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Macro- and Microelement Fertilizers Influence the Severity of Fusarium Crown and Root Rot of Tomato in a Soilless Production System

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Abstract. **Host nutritional variables were evaluated for their effects on the severity of crown and root rot of tomato caused by *Fusarium oxysporum* f.sp. *radicis-lycopersici*. Tomato (*Lycopersicon esculentum* Mill.) seedlings (cv. Bonnie Best) were grown in a pathogen-infested, soilless rockwool system in the greenhouse and were fertilized with a nutrient solution that was amended with macro- and microelements at various rates. Disease was evaluated after 2 weeks using an index of 0 to 4, and plant fresh weight was measured. Regression analysis indicated that disease severity was significantly increased by ammonium-nitrogen [NH_4Cl, $(NH_4)_6Mo_7O_{24}$, and $(NH_4)_2SO_4$], $NaH_2PO_4 \cdot H_2O$, Fe-EDDHA, $MnSO_4$, MoO_3, and $ZnSO_4 \cdot 7H_2O$. Disease severity was reduced by nitrate-nitrogen [$Ca(NO_3)_2 \cdot 4H_2O$] and $CuSO_4 \cdot H_2O$. Low rates of NH_4NO_3 (39 to 79 mg·L^{-1} N) reduced disease, but rates above 100 mg·L^{-1} N increased it. Disease was not affected by $MgSO_4 \cdot 7H_2O$. In all cases, plant growth was inversely related to disease severity. Mineral fertilizers had no effect on nutrient solution pH. This information sheds new light on environmental factors that influence plant–pathogen interactions, and may be applied to develop a management strategy for Fusarium crown and root rot based on host nutrition.**

Crown and root rot of tomato (also referred to as foot and root rot) caused by *Fusarium oxysporum* Schlechtend.:Fr. f.sp. *radicis-lycopersici* Jarvis & Shoemaker was first described in Japan in the late 1970s, and has since become an economically important problem in greenhouse tomato production throughout Europe, North America, Japan, and Israel (Jarvis, 1988). It is considered the most destructive tomato disease caused by a nonzoosporic pathogen in soilless hydroponics production systems, where reductions in marketable yield can exceed 60% (Mihuta-Grimm et al., 1990; Stanghellini and Rasmussen, 1994). Tomato plants can be infected at any time, but losses are especially severe when infection occurs at the seedling stage. Symptoms include dark brown necrotic lesions that form on the roots and crown region and may extend up the hypocotyl, stem, and foliage; localized discoloration of the vascular tissues; and subsequent leaf chlorosis, wilting, and death. The pathogen is spread via infected transplants, which often carry latent infections. It can then grow to some extent through soil to infect adjacent plants (Hartman and Fletcher, 1991; Louter and Edgington, 1990). The threat to tomato production is further increased by infection from airborne conidia that are produced in stem lesions and are dispersed by wind and fungus gnats [*Bradysia* sp. (Diptera: Sciaridae)] (Gillespie and Menzies, 1993; Rowe and Farley, 1981).

Control of Fusarium crown and root rot on tomato has been difficult and will probably require multiple approaches. Only a few resistant cultivars are available (Erb and Rowe, 1992; Heremans, 1996; Sugahara and Sakurai, 1991). Fungicides, including benomyl, captafol, imazalil, thiram, and prochloraz-Mn, provide inconsistent control, leave problematic residues in edible tissues, and are often phytotoxic even when applied at recommended rates, especially on seedlings (Hartman and Fletcher, 1991; Jarvis, 1988, 1992; Mihuta-Grimm et al., 1990). Biological control utilizing fungal (i.e., *Trichoderma harzianum* and nonpathogenic *Fusarium oxysporum* and *F. solani*) and bacterial agents (i.e., *Bacillus subtilis* and *Pseudomonas* sp.) typically provides only a moderate level of disease suppression in the greenhouse and field (Bochow et al., 1996; Duffy and Défago, 1997; Hartman and Fletcher, 1991; Louter and Edgington, 1990; M'Piga et al., 1997; Sivan et al., 1987). Allelopathy from lettuce (*Lactuca sativa* L.) and dandelion (*Taraxacum* Weber sect. *ruderalia* sp. Kirschner) residues incorporated into soil provides limited control (Jarvis, 1992; Jarvis and Thorpe, 1981), but is technically impractical in hydroponic production systems. Alternative control measures are needed, ideally with the aim of developing an integrated disease management strategy.

The nutritional status of a plant has a major impact on disease susceptibility, and this has been exploited for suppressing a variety of diseases (Engelhard, 1989). Notable examples are Fusarium wilts caused by *F. oxysporum* formae speciali, with reports dating to the 1920s that describe the beneficial effect of lime amendments (Jones et al., 1989). Since then, the effects of most major and minor nutrients on wilt diseases have been studied. Jones and coworkers (Jones et al., 1989) applied this information to develop an effective fertilizer-based management strategy for Fusarium wilt of tomato that is used in commercial production systems in the United States. Similar approaches have been successful for control of Fusarium wilts of other vegetable and ornamental crops (Elmer, 1992; Jones et al., 1989; Schneider, 1985).

In contrast, little is currently known about the influence of plant nutrition on crown and root rot of tomato. Previous studies tested single concentrations of nitrogenous fertilizers and sodium chloride (Jarvis and Thorpe, 1980; Woltz et al., 1992), and did not examine the influence of other potentially critical mineral nutrients, particularly microelements. The objective of our study was to compare the effects of several macro- and microelements (various ammonium-N sources, nitrate-N, sodium phosphate, iron, molybdenum, and copper-, magnesium-, manganese-, and zinc-sulfates) on disease severity and growth of tomato seedlings. Mineral nutrients were tested across a range of concentrations to provide more information that can be applied to develop a fertilizer-based management strategy and for integrating mineral fertilizers with other control approaches (e.g., biocontrol) that may be sensitive to mineral levels.

Materials and Methods

The influence of various mineral nutrients on Fusarium crown and root rot was evaluated in a noncirculating hydroponics system. Pregerminated [2–3 d on 0.85% water agar (Oxoid, Hampshire, England) at 24 °C; 2–4 mm-long primary root] tomato seeds cv. Bonnie Best were planted on rockwool cubes (3.5 cm^2 diameter × 4 cm deep; one seed per cube; Grodania A/S, Hedehusene, Denmark) in square plastic trays (5.5 cm deep). The rockwool was saturated with 800 mL of dilute (1/4 strength) Knop nutrient solution (Ziegler, 1983) containing (mg·L^{-1}): $Ca(NO_3)_2 \cdot 4H_2O$ (250); KH_2PO_4, KCl, and $MgSO_4 \cdot 7H_2O$ (62.5 each); and Fe-EDDHA [ethylenediamine-di(*o*-hydroxyphenyl-acetic acid); Sequestrene 138 Fe, Novartis AG, Basel, Switzerland] (5). Autoclave-sterilized stock solutions of the various minerals tested [$Ca(NO_3)_2 \cdot 4H_2O$, $CuSO_4 \cdot 5H_2O$, $MgSO_4 \cdot 7H_2O$, $MnSO_4$, MoO_3, $NaH_4PO_4 \cdot H_2O$, NH_4Cl, $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$, NH_4NO_3, $(NH_4)_2SO_4$, $ZnSO_4 \cdot 7H_2O$] were added to the nutrient solution just before use to

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give a range of final concentrations (see Figs. 1–5) and the pH was measured with a Digitalmeter (Auer Bittmann Soulié AG, Zürich, Switzerland). Prior to saturating the rockwool, the nutrient solution was inoculated with *F. oxysporum* to give ≈10^5 microconidia plus mycelial fragments per mL, as previously described (Duffy and Défago, 1997). Mycelial fragments were included because in preliminary experiments, inoculation with microconidia alone resulted in little or no disease. Inoculum was produced by growing the pathogen in 150 mL of 2% malt extract broth (pH 5.5; Oxoid) in 500-mL baffled Erlenmeyer flasks at 24 °C for 5–7 d with shaking at 130 rpm. Cultures were centrifuged (15 min at 2200 g_n) to collect fungal biomass, which was then briefly homogenized in an electric blender immediately before adding to the nutrient solution.

Plants were grown in a growth chamber in the greenhouse with 16 h light/8 h darkness, 22 °C day/18 °C night, and 70% relative humidity. Lower temperatures are favorable for development of crown and root rot, in contrast with the warmer temperatures (≈28 °C) that favor Fusarium wilt (Jones et al., 1991). Millipore-filtered bi-distilled water (0.05 µm, Elgastat Ultra High Polishing unit, O. Kleiner AG, Wohlen, Switzerland) was added as needed to maintain a solution level of 1 to 2 cm. Fourteen days after planting, tomato seedlings were carefully removed from the rockwool with the upper 1.5 cm of the root system attached. They were weighed and disease severity was rated on a scale of 0 to 4 (adapted from Mihuta-Grimm et al., 1990) where 0 = symptomless; 1 = slight brown discoloration of the upper root system; 2 = moderate brown discoloration of two-thirds or less of the upper root system; 3 = extreme brown discoloration of the upper root system and numerous necrotic lesions extending up the crown and stem; and 4 = seedling dead or nearly so. Representative samples of necrotic tissue were plated onto Komada's selective medium (Komada, 1975) to confirm *F. oxysporum* f.sp. *radicis-lycopersici* as the cause of symptoms.

Mineral nutrient treatments were used at seven rates, each consisting of three replicates over time with 12 to 20 plants per replicate, and were arranged in a completely randomized design. Data for each mineral nutrient treatment were analyzed separately. Relationships between nutrient rate and disease severity and plant weight were evaluated using regression procedures (SAS Institute, Cary, N.C.). Adjusted regression coefficients, which stabilize to a certain value when an adequate set of variables is included in the model, were derived as an alternative to r^2, which can be driven to 1 by adding superfluous variables to the model with no real improvement of fit (Littell et al., 1991).

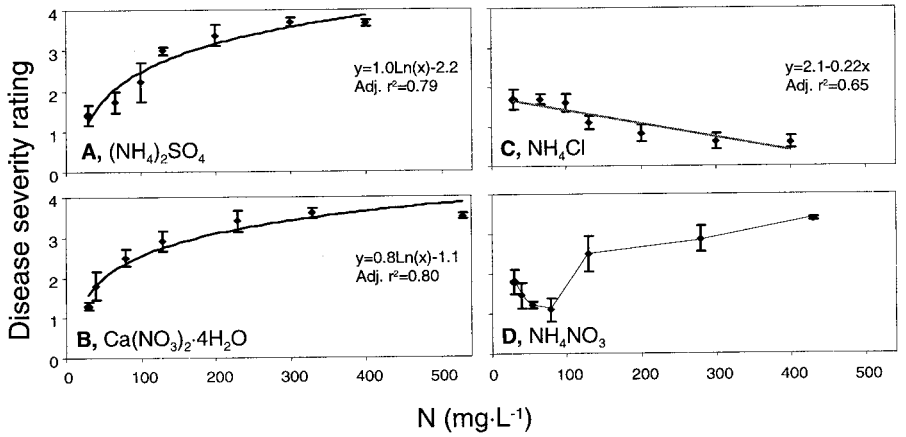

Fig. 1. Influence of the amount and form of nitrogen on Fusarium crown and root rot disease severity after 2 weeks. Nitrogen was supplied at planting as (**A**) $(NH_4)_2SO_4$, (**B**) $Ca(NO_3)_2 \cdot 4H_2O$, (**C**) NH_4Cl, or (**D**) NH_4NO_3. Values represent the means per plant in three trials. Adjusted regression coefficients and line derivations were significant at $P \leq 0.0001$. Low adjusted r^2 values for **D** (0.45) reflected the different trends at low- and high-N concentrations, and line derivations have not been forced. Vertical bars represent ± standard error of the mean.

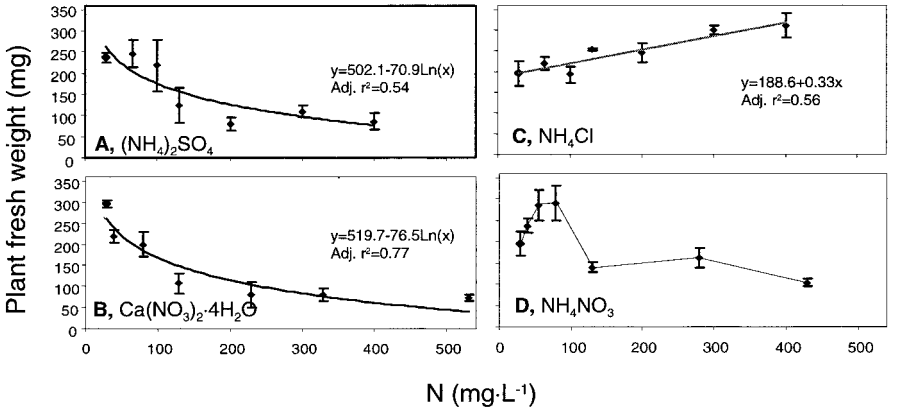

Fig. 2. Influence of the amount and form of nitrogen on growth of Fusarium-infected tomato seedlings after 2 weeks. Nitrogen was supplied at planting as (**A**) $(NH_4)_2SO_4$, (**B**) $Ca(NO_3)_2 \cdot 4H_2O$, (**C**) NH_4Cl, and (**D**) NH_4NO_3. Values represent the means per plant in three trials. Adjusted regression coefficients and line derivations were significant at $P = 0.0001$. Low adjusted r^2 values for **D** (0.25) reflected the different trends at low- and high-N concentrations, and line derivations have not been forced. Vertical bars represent ± standard error of the mean.

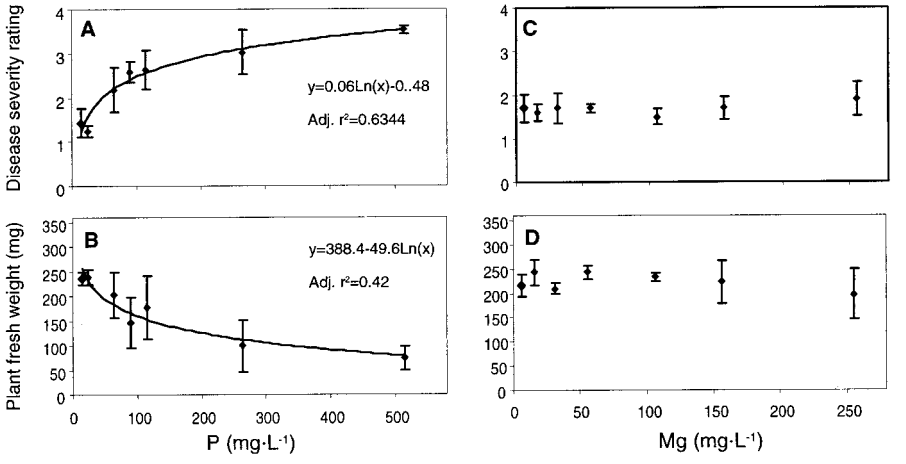

Fig. 3. Influence of sodium phosphate (**A, B**) and magnesium sulfate (**C, D**) on Fusarium crown and root rot severity and on tomato seedling growth after 2 weeks. Values represent the means per plant in three trials. Adjusted regression coefficients and line derivations in **A–B** were significant at $P \leq 0.0009$. Differences in **C–D** were nonsignificant ($P \geq 0.6000$). Vertical bars represent ± standard error of the mean.

Results and Discussion

Twelve mineral nutrients were tested separately for their influence on Fusarium crown and root rot. A similar and moderate level of disease (1–2 rating on a scale of 4) developed in all control treatments that were provided with the standard nutrient solution (no additional minerals) (Figs. 1–4). Disease developed rapidly in affected seedlings, with necrotic lesions forming at the crown generally within a week of emergence. This was often followed by severe chlorosis and turgor loss. No signs of vascular infection were observed beyond the area of superficial necrosis. Severe

disease developed (mean rating 3–4) in treatments provided with ammonium-N (Fig. 1), phosphate (Fig. 3), iron, zinc, manganese, and molybdenum (Fig. 4). At the higher concentrations tested, infected seedlings often failed to emerge. Seedlings with no symptoms after 10 d usually remained healthy even when left to mature (data not shown), probably because of poor spread of the pathogen in rockwool (Mihuta-Grimm et al., 1990). In all treatments, fresh weight of seedlings was inversely correlated with the severity of Fusarium crown and root rot (Figs. 1–5), supporting previous observations for this disease (Duffy and Défago, 1997; Jones et al., 1991; Woltz et al., 1992). Windborne and insect-transmitted spores were not a factor in this study, because noninoculated plants that were placed in the greenhouse (but not included in the experiments) remained disease-free.

Nitrogen form had a major influence on the severity of Fusarium crown and root rot and on growth of tomato seedlings in a soilless rockwool system (Fig. 1). Increasing concentrations of nitrate-N reduced disease and improved plant growth in comparison with ammonium forms. Ammonium sulfate and ammonium chloride gave similar responses, implicating NH_4^+ as the deleterious component (Fig. 1). Ammonium nitrate has been reported to either have no influence on Fusarium diseases or to increase disease just as ammonium-N (Jones et al., 1989; Schneider, 1985). While this was generally true for Fusarium crown and root rot, by testing a range of concentrations we were able to observe that at low concentrations (10 to 100 mg·L^{-1} N), ammonium nitrate reduced disease in a fashion similar to nitrate-N (Figs. 1D, 2D). However, the negative influence of the NH_4^+ ion became evident at concentrations above 125 mg·L^{-1} N (Figs. 1D, 2D). At higher concentrations, seedlings may have had insufficient available carbohydrates to convert the excess ammonium, which is toxic for tomato seedlings (Woltz et al., 1992), to nontoxic amino acids (Pate, 1973).

Nitrates have long been recognized for reducing seedling disease caused by *Rhizoctonia solani* (Huber and Watson, 1974); however, contradictory results have been reported for Fusarium crown and root rot. Mihuta-Grimm et al. (1990) reported that nitrogen supplied as a 20N–20P–20K fertilizer had no effect on growth of *F. oxysporum* f.sp. *radicis-lycopersici* in rockwool compared to nonfertilized treatments. Jarvis and Thorpe (1980) found no effect of nitrogen form (total N applied was not specified) on disease or yield when adequate lime was provided to negate potential pH effects. Indeed, a differential effect of nitrogen form on pH is a major mechanism of action for suppression of many soilborne pathogens (Huber and Watson, 1974). In contrast, Woltz et al. (1992) reported that nitrate- vs. ammonium-N (each at 225 mg·L^{-1} N) reduced severity of crown and root rot without affecting soil pH (pH 4.81 and 4.85, respectively). Similarly, we observed no effect of nitrogen fertilization (or any other mineral amendment) on pH of the hydroponic solution. In both studies, though, only pH of

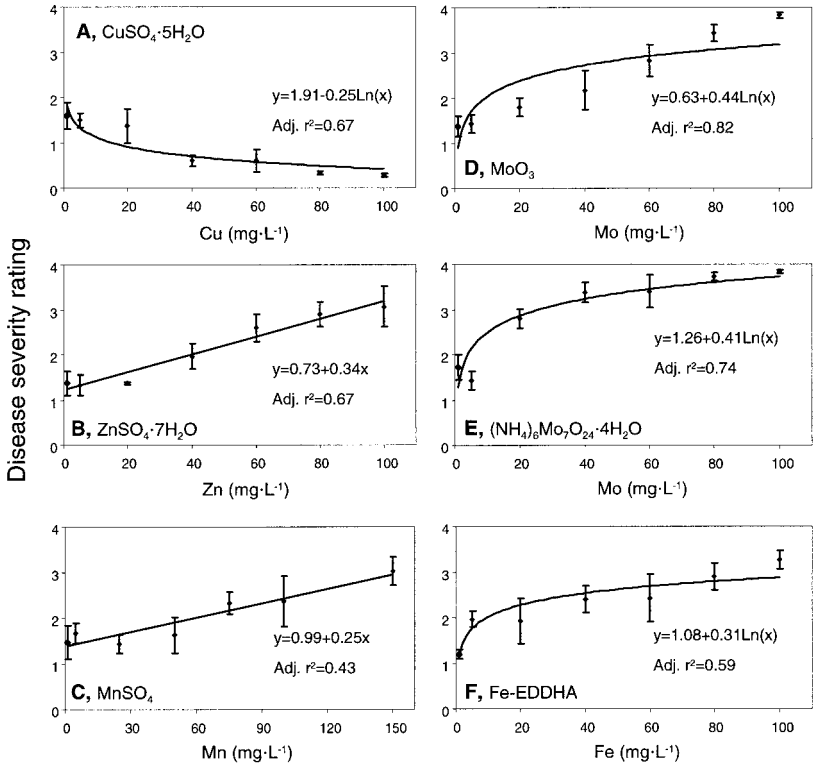

Fig. 4. Influence of micronutrients on the severity of Fusarium crown and root rot of tomato. Amendments of (**A**) $CuSO_4·5H_2O$; (**B**) $ZnSO_4·7H_2O$; (**C**) $MnSO_4$; (**D**) MoO_3; (**E**) $(NH_4)_6Mo_7O_{24}·4H_2O$; or (**F**) Fe-EDDHA were provided at planting. Values represent the means per plant in three trials. Adjusted regression coefficients and line derivations were significant at $P \leq 0.0008$. Vertical bars represent ± standard error of the mean.

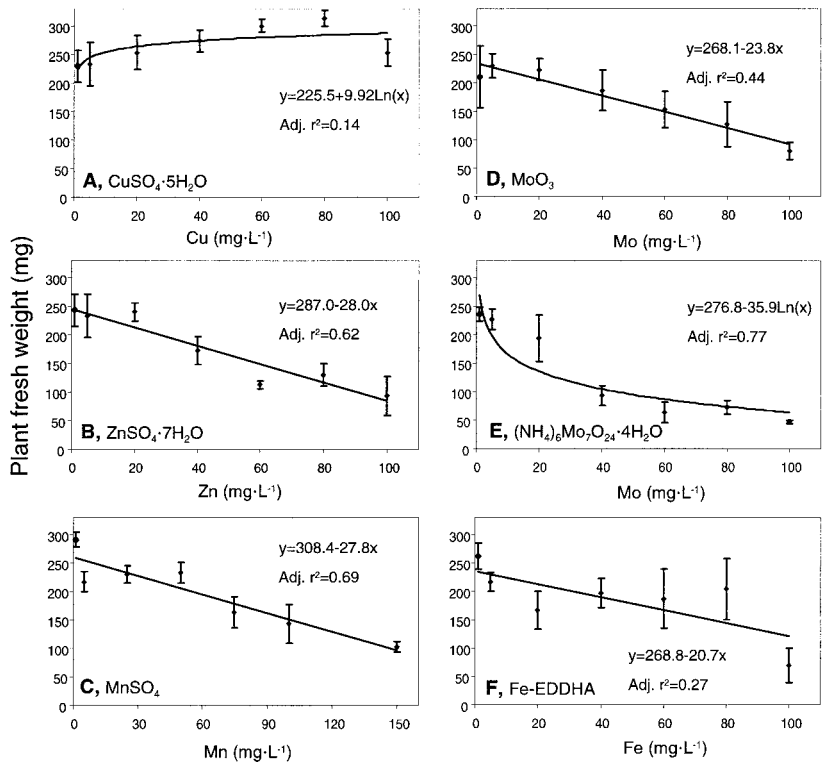

Fig. 5. Influence of micronutrients on tomato seedling growth after 2 weeks in rockwool infested with *Fusarium oxysporum* f.sp. *radicis-lycopersici*. Amendments of (**A**) $CuSO_4·5H_2O$; (**B**) $ZnSO_4·7H_2O$; (**C**) $MnSO_4$; (**D**) MoO_3; (**E**) $(NH_4)_6Mo_7O_{24}·4H_2O$; and (**F**) Fe-EDDHA were provided at planting. Values represent the means per plant in three trials. Adjusted regression coefficients and line derivations were significant at $P \leq 0.0007$ for all except **A** and **F,** where $P = 0.0504$ and 0.0091, respectively. Vertical bars represent ± standard error of the mean.

the bulk media was measured and possible localized pH effects in the rhizosphere where disease actually occurs cannot be excluded (Smiley, 1975). Another possible factor may be total calcium concentrations, which are increased with liming and with calcium nitrates as used in our study and that of Woltz et al. (1992). They found that all treatments that increased calcium content also reduced disease. While adequate calcium in tomato tissues appears to be important for resistance to cell-wall-degrading enzymes (e.g., polygalacturanose) produced by *Fusarium* sp., it is generally considered a minor factor in controlling disease (Jones et al., 1989).

Sodium phosphate increased disease severity and reduced tomato growth (Fig. 3). Similar results with various phosphorus forms have been reported for wilt diseases caused by related formae speciali (Jones et al., 1989), and this has been attributed in part to the enhanced uptake of calcium (Jarvis, 1992). While possible effects of sodium cannot be excluded, exhaustive studies with other Fusarium diseases [i.e., celery yellows (Schneider, 1985) and asparagus wilt (Elmer, 1992, 1995)] revealed no influence of the Na^{2+} ion. Magnesium sulfate fertilization had absolutely no effect on Fusarium crown and root rot at concentrations up to 250 mg·L^{-1} Mg (Fig. 3). To our knowledge, this is the first examination of magnesium on *F. oxysporum* independent of the Cl^{2+} ion. Previous work has demonstrated that fertilization with $MgCl_2$ increased wilt caused by *F. oxysporum* formae speciali on tomato (Jones et al., 1989) and celery (Schneider, 1985). In these studies, Cl^{2+} and not Mg^{2+} was suspected to be the problematic ion, a conclusion that is further supported by our results.

Copper sulfate effectively reduced disease severity (Fig. 4) and improved tomato growth (Fig. 5) at concentrations above 20 mg·L^{-1} Cu. This is not surprising, considering the historical use of Cu^{2+} as a broad-spectrum fungicide (Schumann, 1991). No phytotoxicity was observed, even at the highest concentrations tested. In contrast, all other micronutrients tested aggravated disease (Fig. 4) and stunted growth (Fig. 5). Zinc and manganese increased disease at concentrations above 40 and 50 mg·L^{-1}, respectively. Molybdenum increased disease at concentrations of 20 mg·L^{-1} and above. Ammonium molybdate (Fig. 4E) was more conducive to disease than molybdenum oxide (Fig. 4D), perhaps because of the additive influence of the NH_4^+ ions. Iron added as Fe-EDDHA increased disease at concentrations of just 5 mg·L^{-1} and greater, with only slight further increases until over 80 mg·L^{-1} (Fig. 4F). We found no evidence for induction of host defenses by zinc, iron, or manganese, as suggested by Mandal and Sinha (1992). Plants supplied with zinc or ammonium molybdate at 33 mg·L^{-1} exhibited no signs of toxicity in the absence of the pathogen (Duffy and Défago, 1997). However, node length declined with higher concentrations, suggesting that phytotoxicity as well as increased disease possibly contributed to reductions in fresh weight (Fig. 5). While excessive concentrations are uncommon in agricultural soils and hydroponics, their availability can be increased under certain conditions, such as acidification. Incidentally, acidic pH also favors crown and root rot (Woltz et al., 1992). Inert materials such as rockwool tend to reduce plant sensitivity to minerals (Jarvis, 1992). Plants may also be exposed to elevated mineral concentrations applied to improve the beneficial activity of biological control strains of *Pseudomonas fluorescens* (Duffy and Défago, 1997). Results of our study facilitate the development of such microbe–mineral fertilizer treatments with minimal adverse side effects on the host plant, information that has been lacking. They also accentuate the need to develop methods for more efficient delivery of potentially phytotoxic minerals.

Exactly how mineral nutrients influence disease is uncertain, but effects on pathogen activity and host susceptibility are probably involved. *Fusarium oxysporum* has a relatively high requirement for micronutrients (Jones et al., 1989). Concentrations of zinc, iron, manganese, and other metals above those typically found in soil and nutrient solutions stimulate fungal growth and sporulation (Duffy and Défago, 1997; Jones et al., 1989). The profile of secondary metabolites produced by the pathogen, including phytotoxic compounds like fusaric acid, is also altered (Duffy and Défago, 1997; Egli, 1969). Nitrates inhibit both sporulation and spore germination, while ammonium has the opposite effect (Jones et al., 1989). Fertilization with nitrate-N decreases the sensitivity of tomato to fusaric acid, a phytotoxin produced in infected plants by *Fusarium oxysporum* (Barna et al., 1983). Susceptibility of tomato to fungal attack is increased by zinc, in part because zinc raises the sugar level in plant tissues (Jarvis, 1992). Host susceptibility can also be altered by interactions between minerals, particularly at elevated concentrations, which impact the availability of other nutrients. For example, ammonium-N interferes with the uptake of nitrates and potassium, which in turn stimulates chloride uptake, leading to increased susceptibility of tomato to *F. oxysporum* f.sp. *lycopersici* (Jarvis, 1992). Disease suppression with minerals has also been attributed to the stimulation of indigenous populations of antagonistic microorganisms in the soil and rhizosphere (Elmer, 1995; Engelhard, 1989). While this is generally not relevant to hydroponics, recent work indicates that minerals can be exploited to improve the beneficial activity of introduced biocontrol agents in soilless culture (Duffy and Défago, 1997).

Our results build on those of Woltz et al. (1992) and provide a foundation for developing a control strategy based on plant nutrition. Such an approach has been successfully applied to manage other Fusarium diseases (Jarvis, 1992; Jones et al., 1989). Mineral nutrient effects on crown and root rot of tomato caused by *F. oxysporum* f.sp. *radicis-lycospersici* were similar to those reported for other formae speciali, which reflects the adaptability of control strategies for various Fusarium diseases. It further suggests biological similarity of these pathogens and/or similar responses of diverse hosts to these fungi. Fusarium crown and root rot, however, is not the only problem threatening hydroponically grown tomato, and nontarget effects of certain mineral nutrients on other diseases need to be considered. A prominent example, nitrate-N, which reduced crown and root rot, increases the severity of economically devastating diseases caused by *Pythium* and phytopathogenic bacteria (Stanghellini and Rasmussen, 1994). Integrating mineral nutrients with newly developed resistant cultivars, biocontrol agents, and/or fungicides used at reduced, nonphytotoxic concentrations may enhance the level and spectrum of disease control.

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