Reduction of Fusarium Wilt of Carnation with Suppressive Soils and Antagonistic Bacteria

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ABSTRACT

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Severity of Fusarium wilt caused by *Fusarium oxysporum* f. sp. *dianthi* in greenhouse-grown carnations was reduced 18–66% for 90 days when two wilt-suppressive soils were incorporated into an infested wilt-conducive soil mix at a rate of 1% (v/v). Preplant treatment of carnation cuttings by dipping roots in a slurry of suppressive soil resulted in 68 and 35% reductions in disease severity at 50 and 90 days, respectively. Application of an unsterile filtrate of a suppressive soil slurry was comparable in reducing disease severity to the incorporation of suppressive soil into conducive soil at rates of 1 and 10%. Ten soils from the Salinas Valley, when applied to rooted cuttings as slurries, reduced wilt severity by amounts ranging from about 25% to more than 75% at 5 mo. *Alcaligenes* sp. MFA1 and *Pseudomonas putida* C88, both isolated from the roots of carnations grown in a suppressive soil, significantly reduced wilt severity by 40 and 30%, respectively, for about 75 days in repeated experiments. *Bacillus subtilis* A13 and *Pseudomonas* sp. B10, strains previously tested for plant growth promotion in greenhouse and field trials, gave similar levels of disease control. Treatments with specific bacteria, however, were not as effective in reducing Fusarium wilt as treatments with suppressive soil slurries for intervals of 120 days. Survival of strain MFA1 on the root system of carnation was influenced by the texture and pH of the soil in which the plant was grown. The root population densities of MFA1 detected over a 5-mo period were lower in sand and loamy sand soils with low pH than in sandy loam and clay loam soils with near-neutral pH. In evaluations of suppressive soil and specific bacteria for control of Fusarium wilt of carnations grown in commercial greenhouse beds, only the suppressive soil significantly reduced disease incidence.

Additional key words: biological control, *Dianthus caryophyllus*, root colonization

Fusarium wilt of carnation caused by *Fusarium oxysporum* Schlecht. f. sp. *dianthi* (Prill. & Del.) Snyd. & Hans. causes widespread, heavy economic losses in commercially grown carnation (*Dianthus caryophyllus* L.). Most carnations grown in commercial plantings in the United States carry little or no resistance to the disease. Although wilt-tolerant cultivars have been developed, they have not gained wide commercial acceptance. Thus, control of Fusarium wilt in carnation has been limited to eliminating the pathogen in soil and planting pathogen-free stock. However, complete eradication of the pathogen from soil by steaming or fumigating with chemicals is seldom achieved. The treatments also may eliminate the antagonistic microflora that normally inhibit the pathogen.

The introduction of biological control agents to soil or planting stock has potential for control of another disease of carnation, Fusarium stem rot (2,4,12,16). Application of certain fungi to carnation cuttings and wounds has provided protection from the disease by the mechanism of cross-protection (4). Reduction of stem rot by an unidentified bacterium (12) was related to its ability to lyse mycelia of the pathogen. The bacterium, later identified as an *Arthrobacter* sp., was tested for control of Fusarium wilt of carnation (23). Inoculation of roots of greenhouse-grown carnation seedlings with this bacterium reduced the incidence of wilt up to 150 days, whereas similar treatments of rooted cuttings transplanted into the field had less effect on wilt incidence.

Control of Fusarium wilt of carnation by incorporating small amounts of Fusarium wilt-suppressive soil into pasteurized conducive soil has been demonstrated (1,3,15,19). The factors responsible for suppressiveness are primarily biotic, as shown by their transmissibility and their susceptibility to heat and gamma-irradiation (14,19). Both fungi and bacteria have been implicated in wilt-suppressive soils. Saprophytic forms of *F. oxysporum* and *F. solani* were important in imparting suppressiveness to soils of Chateaurenard (18). *Arthrobacter* sp., although never shown to be specifically involved in suppressiveness, was isolated in higher numbers and multiplied faster in wilt-suppressive soils of the Salinas Valley than in wilt-conducive soils (21). *Pseudomonas* strains isolated from a Salinas Valley suppressive soil reduced the incidence of Fusarium wilts of flax, cucumber, and radish (19,20,24) when added to conducive soil.

This study examined the feasibility of using aqueous soil suspensions, or slurries, as root dips to control Fusarium wilt in commercially grown carnations and to compare the efficacy of these treatments with treatments using several antagonistic bacterial strains. These included strains isolated from wilt-suppressive soils and strains previously tested for growth promotion and biological control (6,10). Population dynamics of the antagonistic bacteria on carnation roots were also studied to determine the relationship of soil type to root colonization. Preliminary results have been reported (28).

MATERIALS AND METHODS

Soils. Soils were collected from the top 30-cm layer at various agricultural sites in California. The series and type of soil from each site were determined from soil survey maps (8,25,27). The pH was measured using the saturated soil paste method (17). The soils were sifted through a 5-mm screen and stored in plastic bags at 18–23 C for up to 2 mo before use. Of the soils studied, Chualar sandy loam, Metz fine sandy loam, and Mocho silty clay loam were previously reported as suppressive soils (15,19,22).

Soils were applied in tests for suppressiveness by two procedures. In one procedure, they were incorporated at rates of one to 10% (v/v) into a wilt-conducive soil mix (loam soil, peat, and sand; 2:1:1, v/v), typical of those used in carnation beds. It had been steam-sterilized previously and exposed to air to allow recolonization by miscellaneous microorganisms. In the second procedure, root masses of commercially rooted cuttings of Improved White Sim carnations were dipped in slurries made with field soil and water in a 2:1 ratio (v/v) before planting in the conducive soil mix.

Isolation of antagonistic bacteria. Bacteria were isolated from roots of carnations grown for more than 1 mo in wilt-suppressive soil. Root segments, briefly washed under running water, were

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triturated with mortar and pestle in a small volume of sterile water. Final dilutions of the triturate was plated on King's Medium B (KB), potato-dextrose, and trypticase soy (Difco) agar media. After 24–48 hr of incubation, plates containing fewer than 30 bacterial colonies were sprayed with a suspension containing 10^7 microconidia of *F. oxysporum* f. sp. *dianthi* per milliliter. After an additional 24 hr of incubation, the cultures were observed for bacterial strains that inhibited the fungus.

Strains that were inhibitory to *F. oxysporum* f. sp. *dianthi* were tested for antagonism against the pathogen in soil. Seeds of carnation Marguerite were dipped in bacterial suspensions containing 10^8 colony-forming units (cfu) per milliliter and planted in soil mix infested with *F. oxysporum* f. sp. *dianthi* at 10^5 propagules per gram. Previous experiments showed that preemergence and postemergence damping-off of carnation seedlings was caused by *F. oxysporum* f. sp. *dianthi* at this population density. Of the strains that significantly improved the germination and survival of seedlings, two strains, MFA1 and C88, were evaluated further. They were identified as *Alcaligenes* Cast. & Chalm. sp. and *Pseudomonas putida* (Trev.) Mig., respectively, according to Buchanan and Gibbons (7).

Other bacteria used in experiments included *Bacillus subtilis* (Cohn) Prazm. strain A13, which increased germination and growth of plants in greenhouse and field trials (6), and *Pseudomonas* Migula sp. strain B10, a plant growth-promoting rhizobacterium that also suppressed Fusarium wilt of flax and take-all of wheat (10).

Pathogen inoculum. *F. oxysporum* f. sp. *dianthi* (strain 987) was grown on 100 g of sterilized ground barley straw amended with 200 ml of 0.03 M L-asparagine in a 3-L Erlenmeyer flask. Each flask was incubated at room temperature for 4 wk and the contents air-dried for 2 wk. Infested straw was then added to the soil mix to give inoculum densities of 100–10,000 propagules per gram. Pathogen concentrations in infested soil were assessed by dilution plating onto Komada's medium (11).

Inoculation of carnations with bacteria and detection of root populations. Spontaneous mutants of each bacterial strain tolerant to rifampicin at 100 μg/ml were used as inoculum. Before planting, roots of cuttings were dipped in 0.1 M $MgSO_4$ bacterial suspensions containing 10^8 cfu/ml. The numbers surviving on carnation roots were detected by excising 1.5-cm segments of roots growing beyond the inoculated root mass with a cork borer and shaking the segments in sterile water for 30 min. The washings were serially diluted and plated on KB agar amended with rifampicin at 100 μg/ml, cycloheximide at 150 μg/ml, and benomyl at 150 μg/ml.

Evaluation of bacteria and suppressive soils in reducing Fusarium wilt severity. One or two rooted carnation cuttings were inoculated with bacteria or soil slurries and planted in 15-cm clay pots containing soil mix infested with *F. oxysporum* f. sp. *dianthi*. Eight to 12 replicate pots, depending on the experiment, were arranged in a randomized block design for each treatment since good uniformity was obtained among replicate treatments in preliminary experiments. The plants were maintained in a greenhouse with night/day temperature extremes ranging from 17 to 32 C and watered and fertilized daily.

Each plant was evaluated for Fusarium wilt severity at weekly intervals on a scale of 0–4, where 0 = no symptoms, 1 = slight chlorosis or wilt in one branch, 2 = wilt in less than half of the plant, 3 = severe wilt, and 4 = dead plant. Stem samples were removed from some diseased plants and cultured for the pathogen to ensure that *F. oxysporum* f. sp. *dianthi* was the cause of the disease. Arc sine transformation (5) was performed on the raw data before testing for statistical significance by analysis of variance.

Test of suppressive soils and bacteria in commercial carnation greenhouses. Bacteria and wilt-suppressive soils were evaluated for their effects on the development of Fusarium wilt in five commercial greenhouses, each with a history of heavy losses caused by Fusarium wilt. Preparation of ground beds varied among locations and involved steaming, fumigation with methyl bromide, or no treatment. The source of pathogen inoculum was from natural reinfestation or residual inoculum.

Bacterial suspensions and suppressive soil slurries were applied to the roots of cuttings of susceptible Sim cultivars

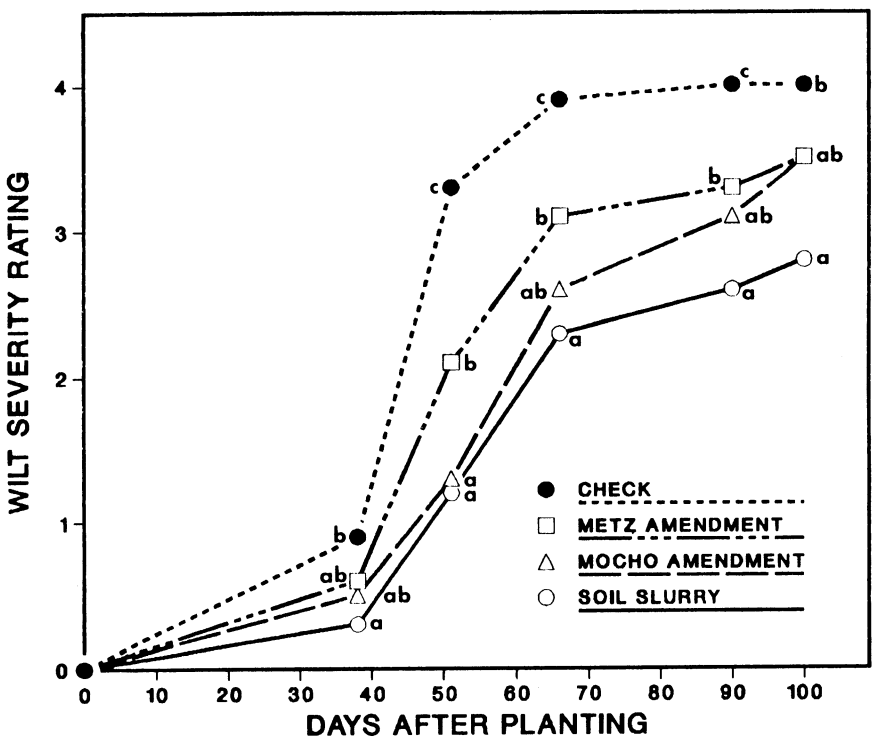

Fig. 1. Fusarium wilt severity of carnations grown in pathogen-infested soil mix as affected by amendments (1%, v/v) with Mocho or Metz suppressive soils, a preplant root dip in a slurry of Mocho and Metz soils, and no treatment (control). Disease severity was rated on a scale of 0 (symptomless) to 4 (dead). Small letters indicate significant differences (P = 0.05) at each observation time according to Duncan's multiple range test.

Table 1. Reduction of Fusarium wilt severity by dipping carnation roots in soil filtrates of Mocho suppressive soil and by planting rooted cuttings in wilt-conducive soil mix[x] amended with suppressive soil

Treatment	Disease severity rating[y] 2 mo	4 mo
Mocho soil filtrate	0.3 a[z]	1.6 ab
Autoclaved Mocho soil filtrate	1.2 bc	2.3 c
Mocho soil amendment (1%, v/v)	0.4 a	1.3 a
Mocho soil amendment (10%, v/v)	0.4 a	1.8 b
Autoclaved Mocho soil amendment (10%, v/v)	1.5 c	2.6 c
No treatment	0.8 b	2.6 c

[x] Soil mix was infested with *Fusarium oxysporum* f. sp. *dianthi* at 100 propagules per gram.

[y] Average of 12 plants rated on a scale of 0 (symptomless) to 4 (dead).

[z] Values within a column followed by the same letter are not significantly different (P = 0.05) according to Duncan's multiple range test.

before planting. The number of plants in each replicate plot varied among experiments from 36 to 100, and the number of replicate plots per treatment varied from four to eight. Because of the proximity of commercial plants, disease severity of individual plants could not be determined; incidence of Fusarium wilt or mortality was measured instead. The experiments were designed as paired plots in which disease incidence or mortality in each treatment plot was compared with levels measured in an adjacent untreated control plot. The *t* test of paired treatments (5) was performed in the statistical analysis of the data.

RESULTS

Reduction of disease by suppressive soils. Two suppressive soils, Metz fine sandy loam and Mocho silty clay loam, significantly reduced symptom severity of Fusarium wilt of carnation compared with controls for 90 days when added separately to infested potting mix at a rate of 1% (v/v) or when applied in combination as a slurry to the roots of cuttings (Fig. 1). The soil slurry treatment was slightly better than the other two treatments, with reduction of disease ranging from about 55% at 40 days to 35% at 90 days. All of the control plants had died by 90 days.

Treatment of rooted cuttings with an unsterile filtrate of Mocho silty clay loam also reduced the severity of Fusarium wilt (Table 1). The filtrate was prepared by filtering a slurry of the suppressive soil through Whatman No. 1 filter paper, thereby removing most of the soil particles and leaving the microflora in suspension. After 2 and 4 mo, symptom severity of plants treated with the filtrate was significantly less than that of untreated control plants. The severity of symptoms was also similar to that of plants grown in potting mix amended with Mocho soil at 1 and 10% (v/v). Amendments of potting mix with sterilized Mocho soil and treatment of cuttings with a filtrate prepared from it did not reduce wilt severity.

In a test comparing slurries of 10 soils from the Salinas Valley as root treatments (Table 2), significant reductions in wilt severity were obtained with all soils. The extent of disease reduction compared with controls at 5 mo varied widely among the soils. The most effective soil reduced disease severity by more than 75%, and the least effective, by about 25%. The three soils known to be wilt-suppressive, Mocho silty clay loam, Chualar sandy loam, and Metz fine sandy loam, reduced wilt severity by 50–60%.

Reduction of disease by antagonistic bacteria. Application of antagonistic bacteria to the roots of carnation cuttings consistently reduced Fusarium wilt severity for about 75 days after treatment in various experiments using three

Table 2. Reduction of Fusarium wilt severity by dipping carnation roots in slurries of Salinas Valley soils

Soil	Subgroup[x]	Disease severity rating[y]
Elkhorn fine sandy loam	Pachic Argixerolls	0.8 a[z]
Pico fine sandy loam	Fluventic Haploxerolls	1.0 a
Mocho silty clay loam	Fluventic Haploxerolls	1.3 ab
Salinas loam	Pachic Haploxerolls	1.3 ab
Arroyo Seco gravelly sandy loam	Fluventic Haploxerolls	1.7 bc
Chualar sandy loam	Typic Argixerolls	1.7 bc
Elder loam	Cumulic Haploxerolls	1.8 bc
Metz fine sandy loam	Typic Xerofluvents	1.8 bc
Oceano loamy sand	Alfic Xeropsamments	2.3 cd
Santa Ynez fine sandy loam	Ultic Palexerolls	2.7 d
Untreated control	...	3.5 e

[x] From Cook (8).
[y] Average of eight plants on a scale of 0 (symptomless) to 4 (dead), 5 mo after planting in a wilt-conducive soil mix infested with the wilt pathogen at 1,000 propagules per gram.
[z] Values followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

Table 3. Reductions in Fusarium wilt severity of carnation by preplant root dips in Mocho soil slurry and bacterial suspensions[a]

Treatment	Time of reading (days)	Disease severity rating[b] in 10 experiments										
		1	2	3	4	5	6	7	8	9	10	Mean
Mocho soil slurry	75	0.4*[c]	0.5*	...[d]	0.1*	2.4*	...	...	1.0*	1.8*	...	1.0
	120	0.4*	0.8*	...	1.8*	...	...	...	2.1*	2.0*	...	1.7
Bacterial antagonists												
MFA1	75	0.9*	1.0*	1.4*	...	...	2.8	2.3*	1.0*	1.8*	2.3*	1.7
	120	1.3	1.3*	2.6	...	...	3.6	...	2.3*	2.5*	3.7	2.5
C88	75	...	1.2	...	...	...	2.2*	2.4*	...	1.7*	...	1.9
	120	...	1.5*	...	...	...	3.4	...	...	2.5*	...	2.5
B10	75	1.5	...	1.4*	0.6*	...	2.6	2.0*	0.8*	2.6	...	1.6
	120	1.7	...	2.8	3.2	...	3.6	...	3.2	3.2	...	3.0
A13	75	...	...	1.9*	1.0*	...	2.9	2.6	0.9*	...	...	1.9
	120	...	...	3.0	3.0	...	3.9	...	4.0	...	...	3.5
MFA1-B10	75	1.1	...	0.8*	...	...	2.3*	2.5	...	...	...	1.7
	120	1.3	...	2.2*	...	...	3.5	...	...	...	...	2.3
MFA1-A13	75	...	...	1.9*	...	...	3.2	2.6	...	...	...	2.6
	120	...	...	3.1	...	...	3.9	...	...	...	...	3.5
MFA1-C88	75	...	...	...	...	...	2.0*	...	...	...	...	2.0
	120	...	...	...	...	...	3.4	...	...	...	...	3.4
A13-B10	75	...	...	2.6	...	...	2.6	...	...	...	...	2.6
	120	...	...	3.4	...	...	3.7	...	...	...	...	3.6
MFA1-B10-A13	75	...	...	...	...	3.6	2.8	...	...	...	...	3.2
	120	...	...	...	...	...	4.0	...	...	...	...	4.0
Untreated check	75	1.4	1.5	2.7	1.9	3.9	3.0	3.1	3.1	3.2	3.5	2.7
	120	1.5	2.0	2.8	3.1	...	3.6	...	4.0	3.9	3.9	3.1

[a] Treated carnations were planted in potting mix infested with various amounts of *Fusarium oxysporum* f. sp. *dianthi*: 100 propagules per gram in experiments 1 and 2, 1,000 propagules per gram in experiments 3 and 4, 10,000 propagules per gram in experiments 5–10.
[b] Average of eight to 12 plants rated on a scale of 0 (symptomless) to 4 (dead).
[c] * = Decreases from control statistically significant at $P = 0.05$.
[d] ... = No data.

Table 4. Populations of the bacterial strain MFA1 on roots of carnations grown in different soils

Soil	Subgroup	Water-holding capacity (cm/cm soil)	Soil pH[w]	Log_{10} cfu/mg of root[x] 2 mo	4 mo
Metz fine sandy loam	Typic Xerofluvents (8)[y]	0.13–0.17 (8)[y]	7.3	5.94 d[z]	4.98 d
Mocho silty clay loam	Fluventic Haploxerolls (8)	0.18–0.21 (8)	6.7	5.11 c	4.00 c
Yolo fine sandy loam	Typic Xerothents (27)	0.19–0.21 (27)	7.2	4.88 bc	3.89 c
Oceano loamy sand	Alfic Xeropsamments (8)	0.05–0.08 (8)	5.9	4.23 b	2.81 b
Delhi sand	Typic Xeropsamments (25)	0.05–0.06 (25)	4.9	3.28 a	1.30 a
Potting mix (2 loam:1 peat:1 sand)	...	Not determined	5.7	3.40 a	1.90 a

[w] Determined by the saturated soil paste method.
[x] Average of five plants inoculated with MFA1 before planting by dipping roots of cuttings in a suspension containing 10^8 cfu/ml.
[y] Numbers in parentheses refer to literature citations.
[z] Values within a column followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

Table 5. Reduction in the incidence of Fusarium wilt of carnations in a commercial greenhouse by preplant root dips in Mocho soil slurry and bacterial cell suspensions

Treatment	Disease incidence (%)[a] 3 mo	5 mo	7 mo
Mocho soil slurry	5***[b]	19**	57**
Check	13	28	67
MFA1 suspension	13*	33	62*
Check	17	37	71

[a] Average percentage of diseased plants in paired plots of seven replicates per treatment, with 36 plants per replicate.
[b] Significant difference from the check: * = 90%, ** = 95%, and *** = 99% confidence levels.

concentrations of pathogen inoculum (Table 3). Inoculation with strain MFA1 resulted in significant reductions in wilt severity averaging about 40% in seven of eight experiments, whereas treatment with C88 caused significant reductions averaging 30% in three of four experiments. Strains A13 and B10, which were not isolated from wilt-suppressive soils, caused similar amounts of disease inhibition. At 120 days after inoculation, however, disease reductions by MFA1 and C88 occurred in only a few experiments, and A13 and B10 no longer had a significant effect on disease.

Bacterial combinations MFA1-C88, MFA1-B10, and MFA1-A13 were effective in reducing wilt severity in some experiments for 75 days but did not sustain effectiveness for 120 days. The combinations A13-B10 and MFA1-A13-B10 had no effect on disease severity, even within the first 75 days. There was no relationship between pathogen inoculum density and the duration in which any one treatment affected disease development.

Populations of antagonistic bacteria on carnation roots. Population densities of antagonistic bacteria on carnation roots declined during the experiments. In general, the inoculated bacteria were found in low numbers (fewer than 100 cfu/mg of root) or were undetectable in the rhizospheres 5 mo after planting in the soil mix.

To study the effect of soil type on the colonization of carnation roots by an antagonistic bacterium, rooted cuttings inoculated with MFA1 were planted in six soils. During a 5-mo period, higher population densities of MFA1 were detected on the roots of plants grown in sandy loam and clay loam soils with near-neutral pH than on roots of plants in sand and loamy sand soils with low pH (Table 4). The greatest numbers were detected on roots of plants grown in Metz fine sandy loam, the suppressive soil from which MFA1 was originally isolated.

Reduction of Fusarium wilt incidence in commercial greenhouses. Inoculation of cuttings with Mocho suppressive soil slurry and MFA1 reduced Fusarium wilt incidence in one commercial greenhouse trial by 15 and 13%, respectively, 7 mo after treatment (Table 5). The MFA1 treatment, however, was statistically significant only at $P = 0.10$ because of the high variability in disease incidence among replicates. No preplant treatments had been applied to reduce *Fusarium* inoculum, and thus, disease incidence in control plots exceeded 65% by 7 mo. In four trials in which methyl bromide or steam had been applied to the ground beds before planting, disease did not occur until 7–12 mo after planting. Treatment of cuttings or amendment of ground-bed soils with Mocho suppressive soil in these trials resulted in reduced losses of 10–20% for up to 16 mo, but the differences were often significant only at the 90% confidence level. Antagonistic bacteria, applied either as single strains or as mixed strains, were not effective in inhibiting Fusarium wilt in these experiments during any time period.

DISCUSSION

This study shows that Fusarium wilt of carnation grown in pots can be reduced for up to 4 mo by dipping carnation roots in slurries of suppressive soils or suspensions of specific bacteria. Although the disease reduction was a relatively consistent event, the amount was variable as indicated by the different experiments. This is expected and presumably occurs because population densities of microorganisms differ among soils and are in a constant state of flux as are environmental factors that influence the interactions among the resident microflora, the pathogen, and the introduced antagonist.

The use of individual strains of bacteria to control Fusarium wilt of carnations in commercial production does not appear practical, since carnations are grown up to 2 yr and are susceptible to the disease during the entire period. Furthermore, the roots are continuously advancing into soils away from sites where population densities of the introduced biological agent are the greatest. This and other studies (9,26) have shown that population densities of root-colonizing bacteria decline with time and that their occurrence on roots is sporatic (13).

The suitability of the soil environment for introduction and sustained survival of antagonistic microorganisms is an important factor in biological control of pathogens. In this study, the survival of strain MFA1 on the root system was affected by the soil in which the plant was grown. The greatest population densities were detected on plant roots in fine-textured soils with neutral pH. This may be an effect of the soils with greater moisture-holding capacity preventing rapid fluctuations in soil matric potential between waterings. As shown in a study on the survival of *P. putida* in soil, long-term survival was favored when the soil was maintained at high matric potentials or was dried slowly (9).

More consistent and durable disease protection was provided by treatments with suppressive soils than by applications of single strains of antagonistic bacteria, suggesting an interplay of a wider spectrum of microorganisms with the *Fusarium* pathogen. Inoculations with a mixture of organisms may achieve a similar level of disease control. However, this and another study with *Fusarium*-antagonistic bacteria (24) show that treatments involving combinations of antagonistic strains do not necessarily prove more effective than single strains. Effective commercial biological control of Fusarium wilt will probably depend on two developments: the selection of an assortment of microorganisms that are mutually compatible and can compete in

combination with *F. oxysporum* over a wide variety of environmental conditions and the identification of environmental factors that favor their activity and survival for extended periods. It may also be necessary to develop methods for reintroducing antagonists to the soil and root systems to offset the decline in population densities that may occur.

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