Effect of Compost on Rhizosphere Microflora of the Tomato and on the Incidence of Plant Growth-Promoting Rhizobacteria

MARCOS A. DE BRITO ALVAREZ,¹ SERGE GAGNÉ,² AND HANI ANTOUN^{1*}

*Science de la Vie et de la Santé, Pavillon Charles-Eugène Marchand, Université Laval, Québec, Québec, Canada G1K 7P4,¹
and Premier Research Center, Premier Peat Moss Ltd., Rivière-du-Loup, Québec, Canada G5R 4C9²*

Received 27 July 1994/Accepted 24 October 1994

Four commercial composts were added to soil to study their effect on plant growth, total rhizosphere microflora, and incidence of plant growth-promoting rhizobacteria (PGPR) in the rhizosphere of tomato plants. Three of the compost treatments significantly improved plant growth, while one compost treatment significantly depressed it. Compost amendments caused only small variations in the total numbers of bacteria, actinomycetes, and fungi in the rhizosphere of tomato plants. A total of 709 bacteria were isolated from the four compost treatments and the soil control to determine the percentage of PGPR in each treatment. The PGPR tests measured antagonism to soilborne root pathogens, production of indoleacetic acid, cyanide, and siderophores, phosphate solubilization, and intrinsic resistance to antibiotics. Our results show that the addition of some composts to soil increased the incidence in the tomato rhizosphere of bacteria exhibiting antagonism towards *Fusarium oxysporum* f. sp. *radicis-lycopersici*, *Pyrenochaeta lycopersici*, *Pythium ultimum*, and *Rhizoctonia solani*. The antagonistic effects observed were associated with marked increases in the percentage of siderophore producers. No significant differences were observed in the percentage of cyanogens, whereas the percentages of phosphate solubilizers and indoleacetic acid producers were affected, respectively, by one and two compost treatments. Intrinsic resistance to antibiotics was only marginally different among the rhizobacterial populations. Our results suggest that compost may stimulate the proliferation of antagonists in the rhizosphere and confirm previous reports indicating that the use of composts in container media has the potential to protect plants from soilborne root pathogens.

Composts used as a soil amendment or in container media may protect plants from diseases caused by soilborne root pathogens (7, 21). Several organisms antagonistic to soilborne root pathogens have been isolated from suppressive composts (25, 26, 39). These findings suggest that suppressive organisms may be at least partly responsible for the decreased disease incidence observed on plants grown in compost substrates. Chen et al. (8) have also found that suppressive composts possess a higher microbial activity than conducive ones. They suggested that a high microbial activity causes a depletion in essential nutrients for the survival and multiplication of the pathogen, thus preventing infection of the host.

Plant growth-promoting rhizobacteria (PGPR) benefit plants through different mechanisms of action, including, for example, (i) the production of secondary metabolites such as antibiotics, cyanide, and hormonelike substances; (ii) the production of siderophores; (iii) antagonism to soilborne root pathogens; (iv) phosphate solubilization; and (v) dinitrogen fixation (2, 10, 12, 17, 30, 42, 48). The establishment in the rhizosphere of organisms possessing one or more of these characteristics is interesting since it may influence plant growth. Composts, depending on the degree of maturity, provide a rich medium supporting a high microbial activity (8) and may also contain a diverse microbial population (37). The objective of this study was to compare the effects of the incorporation of four types of compost on the PGPR microbial composition of the rhizosphere of tomato plants. Our results indicate that the use of compost as an amendment can significantly influence the incidence of PGPR in the rhizosphere of tomato plants.

MATERIALS AND METHODS

Soil and soil-compost mix. A silty clay soil collected from a depth of 15 cm was obtained from the Laval University farm, at St-Louis de Pintendre, Québec, Canada. The soil was air dried and sieved to 2 mm before it was mixed with the composts.

Four types of compost were used: compost 1 was derived from a mix of straw, sawdust, bark, and liquid pig manure; compost 2 was derived from peat moss and cow, chicken, and sheep manure; compost 3 was derived from peat moss and cow and chicken manure; and compost 4 was derived from peat moss and cow, chicken, and sheep manure. The compost treatments consisted of a mix of soil and compost (2:1, vol/vol). A mixture of soil and perlite (2:1, vol/vol) was used for the control treatment.

Chemical characteristics of the soil-compost mix. All composts used in this experiment had good chemical characteristics for tomato growth (Table 1). In all mixtures, the addition of compost increased the organic matter content and the amount of available nutrients. Although the pH of the soil-compost mix was lower than that of the soil alone, it was within the limit for growth of tomato plants.

Plant growth conditions. After the soil and compost or perlite were thoroughly mixed, six 1-liter pots for each treatment were filled with the mix. Each pot was sown with five seeds of tomato (*Lycopersicon esculentum* Red Cherry) and then placed in a growth chamber (16 h of light at 25°C and 8 h of darkness at 18°C). One week after germination, the seedlings were thinned to one seedling per pot. To avoid the nutrient effect of the compost treatments, the plants were irrigated daily with 50 ml of 1/7-strength Hoagland solution (20).

Soil, compost mixes, and plant analysis. Total N was determined by the Kjeldahl method (5). Soil pH was measured in water (1:1, vol/vol), and available nutrients were extracted and measured according to the Mehlich 3 method (38). Organic matter was estimated by a modified Walkley and Black method (36). Plant tissues were digested in a mixture of 15 ml of HClO₄ and 5 ml of HNO₃, and phosphorus was determined colorimetrically by the vanado-molybdate method (43). Other elements were determined by atomic absorption spectrophotometry (14).

Plant growth. Five weeks after planting, the pots were removed from the growth chamber and the shoots were clipped off at the soil surface level. The roots were separated from the soil by gentle shaking. Samples for microbial counts of the rhizosphere were taken (see below), and the sets of roots were rinsed to remove adhering soil particles. Dry weights of shoots and roots were determined after drying at 80°C.

Enumeration of the rhizosphere microflora. Rhizosphere microflora was estimated by a previously described procedure (49). The following culture media were used to enumerate the microorganisms: 10% tryptic soy agar (TSA; Difco)

* Corresponding author. Fax: (418) 656-7176. Electronic mail address: Antoun@rsvs.ulaval.ca.

TABLE 1. Chemical characteristics of soil and soil-compost mixes

Treatment	pH	% Organic matter	N (mg g ⁻¹)	P (µg g ⁻¹)	K (µg g ⁻¹)	Mg (µg g ⁻¹)	Ca (mg g ⁻¹)
Soil	7.92	2.63	1.8	11	167	294	6.4
Soil-compost 1	7.52	5.34	2.4	106	317	462	7.2
Soil-compost 2	7.12	6.83	2.8	148	555	512	7.1
Soil-compost 3	7.04	7.11	2.8	134	710	580	7.3
Soil-compost 4	6.98	7.96	3.0	346	955	558	6.9

for bacteria (28); actinomycete isolation agar (Difco) for actinomycetes; and Martin's rose bengal (33) for fungi. Plates were incubated at 28°C in the dark; bacteria and fungi were counted after 4 to 7 days of incubation and actinomycetes were counted after 10 to 14 days.

Isolation of representative colonies of rhizobacteria and storage. Representative colonies from each treatment were picked and streaked on 10% TSA to obtain pure colonies. After 7 days at room temperature (22°C), individual colonies from each isolate were again streaked, and the process was repeated until a plate with pure microorganisms was obtained. Bacteria were stored in tryptic soy broth (TSB) (Difco) with 15% glycerol in alternate wells of a 96-well tissue culture plate (Falcon 3075). Each plate held 24 bacterial cultures. The plates were kept in a freezer at -80°C for further studies.

Characterization of the rhizobacteria. (i) Inoculation procedure. The bacteria, except as stated otherwise, were inoculated as follows. The tissue culture plates containing the frozen bacterial cultures were left to thaw briefly. A sterilized replicator was inserted in the plate and transferred to a petri dish filled with 18 ml of the specific medium used for each test. Each dish was inoculated with 24 bacterial cultures.

(ii) Gram reaction and cell shape. The bacteria were inoculated as described above and incubated for 12 or 24 h depending on the organism. A smear of each organism was prepared from 12- to 24-h-old cultures, and the standard procedure (Difco) for Gram staining was used. Cell shape (rods or cocci) was recorded during the microscopic observation of the Gram reaction.

(iii) Fluorescent pseudomonads. The two media described by Gould et al. (19) were used to test for the presence of total and fluorescent pseudomonads. Colonies showing the characteristic pigment production in at least one medium were recorded as fluorescent pseudomonads. Few strains produced pigmentation in only one medium.

(iv) Fungal inhibition assays. In vitro inhibition of *Rhizoctonia solani*, *Pyrenochaeta lycopersici*, *Fusarium oxysporum* f. sp. *radicis-lycopersici*, *Pythium ultimum*, *Phytophthora parasitica* var. *nicotianae*, and *Verticillium albo-atrum* was measured on agar plates containing 18 ml of nutrient broth-yeast extract medium (41). The mycelia of 5- to 7-day-old liquid cultures of the fungi were ground in a blender and filtered through four layers of cheesecloth. The mycelial suspension was used to spray an nutrient broth-yeast extract agar plate that had been inoculated with bacterial cultures 24 h previously. Each plate included 24 organisms and was done in triplicate. Control plates with bacteria and fungi alone were inoculated concomitantly. The plates were incubated for 5 to 7 days at 28°C. A test was considered positive when a clear inhibition zone was observed around the bacterial growth in the three replications.

(v) Production of siderophores. Two methods were used to test for production of siderophores, as described by Alexander and Zuberer (1). In the first method, chrome azurol S agar plates were inoculated as described above and incubated at 28°C for 5 days. Microorganisms exhibiting an orange halo were considered positive for the production of siderophores. In the second method, 8-hydroxyquinoline (50 mg liter⁻¹) was added to TSA (10%). Organisms growing on this medium were considered positive for siderophore production. Strains scoring positive in either medium were considered siderophore producers.

(vi) Production of IAA and/or IAA analogs. A modified method (6) was used to screen indoleacetic acid (IAA) and/or IAA analog producers. TSA (10%) amended with 5 mM 1-tryptophan was overlaid with an 82-mm-diameter nitrocellulose membrane disk (Amersham). Agar plates were inoculated with bacte-

rial cultures, 24 per plate, and incubated at 28°C for 3 days. The membranes were overlaid on a Whatman no. 2 filter paper saturated with Salkowski reagent (18). Organisms producing IAA and/or IAA analogs were separated from organisms producing other indoles (producing yellow to yellow-brown pigment) by their characteristic pink to red color after 0.5 to 3 h.

(vii) Cyanogenesis. Cyanide production by rhizobacteria was detected as previously described (2). Petri plates containing TSA (10%) supplemented with 4.4 g of glycine liter⁻¹ were inoculated. The plates were incubated at 28°C for 3 days. The bacterial cultures were transferred with toothpicks to individual agar plates containing the same medium as before and inverted after a piece of filter paper impregnated with 0.5% picric acid-2% sodium carbonate had been placed in the lid of each petri dish. The plates were incubated at 28°C for 3 to 5 days. A change in color from yellow to orange-brown on the filter paper indicated the production of cyanide.

(viii) Phosphate solubilization. The medium described by Goldstein (17) was used to screen phosphate solubilizers. Dicalcium phosphate agar plates were inoculated with 24 bacterial cultures and incubated at 28°C for 5 days. The bacterial colonies forming clarification halos were considered phosphate solubilizers.

(ix) Intrinsic resistance to antibiotics. Resistance to streptomycin, novobiocin, chloramphenicol, nalidixic acid, and aureomycin each at concentrations of 20, 50, and 100 µg ml⁻¹ was determined. TSA (10%) plates amended with an antibiotic were inoculated with 24 bacterial cultures, and the plates were incubated at 28°C for 3 days. Control plates (nonamended TSA) were inoculated concomitantly, and organisms exhibiting growth on both media were considered resistant to the antibiotic.

Experimental design and statistical analysis. A fully randomized design with six replications was used for the growth chamber experiment. The microbiological determination was carried out with only three randomly chosen replications. All statistical analyses were carried out on a Vax 8650 minicomputer, using the software Genstat 5 release 2.2 (Numerical Algorithms Group Limited, Oxford, England).

The results were arranged on 30 by 10, 15 by 4, and 709 by 26 matrices respectively, for the (i) shoots and roots biomass and N, P, K, Ca, Mg, Cu, Zn, and Mn accumulation in the biomass; (ii) bacterial, actinomycete, fungal, and yeast counts; and (iii) microbiological characterization. The matrices of results were analyzed by using generalized linear models and summarized by analysis of deviance (29, 35). The gamma distribution, a compound Poisson distribution, and the binomial distribution were used as the theoretical distributions for the three data matrices, respectively. In the framework of Genstat, the compound Poisson distribution was fitted by specifying a gamma distribution with a log link function. To separate the means, contrasts were established and analyzed separately.

RESULTS

Plant growth. The dry matter of plants grown on the composts was significantly higher than that of the control plants. However, compost 1 caused a significant decrease in the shoot dry weight (Table 2). Similarly, the root dry weight was signif-

TABLE 2. Effect of composts on growth and nutrient accumulation in tomato plants^a

Treatment	g plant ⁻¹		mg g of dry matter ⁻¹					µg g of dry matter ⁻¹		
	Shoots	Roots	N	P	K	Ca	Mg	Mn	Zn	Cu
Control	3.6 (1.76)	0.6 (0.06)	15.2 (0.73)	2.3 (0.16)	17.8 (0.96)	22.8 (0.58)	4.9 (0.23)	105.0 (18.1)	44.2 (5.47)	12.7 (2.47)
Compost 1	2.4 (1.18)	0.5 (0.04)	11.3 (0.55)	2.3 (0.16)	17.8 (0.95)	20.3 (0.52)	4.1 (0.19)	102.0 (17.6)	52.2 (5.89)	14.0 (2.73)
Compost 2	6.3 (3.06)	0.9 (0.09)	22.5 (1.09)	2.7 (0.20)	31.4 (1.69)	23.3 (0.59)	4.9 (0.23)	80.0 (13.8)	34.2 (4.23)	9.5 (1.85)
Compost 3	6.3 (3.05)	0.7 (0.07)	30.5 (1.47)	2.6 (0.19)	33.5 (1.80)	29.3 (0.75)	5.6 (0.30)	91.0 (15.7)	42.1 (4.75)	11.0 (2.14)
Compost 4	6.6 (3.20)	0.7 (0.07)	31.3 (1.51)	2.9 (0.21)	35.5 (1.91)	28.5 (0.73)	5.9 (0.28)	131.3 (22.7)	38.9 (4.38)	10.0 (1.95)

^a Values are means of six replicates. These values are predictions from analysis of the deviance. The predictions are fitted values formed on the scale of the response variable. Number in parentheses are standard errors. Standard errors are approximate since the model is not linear.

TABLE 3. Effect of addition of compost on number of rhizosphere microorganisms of tomato plants

Treatment	Mean no. (SE) g ^{-1a}		
	Bacteria (10 ⁶)	Actinomycetes (10 ⁵)	Fungi (10 ⁴)
Control	8.9 (1.9)	1.4 (0.3)	6.4 (3.0)
Compost 1	9.2 (2.9)	3.8 (1.0)	4.6 (3.1)
Compost 2	8.0 (0.8)	1.4 (0.3)	4.7 (2.2)
Compost 3	8.5 (0.9)	1.9 (1.0)	3.6 (1.2)
Compost 4	12.5 (3.4)	2.2 (0.5)	4.3 (0.1)

^a Values are means of three randomly chosen replicates.

icantly higher for plants grown in composts except for compost 1, which did not affect root dry matter accumulation (Table 2).

Nutrient accumulation in the biomass. Table 2 shows the accumulation of macro- and micronutrients in the biomass of tomato plants. Composts 2, 3, and 4 significantly stimulated the accumulation of N and K in the shoot dry matter of tomato plants. Compost 1 caused a decrease in the accumulation of N and did not affect the accumulation of K. The accumulation of Ca was depressed by compost 1, and in turn, it was stimulated by composts 3 and 4. Mg accumulation was significantly stimulated by composts 3 and 4 and slightly depressed by compost 1. The accumulations of P, Mn, Zn, and Cu were not affected by any composts under study.

Enumeration of rhizosphere microorganisms. Total viable bacteria, actinomycetes, and fungi were enumerated in the rhizosphere of tomato plants 4 weeks after planting (Table 3). No significant difference in the microbial counts among the four composts and the soil control was observed.

Bacterial characterization. Table 4 shows the percentage of gram-negative bacteria, rods, and fluorescent pseudomonads and of the selected PGPR attributes analyzed for the five

rhizobacterial populations. The results show significant differences in the percentage of gram-negative bacteria in the five bacterial populations. The control and compost 1 treatments had the highest percentages of gram-negative bacteria, while the compost 4 treatment had the lowest percentage. Similarly, the percentages of rod-shaped bacteria were highest in the control and compost 1 treatments and lowest in the compost 4 treatment. The same trend was observed in the percentage of fluorescent pseudomonads, with the control and compost 1 treatments showing the highest percentages and compost 4 treatment showing the lowest percentage.

Significant differences were observed in the percentages of bacteria antagonistic towards the phytopathogens tested. The compost 2 and 4 treatments had the highest percentages of bacteria antagonistic toward *F. oxysporum* f. sp. *radicis-lycopersici*, while the compost 1 population had the lowest percentage. Similarly, compost 2 treatment had the highest percentage of bacteria antagonistic toward *Pyrenochaeta lycopersici*, while compost 4 had the lowest percentage. For antagonism towards *Pythium ultimum*, only compost 2 treatment was different, with a higher percentage than the remaining treatments. On the other hand, compost treatments had lower percentages of antagonists toward *V. albo-atrum* and *Phytophthora parasitica* var. *nicotianae* compared with the control. For antagonism toward *R. solani*, composts 2 and 4 treatments had the highest percentages and control and compost 1 treatments had the lowest percentages.

The percentage of cyanogens was very low and present only in the control and compost 1 and 4 populations. A higher percentage of isolates from compost treatments produced detectable siderophores. Bacteria producing IAA and/or IAA analogs were more frequent in compost 1 and 3 treatments, whereas the incidence of phosphate solubilizers increased only in the presence of compost 3.

TABLE 4. Percentages of tomato rhizobacterial populations exhibiting PGPR characteristics as affected by compost

Test determination	% Predicted (SE) ^a				
	Control (n = 147)	Compost 1 (n = 132)	Compost 2 (n = 199)	Compost 3 (n = 87)	Compost 4 (n = 144)
Gram-negative bacteria	76.19 (3.51)	73.48 (3.83)	61.31 (3.44)	66.67 (5.04)	43.06 (4.13)
Rods	97.96 (1.14)	98.48 (1.02)	89.95 (2.13)	90.80 (3.10)	83.33 (3.11)
Fluorescent pseudomonads	43.54 (4.09)	41.67 (4.29)	31.66 (3.29)	19.54 (4.24)	14.58 (2.94)
Antagonism towards					
<i>Fusarium oxysporum</i> f. sp. <i>radicis-lycopersici</i>	25.85 (3.60)	8.33 (2.41)	41.71 (3.49)	24.14 (4.57)	48.61 (4.17)
<i>Pyrenochaeta lycopersici</i>	15.65 (2.99)	10.61 (2.68)	28.14 (3.18)	8.05 (2.92)	6.94 (2.12)
<i>Pythium ultimum</i>	5.44 (1.87)	4.55 (1.80)	10.05 (2.13)	4.60 (2.23)	4.86 (1.78)
<i>Verticillium albo-atrum</i>	23.81 (3.50)	12.88 (2.92)	9.55 (2.08)	2.32 (1.52)	4.86 (1.78)
<i>Phytophthora parasitica</i> var. <i>nicotianae</i>	87.75 (2.67)	65.15 (4.13)	45.23 (3.53)	47.13 (5.35)	75.00 (3.60)
<i>Rhizoctonia solani</i>	25.85 (3.60)	20.45 (3.50)	55.78 (3.52)	31.04 (4.95)	59.03 (4.09)
Cyanogens	1.36 (0.96)	1.52 (1.06)	0.02 (0.06)	0.02 (0.09)	1.39 (0.98)
Siderophore producers	23.13 (3.47)	34.85 (4.14)	37.69 (3.43)	42.53 (5.30)	31.95 (3.88)
IAA producers	30.61 (3.79)	41.67 (4.29)	23.62 (3.00)	35.63 (5.13)	24.31 (3.56)
Phosphate solubilizers	6.13 (1.92)	6.82 (2.16)	8.54 (1.98)	16.12 (3.85)	9.72 (2.47)
Resistance to					
Streptomycin (100 µg ml ⁻¹)	68.03 (3.83)	68.94 (4.02)	63.82 (3.40)	71.26 (4.84)	59.72 (4.08)
Novobiocin (20 µg ml ⁻¹)	75.51 (3.54)	69.70 (3.99)	66.33 (3.34)	65.52 (5.08)	50.69 (4.17)
Novobiocin (100 µg ml ⁻¹)	61.90 (3.99)	58.33 (4.28)	51.76 (3.54)	58.62 (5.27)	38.89 (4.06)
Nalidixic acid (20 µg ml ⁻¹)	91.16 (2.34)	92.42 (2.29)	89.45 (2.18)	78.16 (4.43)	84.03 (3.05)
Aureomycin (100 µg ml ⁻¹)	90.48 (2.42)	87.88 (2.84)	90.95 (2.03)	91.95 (2.91)	90.97 (2.38)
Chloramphenicol (20 µg ml ⁻¹)	44.90 (4.10)	43.94 (4.32)	48.74 (3.54)	43.68 (5.32)	30.56 (3.83)

^a Values are predictions from analysis of deviance. These predictions are fitted proportions, ignoring the numbers of binomial trials. Standard errors are approximate since the model is not linear.

Generally, the percentages of bacteria resistant to the antibiotics tested in each of the five rhizobacterial populations were similar except for novobiocin, nalidixic acid, and chloramphenicol. Table 4 shows the results of the concentrations in which we detected variations among the populations. The compost 4 population had a significantly lower percentage of bacteria resistant to 20 and 100 μg of novobiocin g^{-1} . Composts 2 and 4 had significantly lower percentages of bacteria resistant to 20 μg of nalidixic acid g^{-1} . The compost 4 population also had a significantly lower percentage of organisms resistant to 20 μg of chloramphenicol g^{-1} .

DISCUSSION

Compost amendments to soil either stimulated or inhibited growth and nutrient uptake of tomato plants. Reports on the fertilizer effect of composts have been published by many authors (13, 22–24, 34). Composts may affect the release of nutrients to plants directly through the nutrients present in them or indirectly by their effect on the cation-exchange capacity (13). In our experiment it is likely that both effects took place. The nutrient content of composts was high. Furthermore, the plants were irrigated daily with a nutrient solution to ensure an equal nutrient supply in every treatment. Thus, a cation-exchange capacity effect may have been reflected in the nutrient uptake by plants. However, compost 1 was inhibitory to growth and nutrient uptake by tomato plants. A nutrient deficiency can be excluded because the plants were fertilized and the nutrient analysis showed that the compost 1 mix had a higher nutrient level than the control soil. According to these results, we hypothesize that compost 1 produced phytotoxins (32) that likely inhibited plant growth and nutrient uptake. This speculation is corroborated by the fact that no other compost treatment inhibited plant growth. A similar observation was reported by Gamliel and Stapleton (15) for lettuce grown in the field. Inhibition of tomato growth can also be attributed to the presence of a high percentage of IAA producers in the rhizosphere of compost 1. Loper and Schroth (31) have shown, under controlled conditions, that bacteria producing a high level of IAA were deleterious to beet seedlings. Similar results have been published by Dubeikovsky et al. (12) studying sour cherry.

The lack of differences in the total number of rhizosphere microorganisms confirms previous reports that composts do not stimulate the growth of microorganisms in the rhizosphere. They do affect the species composition of the rhizosphere (4), thus causing a shift in specific groups of microorganisms, such as antagonists to pathogens in suppressive composts (7) and/or functional groups of rhizobacteria (40). We observed large variations in the percentage of rhizobacteria antagonistic to selected soilborne root pathogens in vitro. Although antagonistic rhizobacteria were found in the control treatment, in only two cases did the control population have higher percentages than the compost treatments. These were antagonistic toward *V. albo-atrum* and *Phytophthora parasitica* var. *nicotianae*. For the remaining pathogens tested, the rhizobacteria of compost treatments were either superior or equal to those of the control. In addition, compost amendments enhanced the population of siderophore producers, giving further support to the idea that composts have the potential to provide a conducive environment for the proliferation of rhizobacteria antagonistic to certain soilborne root pathogens. These two factors, as has been suggested, may be correlated (3, 30). Among the pathogens tested, *Pyrenochaeta lycopersici* and *Pythium ultimum* had the lowest percentages of antagonists. The rhizobacteria from compost 2 contained the highest percentage of rhi-

zobacteria antagonistic to these phytopathogens. Although the antibiosis test in vitro does not always correlate with suppression of soilborne plant disease, because of the magnitude of the rhizosphere population and the lack of a more reliable method, in vitro screening of potential antagonists is valuable (9).

Fluorescent pseudomonads in the five rhizobacterial populations ranged from 14 to 43% of the total rhizobacteria in the five treatments. This signifies a high percentage for a single group of microorganisms and gives support to previous reports that fluorescent pseudomonads make up a substantial proportion of bacteria that can be cultured from the rhizosphere. Similar results were reported by Lambert et al. (27) for the rhizosphere of maize. A very low percentage of cyanogens was detected, suggesting that this feature may not play an important ecological role in the populations studied.

Only a small percentage of bacteria from each population were phosphate solubilizers, and the percentages of these were comparable throughout the treatments. On the other hand, a high percentage of rhizobacteria in each population produced indoles in vitro. However, there were no great differences among the treatments. Similarly, the tests on antibiotic resistance showed that the five rhizobacterial populations had high proportions of organisms intrinsically resistant to the antibiotics tested. Gilbert et al. (16) also found a high proportion of rhizosphere bacteria resistant to antibiotics. A PGPR resistant to high levels of antibiotics might have an ecological advantage for survival in the rhizosphere when introduced as an inoculum (11). We noticed that the percentage of rhizobacteria resistant to chloramphenicol was very low compared with that resistant to the other antibiotics tested.

The heterogeneous nature of the PGPR composition from the five populations shows that the population shift in the rhizosphere is clearly affected by the type of compost used. Antagonism to soilborne root pathogens was the characteristic that varied most among these populations. However, this effect was not consistent; rather, it varied with the type of compost and the type of pathogen tested. Clearly, compost amendment always has an effect on the microbial composition of the rhizosphere. However, there is a need to determine the factors that stimulate the specific groups of rhizobacteria, such as antagonists. This would enable researchers to predict whether a compost would be beneficial or detrimental to plants. Finally, recommendations could be made for the types of composts and mixes to be used in container media. We did not evaluate the level of organic matter decomposition of the composts used, so we do not know the impact that this trait had on the PGPR population of the rhizobacteria of compost-treated plants. However, our results showed that every compost possessed microorganisms with PGPR attributes even though compost 1 depressed plant growth. Kwok et al. (26) have also found that a substrate conducive to disease also possessed bacteria antagonistic to *Rhizoctonia* damping-off. In addition, our results show that the only consistent effect caused by compost amendment on the tomato rhizobacteria was the percentage of bacteria producing detectable amounts of siderophores. Interestingly, this substance is believed to contribute to pathogen inhibition by biological control agents (30). The suppressive effect of certain compost-peat mixes is best explained by microbiostasis (4), and this is consistent with our findings.

Research on the factors that are responsible for a compost effect is necessary if manipulations to exploit the compost effect are to take place in the future. Chen et al. (8) have suggested that compost suppression of soilborne root pathogens is due to the high microbial activity caused by compost amendment and, for *Rhizoctonia* spp. damping-off, to the level

of *Trichoderma* sp. colonization of the compost. Our results show that an increase in the percentage of rhizobacterial antagonists to soilborne root pathogens may also contribute to compost suppression of soilborne root pathogens. However, our work differs from the work reported by Chen et al. in that they included the pathogen in their investigation. In addition, it is possible that compost amendments to soils or used in container media may benefit plants through the effects of its humic fraction on the soil microflora and the plants. Vallini et al. (44) have reported on the increase in the number of total aerobic bacteria and actinomycetes in the rhizosphere of laurel caused by humic acid treatments. In addition, humic substances may affect the plant biochemical process (45) and/or bacteria (46, 47). Changes in the metabolism process of plants may induce a resistance to certain phytopathogens. Similarly, changes in the microbial activity may negatively affect certain soilborne root pathogens. These factors are being considered for future research. Additionally, a number of antagonists have been selected for a more rigorous test in vitro and in vivo. Our results support the literature in that certain composts have the potential to protect plants from soilborne root pathogens. They show that there is an enrichment of microorganisms capable of inhibiting root pathogens in vitro.

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