lead to predictions of disease severity (10).

This study examines the effects of nitrogen and potassium fertilization of tomato plants on the development of bacterial spot by monitoring epiphytic populations of *X. c. vesicatoria* and subsequent defoliation. Populations and defoliation were then correlated with changes in the mineral concentrations within leaves and with differences in soil salinity. Drip irrigation was used to optimize fertilization.

MATERIALS AND METHODS

Tomato culture. Tomato seedlings (*Lycopersicon esculentum* L. 'Sunny') were transplanted into field plots of EauGallie fine sand. Beds on centers of 137 cm were 76 cm wide and 23 cm high and were covered with black polyethylene mulch. Superphosphate (0-8.74-0 [N-P-K]) was applied at a rate of 656 kg of phosphorus per hectare in the bed before planting, along with 20% of the total nitrogen and potassium, in an incorporated band 15 cm wide and 7 cm from the plant row. Individual plants then were fertilized three times each week through polyethylene tubing as previously described (7), and plants received rates of NH_4NO_3 which, when combined with what was applied in the starter, were equivalent to either 336 or 672 kg of nitrogen per hectare. In addition to the potassium in the starter fertilizer and in combination with nitrogen applications, KCl also was supplied through the tubing to total 336, 672, or 1,344 kg of potassium per hectare. Six treatments or fertilizer combinations were produced. An approximation of the salinity associated with each treatment was made by measuring the conductivity of solutions containing NH_4NO_3 and KCl at the concentrations applied in the field. The six treatments, each consisting of a row of 10 plants, were arranged in a randomized complete block design, which was replicated four times.

Inoculation and sampling procedures. The first season, fall 1983, 6-wk-old plants were sprayed with a suspension of a spontaneously derived mutant strain of *X. c. vesicatoria* resistant to streptomycin and rifampicin. Strain 81-18sr was initially cultured on plates of nutrient yeast-dextrose agar (NYDA) (13). Cells were subsequently suspended in 20 L of 0.01 M $MgSO_4$ at a concentration of 10^8 cfu/ml. With a backpack sprayer, plants were inoculated in the early morning while leaves were still wet with dew. Epiphytic populations of this mutant were monitored weekly by plating leaflet washings on NYDA supplemented with streptomycin, rifampicin, and cycloheximide (Sigma Chemical Co.) at 100, 100, and 50 mg/L, respectively. In spring and fall of 1984, plants were sprayed with a suspension of 10^8 cfu/ml of a mixture of wild-type strains (81-18, 83-44, and 84-1 [13]), and populations were measured weekly by plating leaflet washings on a semiselective Tween medium (13). Populations of *X. c. vesicatoria* were estimated by collecting one newly expanded and asymptomatic leaflet in the upper canopy from each of the 10 plants in a treatment replicate. The 10 leaflets, combined into a composite sample, were weighed and vigorously washed for 30 min on a wrist action shaker in 100 ml of a 0.1 M phosphate buffer (pH 7.0) containing, per liter, 5.3 g of KH_2PO_4, 8.61 g of Na_2HPO_4, and 1 g of Bacto peptone. Aliquots of 0.1 ml from serial dilutions of the wash were then spread over the surface of each of three plates of the appropriate medium and were subsequently incubated at 28 C for 96 h. Colonies typical of *X. c. vesicatoria* were counted and recorded relative to the fresh weight of the leaf samples.

Assessments of bacterial spot were made three times each season by estimating the percentages of defoliation of three of the 10 plants within each of the six replicated treatments (7). Leaves were collected at fruit set and at first harvest and were analyzed for nitrogen by the total Kjeldahl method and for phosphorus by ammonium molybdate colorimetry at the Gulf Coast Research and Education Center, and for potassium, calcium, and magnesium by atomic absorption spectrophotometry at the Analytical Research Laboratory of the University of Florida.

Statistical methods. Because each experiment involved the quantification of bacteria and defoliation over several weeks, data were analyzed seasonally to determine the effects attributable to

TABLE 1. Univariate analysis of variance, repeated measures design, of the effects of nitrogen and potassium fertilization of tomato on epiphytic populations of *Xanthomonas campestris* pv. *vesicatoria*

Source of variation	Fall 1983[y]			Spring 1984			Fall 1984		
	df	MS	*F*	df	MS	*F*	df	MS	*F*
Between plot effects									
Potassium (K)									
Linear	1	0.11	0.38	1	4.48	5.82*	1	31.49	17.30**
Quadratic	1	0.56	1.93	1	1.97	2.56	1	0.00	0
Nitrogen (N)	1	1.04	3.60*	1	2.71	3.53*	1	2.25	1.24*
N × K linear	1	1.87	6.45**	1	8.95	11.62**	1	31.85	17.50**
N × K quadratic	1	0.43	1.48	1	0.14	0.18	1	0.89	0.49
Replication (*R*)	3	1.03	3.56*	3	0.08	0.10	3	1.22	0.67
Error	15	0.29		15	0.77		15	1.82	
Within plot effects[z]									
Day	6	32.24	90.77***	11	34.04	43.24***	3	81.41	69.72***
Day × K	12	0.69	1.96	22	1.11	1.41	6	1.02	0.88
Day × N	6	0.19	0.54	11	2.01	2.56*	3	1.22	1.04
Day × K × N	12	1.00	2.81*	22	1.02	1.30	6	2.08	1.78
Day × R	18	0.47	1.31	33	1.33	1.69	9	1.22	1.05
Error (day)	90	0.36		165	0.79		45	1.17	

[y] MS = mean square. Asterisks indicate: * significance at $P = 0.05$, ** significance at $P = 0.01$, and *** significance at $P = 0.001$.
[z] Based on an adjusted *F* value proposed by Greenhouse and Geisser for repeated measures analyses (19).

time, fertilization, and soil salinity by using a repeated measures analysis of variance (11) available through SAS (19). Bacterial populations were analyzed as $\log_{10}$, and the percentages of defoliation were transformed before analysis with an arcsine square-root transformation. Within each experiment, as determined by the date of the two tissue analyses, early and late season comparisons were made between epiphytic populations or percentages of defoliation and the mineral concentrations of leaves. To eliminate the effect of seasonal variability, early season readings were combined into one analysis (N = 24: three potassium rates × two nitrogen rates × four replications), and late season readings were combined into a second analysis. Correlation analyses then were made to relate the epiphytic populations and percentages of defoliation to foliar concentrations of nitrogen, potassium, phosphorus, calcium, and magnesium.

RESULTS

Effects on epiphytic populations of *X. c. vesicatoria*. Univariate analysis of variance, through repeated measures, of the epiphytic populations of *X. c. vesicatoria* on tomato demonstrated highly significant changes ($P = 0.001$) accompanying sampling days in all three seasons (Table 1). Changes were erratic and occurred primarily in response to rainfall (data not shown). The confirmation of this effect, however, and the role of environment, were not objectives of this research.

Fertilizer applications significantly affected populations of *X. c. vesicatoria* (Table 1). In each of three seasons, the effect of fertilizer on *X. c. vesicatoria* was due to a linear interaction between nitrogen and potassium ($P = 0.01$). At both rates of nitrogen fertilization, increasing the rate of potassium application reduced numbers of epiphytic *X. c. vesicatoria*, but the reduction was sharper for the higher level of nitrogen (Table 2). At a particular level of potassium fertilization, except at the lowest, increasing the rate of nitrogen application similarly reduced epiphytic numbers of the pathogen.

Differences in the six fertilizer combinations produced a range of estimated soil salinity values from 0.48 to 1.40 dS/m for treatments with the lowest and highest combined rates of nitrogen and potassium applications, respectively. These values approximate those found in the root zone of plants grown in sand. Epiphytic populations of *X. c. vesicatoria* were significantly affected each season by the linear component of salinity ($P = 0.01$; data not shown). As the estimated salinity of the soil solution increased, population means generally declined; $r = -0.898$. By separating the populations into those that received low or high rates of nitrogen fertilization, however, the lines of regression became more significant. For low nitrogen fertilization, $\log_{10}$ population $= 5.091 - 0.416 \cdot$ dS/m ($r^2 = 0.910$); for high nitrogen fertilization, $\log_{10}$ population $= 5.764 - 1.221 \cdot$ ds/m ($r^2 = 0.969$) (Fig. 1).

Effects on defoliation. The percentage of defoliation resulting from bacterial spot was significantly and inversely related to the rate of nitrogen application and was reduced an average of 35% at the higher rate (Tables 2 and 3). Potassium rate had no significant effect on the percentage of defoliation, nor was there a significant nitrogen × potassium interaction. For the group of six fertilizer treatments, no relationship existed between the average percentage of defoliation and estimated soil salinity; $r = -0.535$. Within subpopulations of plants receiving low and high rates of NH_4NO_3, the same correlations were −0.280 and

TABLE 2. Comparison of mean epiphytic populations of *Xanthomonas campestris* pv. *vesicatoria* and percentage of defoliation on tomato receiving nitrogen (N) and potassium (K) fertilization

Rates of nitrogen fertilization (kg/ha)	Epiphytic populations and percentages of defoliation[z] per rates of potassium fertilization (kg/ha)			
	336	672	1,344	N effect
336	84,192 (13.5)	54,880 (11.7)	41,915 (12.6)	57,810 (12.6)
672	96,269 (8.9)	36,523 (8.7)	12,106 (7.0)	34,914 (8.2)
K effect	89,950 (11.2)	44,771 (10.2)	22,542 (9.8)	

[z] Colony-forming units per gram (fresh weight) of leaf; conversion from $\log_{10}$ values. Numbers in parentheses are the percentages of defoliation. Means of three seasons. LSD (population): N, K, treatment effects, response = 32,900, 19,503, 24,221. LSD (defoliation): N, K, treatment effects, response = 2.37%, 4.56%, 4.14%.

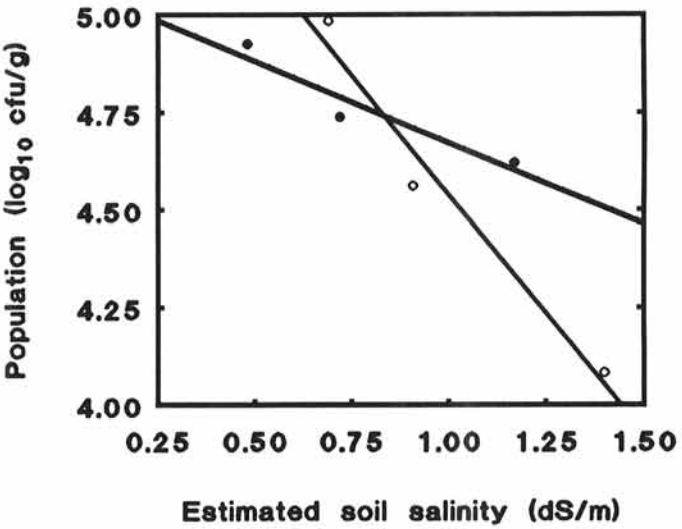

Fig. 1. Relationship between estimated soil salinity and populations of *Xanthomonas campestris* pv. *vesicatoria* on leaves of tomato receiving six combinations of nitrogen and potassium fertilization. Data points are means of three seasons and represent potassium rates (336, 672, or 1,344 kg/ha) at low (● = 336 kg/ha) and high (○ = 672 kg/ha) rates of nitrogen fertilization. LSD = 0.384.

TABLE 3. Univariate analysis of variance, repeated measures design, of the effects of nitrogen and potassium fertilization of tomato on defoliation caused by *Xanthomonas campestris* pv. *vesicatoria*

Source of variation	Fall 1983[y]			Spring 1984			Fall 1984		
	df	MS	*F*	df	MS	*F*	df	MS	*F*
Between plot effects									
Potassium (K)	2	0.002	0.33	2	0.004	0.17	2	0.027	1.96
Nitrogen (N)	1	0.000	0.04	1	0.098	4.45*	1	0.304	22.40***
N × K	2	0.004	0.85	2	0.023	1.03	2	0.001	0.07
Replication	3	0.004	0.75	3	0.039	1.79	3	0.085	6.30**
Error	15	0.005		15	0.022		15	0.014	
Within plot effects[z]									
Day	2	0.050	23.11***	2	0.358	107.25***	2	0.948	174.64***
Error (day)	46	0.002		46	0.004		46	0.011	

[y] MS = mean square. Asterisks indicate: * significance at $P = 0.05$, ** significance at $P = 0.01$, *** significance at $P = 0.001$.
[z] Based on an adjusted *F* value proposed by Greenhouse and Geisser for repeated measures analyses (19). Error is pooled.

−0.966, respectively, but the lines of regression could not be significantly differentiated at $P < 0.10$.

Relationships with mineral content of leaves. Between fruit set and first harvest, the concentrations of nitrogen and potassium decreased in leaves, whereas calcium and magnesium increased (Tables 4 and 5). Rate of potassium application, however, was correlated at both sampling times with an increase in the dry weight percentages of potassium in leaves, and a similar effect of nitrogen rate on leaf nitrogen was noted (Table 5). Early in the season, increased rates of NH_4NO_3 and KCl fertilizers reduced leaf concentrations of potassium and nitrogen, respectively, but this effect was not significant later in the season. Both fertilizers also reduced leaf concentrations of magnesium throughout the season, but only applications of NH_4NO_3 similarly affected calcium. No significant effect was seen on phosphorus (data not included). The estimated soil salinity was not significantly correlated with the accumulation of nitrogen within leaves but was positively correlated with the dry weight percentage of potassium and inversely correlated with dry weight percentages of calcium and magnesium.

Epiphytic populations of *X. c. vesicatoria* were negatively correlated with leaf potassium earlier in the growth of the tomato plant, specifically at fruit set, and were positively correlated with magnesium later in the season, at harvest. Defoliation was positively related to the magnesium content of leaves at both sampling dates and, to a lesser extent, with calcium, which increased in the leaf later in the season. Defoliation was not correlated with epiphytic populations of *X. c. vesicatoria* at the time of fruit set; however, by harvest a slight relationship was apparent (data not shown). The correlation at harvest was $r = 0.351$ ($P = 0.09$).

TABLE 4. Nutrient concentrations in tomato leaves as influenced by nitrogen (N) and potassium (K) fertilization

Rates of nitrogen fertilization (kg/ha)	Mineral content of nitrogen/potassium and calcium/magnesium (% dry weight)[z] per rates of potassium fertilization (kg/ha)			
	336	672	1,344	N effect
Early season				
336	4.64/4.69 (2.05/0.57)	4.47/4.72 (2.05/0.58)	4.36/5.12 (1.93/0.52)	4.49/4.84 (2.01/0.56)
672	4.95/4.24 (1.86/0.53)	4.77/4.65 (1.86/0.51)	4.65/4.88 (1.71/0.48)	4.79/4.59 (1.81/0.51)
K effect	4.80/4.47 (1.96/0.55)	4.62/4.69 (1.96/0.55)	4.51/5.00 (1.82/0.50)	
Late season				
336	3.01/2.70 (4.56/0.90)	2.89/2.92 (4.61/0.90)	2.89/3.45 (4.24/0.79)	2.93/3.02 (4.47/0.86)
672	3.41/2.14 (4.01/0.79)	3.36/3.07 (3.60/0.70)	3.40/3.26 (3.48/0.68)	3.39/2.82 (3.70/0.72)
K effect	3.21/2.42 (4.29/0.85)	3.13/3.00 (4.11/0.80)	3.15/3.36 (3.86/0.74)	

[z]Numbers in parentheses are the percentages of leaf calcium/magnesium mineral content. Means of three seasons (early) or two seasons (late). LSD (early): N, K, treatment effects, response = N: 0.21, 0.32, 0.30; K: 0.32, 0.08, 0.29; Ca: 0.12, 0.07, 0.13; Mg: 0.04, 0.04, 0.05. LSD (late): N, K, treatment effects, response = N: 0.16, 0.30, 0.25; K: 0.53, 0.42, 0.71; Ca: 0.40, 0.63, 0.66; Mg: 0.09, 0.09, 0.11.

DISCUSSION

The literature on the use of improved nutrition for control of plant diseases has been reviewed extensively (6). Cultural methods of disease control are often the only ones available when chemical means are inadequate and resistant cultivars are lacking. This is the case with bacterial spot of tomato. Losses in Florida because of this disease may reach 40% (17). Defoliation of plants is an important factor in reduced yields, and spotted fruits substantially lower the value of a crop.

The Cooperative Extension Service in west central Florida currently recommends fertilizing tomatoes with 180–225 kg/ha of both nitrogen and potassium. Growers have historically exceeded these levels, however, and often use rates that surpass 336 kg of nitrogen per hectare and/or 448 kg of potassium per hectare. In an attempt to better examine a potential relationship between bacterial spot, epiphytic populations of *X. c. vesicatoria*, and the nutrition of tomatoes, the highest fertilization rates used in this study were much higher than those used even by growers. These high rates would be impractical except to demonstrate this relationship and to show what effect soil salinity may have on pathogen populations and disease.

Fertilization rates or the effects of soil salinity significantly affected epiphytic populations of *X. c. vesicatoria*. That bacterial populations may possess an epiphytic stage of growth without producing symptoms of disease was first established by Crosse (2). During this phase, populations may increase to such a level that they overcome some threshold number required to initiate disease (10). They also may establish a reservoir for their subsequent dissemination (9).

Hirano et al (4) have described a lognormal distribution for epiphytic bacteria on leaves of corn, rye, snapbean, soybean, and tomato. For statistical comparison of epiphytic populations, they recommend sampling a large number of single leaves that are consistently selected from similar locations from a number of plants in a treatment. This becomes increasingly laborious as the number of treatments increases. Bulk sampling, used in the tomato experiments reported here, is a second alternative for determining epiphytic populations. Because the method produces an arithmetic mean for a population that is lognormally distributed, the number of epiphytes recovered may appear to be greater than is actually the case (4). Such an estimate would suffice when relative approximations are adequate (4). In these trials, bulk sampling was sufficient to demonstrate statistically significant differences in epiphytic populations of *X. c. vesicatoria*.

Epiphytic populations and defoliation increased throughout each season concurrently with a decrease in foliar levels of nitrogen and potassium and with an increase in calcium and magnesium. But, because a redistribution of nitrogen and potassium from leaves to fruit and an increase in foliar calcium and magnesium naturally occur as tomato plants age, a direct relationship between

TABLE 5. Correlation coefficients over time between leaf mineral content (% dry weight) and fertilization rates, soil salinity, epiphytic populations of *Xanthomonas campestris* pv. *vesicatoria*, and defoliation of tomato[z]

Leaf mineral	Day	Fertilization rates: Potassium Early	Fertilization rates: Potassium Late	Fertilization rates: Nitrogen Early	Fertilization rates: Nitrogen Late	Soil salinity Early	Soil salinity Late	Epiphytic population Early	Epiphytic population Late	Defoliation Early	Defoliation Late
Nitrogen	−0.884***	−0.436*	NS	0.579**	0.708**	NS	NS	NS	NS	NS	NS
Potassium	−0.777***	0.677***	0.530**	−0.396*	NS	0.500**	0.445*	−0.440*	NS	NS	NS
Calcium	0.902***	NS	NS	−0.613***	−0.633***	−0.567**	−0.480**	NS	NS	NS	0.369#
Magnesium	0.682***	−0.359#	−0.413*	−0.704***	−0.636***	−0.574*	−0.600**	NS	0.339#	0.372#	0.397*

[z]From an analysis of the seasonal means incorporating three early season samples (Fall 1983, and Spring and Fall 1984) and two late season samples (Spring and Fall 1984). N = 24: three potassium rates × two nitrogen rates × four replications. # indicates significance at $P = 0.10$; * is significance at $P = 0.05$; ** is significance at $P = 0.01$; *** is significance at $P = 0.001$. NS = not significant ($P > 0.10$).

disease and the concentrations of these nutrients does not necessarily follow. Superimposed on this seasonal trend were the effects of the fertilizers which, in combination and at each sampling date, raised potassium levels while lowering calcium and magnesium levels. A positive correlation between foliar magnesium and bacterial spot, similar to that reported here with epiphytic populations and defoliation, has previously been reported (22).

Factors influencing the development of populations of *X. c. vesicatoria* on the leaf surface may be quite different from factors influencing growth within. Leaching of chemicals can influence populations on the leaf surface, but growth does not begin without free water (5). Within a leaf, however, protected from desiccation, nutritional changes can have a profound effect on a bacterial population; here, differences in nitrogen and potassium fertilization will definitely affect host physiology. For example, the onset of reproduction is delayed in a plant receiving excessive amounts of nitrogen, concentrations of reducing and nonreducing sugars decline with increasing potassium fertilization, and higher amounts of soluble carbohydrates promote susceptibility to species of *Xanthomonas* (14). Similarly, low potassium causes an accumulation of free amino acids in leaves (15).

Measuring lesion development on leaves of potted tomato plants, Nayudu and Walker (16) reported a decrease of bacterial spot in plants treated with high levels of nitrogen, potassium, and phosphorus fertilization. In an otherwise balanced nutrient solution with an osmotic value of 0.1 MPa (=1 atm), the addition of sodium chloride to achieve a value of 0.24 MPa reduced disease to the same extent as the addition of potassium to 1,600 ppm. Further addition of sodium chloride to 0.57 MPa was more effective at reducing disease than the addition of nitrogen to 1,600 ppm, which produced the same osmotic value. Plants grown at high osmotic concentrations were stunted and dark green, and the leaves were occasionally flaccid in weather favoring high transpiration. In the trials reported here, however, osmotic conditions were much less extreme; no symptoms of water stress developed.

Soil factors also affect bacterial leaf spot of pepper (12). Plants grown in well-aerated sandy soils were more susceptible to *X. c. vesicatoria* than were those grown in heavier soils with a lower oxygen supply. Leaves of the former plants developed a lower water diffusion pressure deficit because roots well supplied with oxygen absorbed more soil solution, stomata opened maximally, and, under conditions of high humidity, the intercellular spaces below the stomata were maximally congested with water. This allowed easier entry of the bacteria into the interior of the leaf. A high osmotic concentration in the soil solution might produce an effect similar to insufficient oxygen by retarding the uptake of water. Stomata should then close more readily and restrict the passage of solutes or of microorganisms.

It could be postulated in this case that leakage of nutrients from within the leaf was affected both in quantity and in quality as a result of fertilization or the effects of soil salinity. Further work might investigate this leakage to determine if an imbalance between potassium and other cations on the surface could interfere with the uptake by *Xanthomonas* of minerals such as magnesium. The concentration of foliar magnesium has already been associated with the incidence of bacterial spot (22). In this study, foliar magnesium has been correlated with populations of *X. c. vesicatoria*. Manipulation of this mineral, either through potassium fertilization to reduce root uptake, or through some other mechanism, may offer useful control.

This work demonstrated that epiphytic populations of a plant pathogen can be manipulated through altered plant nutrition, resulting in reduced severity of disease. Although disease did eventually develop, its onset may have been delayed through a reduction in the reservoir of inoculum, or the rate of disease development may have been reduced because of an altered physiological response of the host. For increased fertilization to be practical, these effects must be balanced against the cost of additional fertilizers and the impact on yield. Other soil amendments may mimic the effect. Improved plant nutrition, using drip irrigation to strategically and economically place nutrients in the root zone, may, however, be one way to provide disease management in crops where an adequate chemical control program is not available.

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