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Developing weed-suppressive soils through improved soil quality management

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Abstract

Manipulating soil microbial communities using soil and crop management practices is a basic strategy in developing sustainable agricultural systems. Sustainable farming is based, in part, on the efficient management of soil microorganisms to improve soil quality. However, the identification of biological indicators of soil quality that can be used to predict weed suppression in soils has received little attention. We investigated differences in soil microbial activity among various crop and soil management systems to assess: (i) the microbiological characteristics of these soils; (ii) determine whether any relationships existed that might be used in the development of weed suppression. Soil enzyme activity, water-stable aggregates, and the proportions of weed-suppressive bacteria were compared among seven cropping systems and one native-prairie ecosystem in mid-Missouri, USA. Assays of soil enzymes (fluorescein diacetate hydrolase, dehydrogenase, phosphatase) revealed that organic and integrated cropping systems, and the native-prairie ecosystem had the highest levels of soil activity. Weed rhizospheres from these same ecosystems also had greater proportions of bacterial isolates characterized as "growth suppressive" to green foxtail (*Setaria viridis* {L.} Beauv.) and field bindweed (*Convolvulus arvensis* L.): 15 and 10%, respectively. The proportion of water-stable soil aggregates was the greatest in soils with the highest organic matter and was found to be related to higher enzyme and weed-suppressive activity. Selected biological indicators of soil quality were associated with potential weed-suppressive activity in soil when that soil was managed for high organic matter content under reduced tillage systems. This research study provides further evidence that soil quality and sustainable agricultural practices may be linked to integrated weed management systems for the biological suppression of weeds.

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Keywords: Conservation biological control; Organic matter; Soil enzyme activity; Sustainability; Weed-suppressive bacteria; Water-stable aggregates

1. Introduction

Soil microbial communities, manipulated through soil and crop management, are fundamental to the

development of agricultural systems that are less dependent on non-renewable resources (Pankhurst and Lynch, 1994). Research into sustainable farming options that strive to manage and enhance the beneficial activities of soil microorganisms for soil quality improvement has received relatively little attention.

Soil quality has been defined as the capacity of a soil to function within "ecosystem boundaries" to sustain

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biological productivity, maintain environmental quality, and promote plant and animal health (Doran and Parkin, 1994). Soil quality evaluation, properly characterized, should serve to indicate changes in both the ability of that soil to optimize crop yields and maintain its structural and biological integrity (Parr et al., 1992). Physical soil quality characteristics are generally indicated by increases in water infiltration, macroporosity, aggregate size and stability, and soil organic matter (Karlen and Stott, 1994).

Soil quality is often linked to organic matter content and the activity of beneficial soil organisms. Soil enzymes are both mediators and catalysts of important soil functions and have been used to measure the influence of natural processes and anthropogenic activities on soil quality (Dick, 1997). Soil enzyme activity can be used to evaluate plant productivity, nutrient cycling potential, and improved soil chemical and physical status, especially in soils managed using long crop rotations, conservation tillage practices, and organic amendments (Martens et al., 1992; Jordan et al., 1995; Dick et al., 1988).

The development of agroecosystems with the capacity to suppress weeds using naturally occurring soil–weed interactions has received little study (Gallandt et al., 1999). Such management strategies could be used to promote the development of beneficial microbial communities similar to the “conservation biological control” approach proposed by Newman et al. (1998), thereby undertaking sustainable weed management with reduced or no herbicide inputs (Parr et al., 1992).

Specific microorganisms have been manipulated to produce beneficial effects for agriculture including biological control of plant pests to reduce chemical inputs (Koul and Dhaliwal, 2002). Investigations with deleterious rhizosphere bacteria (DRB) suggest that sustainable management practices for many crops may incorporate the management of indigenous microbial communities for the biological control of weeds. Deleterious rhizobacteria that specifically inhibit various weeds, but do not affect crops, have been isolated from several rhizosphere soils (Kremer and Kennedy, 1996; Ibekwe and Kennedy, 1999).

Soils managed under practices that enhance organic matter accumulation provide an environment for diverse and competitive microbial populations, increased soil enzyme activity (Doran, 1980), and con-

sequently an increased potential for the development of weed-suppressive bacterial communities (Kennedy, 1999; Li and Kremer, 2000). A recent study of crop management practices on claypan soils (Epiaqualfs) that involved reduced tillage, maintenance of high soil organic matter, and limited inputs of agrichemicals, found increased levels of DRB associated with weed seedlings that may contribute to natural weed suppression (Li and Kremer, 2000). Growth of common lambsquarters (*Chenopodium album* L.) in a potato (*Solanum tuberosum* L.) crop was only 25% in soils receiving annual inputs of green manure, composted plant residues, and beef manure compared to non-amended soils (Gallandt et al., 1999). Involvement of antagonistic soil microbes was not indicated although the associated increase in soil quality factors including soil organic matter, was implicated in the development of weed suppressiveness.

Based on the reviews of several studies, Hoitink and Boehm (1999) suggested that high levels of soil hydrolytic enzymes associated with soils with both high organic matter and microbial biomass were correlated to the pest suppressive characteristics in a soil. Because high soil organic matter is generally considered a key indicator of soil quality, these soils may also be expected to have a greater potential for weed suppression relative to those soils where organic matter is low. Several farming practices that maintain or increase soil organic matter can be used to manage soil microorganisms and microbial activity to optimize potential weed suppression (Kremer and Kennedy, 1996; Gallandt et al., 1999; Kennedy, 1999).

By investigating the differences in soil microbial activity among different crops and soil management systems in Missouri, USA, we hope to further develop our understanding of soil agroecosystems that express natural weed suppression. The present study was conducted to determine whether specific soil quality characteristics could be used to predict the potential for natural weed suppression.

2. Materials and methods

2.1. Sampling locations

Seven cropping systems that differed in fertilization practice, method and intensity of tillage, and crop

Table 1
Characteristics of crop management systems at selected study sites

Study site	Code	Management system	Crops
Sanborn Field, plot 6	SF-6	Conventional tillage, monoculture, full fertility for 52 years	Corn
Sanborn Field, plot 26	SF-26	Conventional tillage, crop rotation, full fertility for 112 years	Corn, winter wheat, red clover
Sanborn Field, plot 39	SF-39	Conventional tillage, monoculture, full fertility for 12 years	Soybean
ASEQ cropping system no. 1	CS-1	High agrichemical input, minimum tillage, crop rotation for 12 years	Corn, soybean
ASEQ cropping system no. 5	CS-5	Integrated management, no tillage, crop rotation for 12 years	Corn, soybean, wheat, cover crop
ASEQ cropping system no. 6	CS-6	Cool-season pasture, no fertility, managed as 'conservation reserve program' (CRP) for 12 years	Cool-season grasses and legumes
Organic Farm	OF	Organic farming system, minimum tillage, organic fertilizers and soil amendments for 12 years	Strawberry, onion
Tucker Prairie	TP	Uncultivated native prairie	Native warm-season grasses and forbs

rotation were compared with a native-prairie ecosystem in Missouri, USA (Table 1).

At the long-term experimental research site at the University of Missouri, Columbia, Sanborn Field (SF), full fertility consisted of fertilizer applications sufficient to yield $11,000 \text{ kg ha}^{-1}$ corn. Conventional tillage involved moldboard plowing followed by tandem disk as secondary tillage for seedbed preparation.

The three cropping systems (CS-1, CS-5, CS-6) were established at the USDA-ARS Agricultural Systems for Environmental Quality (ASEQ) site near Centralia, MO. CS-1, was a high agrichemical input, minimum tillage, and corn–soybean rotation receiving 190 kg ha^{-1} N and lime, P and K as needed based on soil test for a corn grain yield of 9400 kg ha^{-1} . Minimum tillage consisted of field cultivation for fertilizer and herbicide incorporation, mid-season in-row cultivation, and fall or spring chisel plow after corn harvest. CS-5, was an integrated crop management of no tillage and corn–soybean–winter wheat–cover crop rotation receiving 150 kg ha^{-1} N and lime, P and K based on soil test only for a corn yield of 7500 kg ha^{-1} . CS-6, was a 10-year continuous cool-season grass and legume pasture system with no agrichemical input representing previously cultivated land taken out of crop production.

An organic farming system (OF) was selected 16 km east of Columbia, MO. It was cropped to strawberry (*Fragaria virginiana* L.) followed by onion (*Allium* sp.) on raised beds with annual applications of 10 Mg ha^{-1} composted beef or poultry manure and no synthetic agrichemical inputs. Finally, Tucker Prairie

(TP), 32 km east of Columbia, MO, consisting of native warm-season grasses and forbs was selected to represent an uncultivated native-prairie reference site. The soil at all the sites was classified as a Mexico silt loam (fine, smectitic, mesic, Aeric Vertic Epiaqualfs). Soils from each site were different for pH, soil organic matter, and mineral nutrient contents (Table 2).

2.2. Sampling procedures

Surface bulk soil samples (0–10 cm depth) were collected using a stainless steel probe (10 cm diameter) along transects established for each plot at the SF and ASEQ sites. Three plots of 100 m^2 were established at the OF and TP sites from which soils were sampled along transects. A minimum of three soil cores was collected along each transect, mixed, and stored in open plastic bags at $15\text{--}20^\circ\text{C}$. Soils were processed within 3 days of collection.

2.3. Soil enzyme analyses

Soil microbial activity expressed as fluorescein diacetate (FDA) hydrolysis was determined following the method of Schnürer and Rosswall (1982). FDA is a general substrate for several hydrolytic enzymes including esterases, lipases and certain proteases (Dick, 1997). FDA hydrolytic activity was detected by spectrophotometrically measuring the product of hydrolysis (fluorescein). The assay consisted of suspending 1.0 g soil in 20 ml phosphate buffer (pH 7.6), shaking for 15 min, and adding $100 \mu\text{l}$ FDA (4.8 mM).

Table 2
Selected chemical and physical characteristics of Mexico silt loam at each crop management site

Site ^a	pH _s	OM (g kg ⁻¹ soil)	P (kg ha ⁻¹)	Ca (kg ha ⁻¹)	Mg (kg ha ⁻¹)	K (kg ha ⁻¹)	Clay (g kg ⁻¹ soil)	Silt (g kg ⁻¹ soil)	Sand (g kg ⁻¹ soil)
SF-6	5.8	32.0	90	1210	75	140	245	677	78
SF-26	5.6	31.0	70	1420	130	210	171	779	50
SF-39	6.5	25.5	80	1700	200	175	180	740	80
CS-1	6.4	31.0	60	1690	180	190	170	754	76
CS-5	6.2	40.0	110	1825	320	275	275	631	94
CS-6	6.2	26.0	30	3260	435	265	190	766	54
OF	6.6	62.0	130	2470	320	280	259	669	72
TP	4.9	55.0	20	1800	315	250	210	750	41

^a See Table 1 for site codes.

The assay mixture was placed on a rotary shaker at 100 rpm and incubated at 30 °C for 105 min. The assay was terminated by extraction with acetone (10 ml) followed by filtration through filter paper (Whatman no. 2, Fisher, Pittsburgh, PA). The optical density of each filtrate was measured at 490 nm and the total amount of product formed was calculated based on a regression equation generated from standards of known concentrations.

Triphenyl-tetrazolium chloride (TTC)-dehydrogenase activity was used to estimate respiratory activity for viable microorganisms (Casida, 1977). Soil (6 g) was incubated in 1.0 ml of 3% TTC and 3.0 ml of 0.2 M CaCO₃ for 24 h at 37 °C. Assays were conducted with three replicates containing TTC and one control with 8 ml deionized water. The reactions were terminated by addition of 50 ml methanol and extracted 30 min on a reciprocal shaker. The reaction mixture was filtered and the concentration of 2,3,4-triphenyl-tetrazolium formazan (product) was determined spectrophotometrically at 485 nm.

Acid and alkaline phosphatase activities were determined using *p*-nitrophenol phosphate (PNP) as the substrate as described by Tabatabai (1994). Half the volume of reagents and PNP was added to 0.5 g soil in 30 ml tubes, gently vortexed, and placed in an incubator at 37 °C for 1 h. After incubation and filtration, presence of *p*-nitrophenol (product) in each sample was determined spectrophotometrically at 410 nm.

All values for enzymatic activities were reported on a dry soil basis. After drying soil at 105 °C for 24 h, soil moisture was determined on each sample.

2.4. Water-stable soil aggregates

Water-stable aggregates in soil samples were determined according to Kemper and Rosenau (1986) with modifications based on Angers and Mehuys (1993). Ten grams of air-dried soil of between 1 and 2 mm aggregate diameter were spread on a 250 µm sieve. The height of the sieve on the wet-sieving apparatus was adjusted to allow immersion of all aggregates in water during its movement (30 vertical strokes/min for 10 min). Soil particles that passed through the sieve were considered the soil fraction that was unstable in water. Soil remaining on the sieve was dried at 105 °C, weighed, and dispersed with 50 ml of 0.5% sodium hexa-metaphosphate to separate water-stable soil fractions from coarse particles. Coarse particles were collected, dried and weighed. The proportion of water-stable soil aggregates was calculated as a percentage of the weight of the stable fraction of the total soil weight.

2.5. Isolation of soil bacteria

Total culturable bacteria were enumerated by serial dilution in sterile phosphate buffered saline (PBS; 10 mM K₂PO₄–KH₂PO₄, 0.14 M NaCl; pH 7.2) and plating on King's B agar medium supplemented with 80 mg g⁻¹ of cycloheximide to suppress fungal growth (Araújo et al., 1996). Although King's B medium was developed to selectively culture pseudomonads, other bacterial genera are readily cultured from soils using this medium (Kremer et al., 1990). Plates were incubated at 27 °C for 3 days, after which bacterial colony forming units (CFUs) were enumerated.

Representative colonies were selected and subcultured onto King's B and tryptic soy agars to obtain pure isolates. Selection criteria included pigmentation, colony morphology, texture and opacity (Smibert and Krieg, 1994). Fluorescent pigment production, an additional selection criterion, was detected by exposing bacterial colonies to ultraviolet light (<260 nm wavelength) for 1–2 s.

2.6. Seedling bioassays

Bacterial isolates were assayed for growth-suppressive activities on the problem weeds green foxtail (*Setaria viridis* [L.] Beauv.) and field bindweed (*Convolvulus arvensis* L.). Seed germination of both weed species was >90%. Weed seeds were surface sterilized by immersion in 1.25% sodium hypochlorite for 1.5 min, rinsing twice with sterile water, immersion in 70% ethanol for 1.5 min, and rinsing five times in sterile water followed by blotting on sterile paper towels. Sixteen seeds of each of the weed species were placed onto an agar (1.1% in de-ionized water) plate. Two-day old bacterial isolates cultured on King's B medium were suspended in 0.1 M MgSO₄ (concentration of 10⁸ cfu ml⁻¹) and applied to the seeds. To assure good contact of bacteria with weed seeds, the volume of the bacterial suspension was adjusted according to seed size. Thus, 30 and 50 ml of bacterial suspension were used to inoculate each seed of green foxtail and field bindweed, respectively. Seedling root lengths were measured after 48 h incubation at 27 °C. The screening experiment was repeated once.

2.7. Statistical analysis

In the primary screening, bacterial isolates that caused 50% of growth inhibition or more were considered phytotoxic and underwent secondary screening. The growth inhibition results of the host screening were subjected to a one-way analysis of variance. The least significant differences were calculated according to Tukey's test and the upper significance bounds of the Studentized range distribution $P = 0.05$ were used.

3. Results and discussion

3.1. Soil bacterial populations

The surface (0–10 cm) soils from the native prairie, organic farm and crop rotation systems under minimum tillage (CS-5) were generally higher in organic matter than soils under intensive crop production (SF-6, SF-39, CS-1) (Table 2). Total number of culturable soil bacteria isolated varied among soils (Table 3) primarily due to differences in recovery of gram-negative bacteria (data not shown). Higher population densities of fluorescent pseudomonads were found also in soil from organically farmed fields and the native-prairie site, as compared to soil from conventionally managed fields (data not shown). Overall, soils under prairie vegetation or under longer crop rotations, reduced tillage, and high inputs of organic matter had more diverse bacterial groups compared

Table 3
Bacterial populations (means ± S.E.; $n = 4$) in soils and selected weed rhizospheres from different cropping systems

Site ^a	Bulk soil (log ₁₀ cfu g ⁻¹ soil)	Rhizosphere ^b (log ₁₀ cfu g ⁻¹ fresh root)		
		Giant foxtail	Morning glory	Field bindweed
SF-6	5.8 ± 0.7	6.9 ± 0.3	6.2 ± 0.2	6.2 ± 0.2
SF-26	7.0 ± 0.7	n.d. ^c	n.d.	6.5 ± 0.1
SF-39	6.6 ± 0.6	n.d.	n.d.	6.8 ± 0.3
CS-1	6.6 ± 0.9	7.3 ± 0.2	7.0 ± 0.1	n.d.
CS-5	7.1 ± 0.8	8.2 ± 0.4	7.2 ± 0.2	7.5 ± 0.4
CS-6	6.9 ± 0.7	8.3 ± 0.3	7.6 ± 0.1	n.d.
OF ^e	7.1 ± 0.6	8.1 ± 0.1	7.9 ± 0.2	n.d.
TP	6.4 ± 0.8	7.7 ± 0.1	6.8 ± 0.2	n.d.

^a See Table 1 for site codes.

^b Rhizosphere bacteria population data modified after Li and Kremer (2000).

^c Not determined.

to soil under conventional tillage and monoculture (data not shown). However, the effects of tillage on soil microbial populations were inherently difficult to assess because of temporal variations in community profiles (Kirchner et al., 1993).

Recent studies have shown that many soil microorganisms are viable but not culturable (Turco et al., 1994; Roper and Ophel-Keller, 1997) thus culturable microorganisms represent only a small fraction of the total soil bacterial population. However, the examination of the culturable component of any soil microbial community is still a useful method to assess specific functions such as weed suppression.

3.2. Soil microbial activity

Soils receiving inputs of organic residues through amendments, or with higher levels of plant residues produced under long crop rotation or permanent vegetation, showed greater FDA hydrolytic, dehydrogenase, and acid phosphatase activities than soils under conventionally managed monoculture (Table 4). Organic amendments and associated plant residues may supply additional sources of labile C and P to soil, which can stimulate microbial growth and biochemical activity (Carpenter-Boggs et al., 2000a). Similarly, soil phosphatase activity was closely related to soil organic matter content, supporting previous reports that elevated organic matter levels promote soil phosphatase activity (Frankenberger and Dick, 1983; Jordan et al., 1995).

FDA hydrolysis is often used as an indicator of microbial activity and is correlated with microbial respiration (Schnürer and Rosswall, 1982). As such it is a simple, non-specific, but sensitive technique that can be used to estimate relative levels of microbial activity in soils, and has been recommended as a useful parameter to assess soil quality (Dick, 1997). In our study, microbial activity based on FDA hydrolytic, phosphatase, dehydrogenase enzymes indicated that soils under grassland vegetation or high-input organic systems were metabolically more active than soils under conventional management systems. FDA hydrolytic activity was the highest in soils under native-prairie vegetation (TP), but similar levels were also observed in soils under organic (OF) and integrated cropping systems (CS-5), and permanent pasture (CS-6) (Table 4). Soils under these management systems had a 0.5 to 2-fold greater FDA hydrolytic activity than soils under more intensive management (SF-6, SF-26 SF-39, CS-1). The increased microbial activity observed in OF, TP, CS-5, and CS-6 soils may reflect a greater availability of substrates that support such activity (Zablotowicz et al., 1998).

Crop production systems that increase inputs of C through cover cropping, crop rotations, or various organic amendments have been shown to have greater microbial biomass and microbial activity than found in systems that utilize chemical inputs for the monoculture of annual row crops (Kirchner et al., 1993; Fraser et al., 1988). Soil enzyme activity measured in our assays were associated with living organisms, especially

Table 4
Microbial enzyme activity and water-stable aggregates in soils under different management systems^a

Site ^b	FDA hydrolase ($\mu\text{mol product g}^{-1}$ soil h^{-1})	Dehydrogenase ($\mu\text{mol product g}^{-1}$ soil h^{-1})	Acid phosphatase ($\mu\text{mol product g}^{-1}$ soil h^{-1})	Alkaline phosphatase ($\mu\text{mol product g}^{-1}$ soil h^{-1})	Water-stable aggregates (%)
SF-6	2440 c	1.70 c	4.33 b	1.50 d	10.0 d
SF-26	2030 c	3.80 b	5.23 b	2.53 b	10.8 d
SF-39	850 d	3.50 b	2.73 c	1.20 d	22.7 c
CS-1	2130 c	3.20 b	3.90 c	2.00 c	6.8 d
CS-5	3480 b	3.70 b	3.00 c	1.40 d	5.8 d
CS-6	3900 b	4.83 b	4.60 b	2.40 b	18.4 c
OF	4100 b	4.43 b	4.50 b	4.10 a	34.5 b
TP	7100 a	17.60 a	11.30 a	1.20 d	68.5 a
LSD ($P = 0.05$)	980	1.80	1.20	0.40	6.8

^a Values within a column followed by the same letter are not significantly different based on LSD ($P = 0.05$).

^b See Table 1 for site codes.

so for dehydrogenase. It is difficult to generalize the relationship between reduced tillage and microbial activity using the enzyme assays. However greater microbial activity was found at TP. Dehydrogenase activity was similar in soils of six agroecosystems, suggesting that there was a threshold level beyond which additional nutrient amendments (organic or synthetic) no longer increased microbial activity.

3.3. Soil aggregate stability

The proportion of water-stable soil aggregates was associated with higher levels of soil organic matter and soil enzyme activity (Tables 2 and 4). Previous studies have also suggested that higher water-stable aggregation improved soil structure providing good soil aeration and water availability for maximum aer-

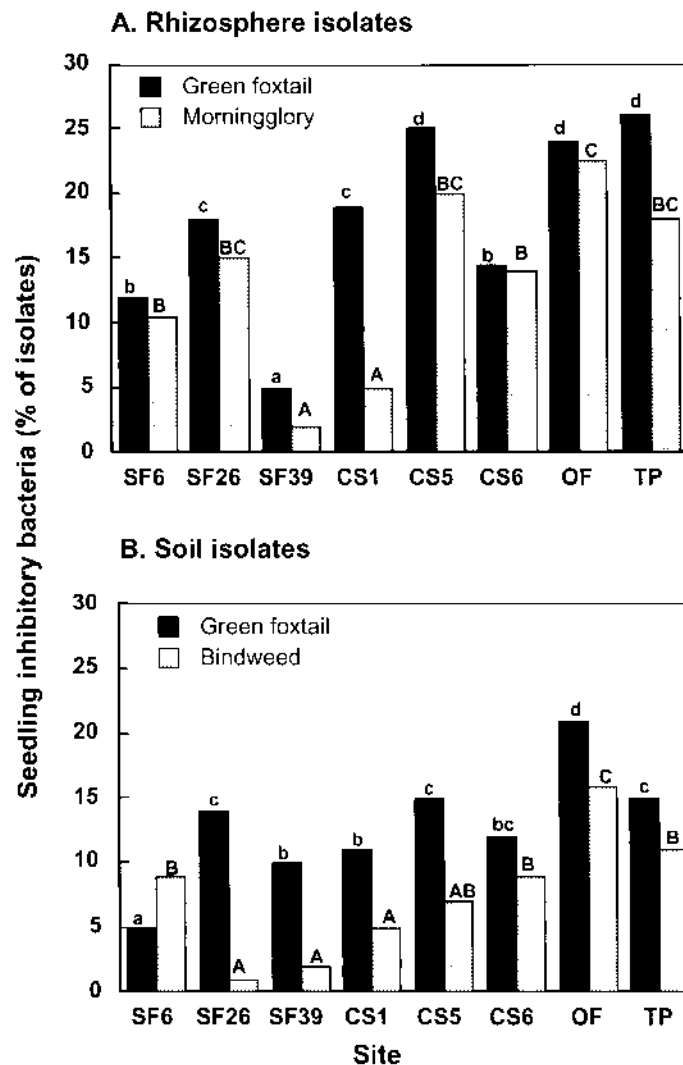


Fig. 1. Proportions of rhizosphere (A) and soil (B) bacteria from selected cropping systems that significantly ($P = 0.05$) inhibited root growth of green foxtail, ivyleaf morning glory, and field bindweed relative to non inoculated checks in seedling bioassays. Values of bars with similar capital or lower-case letters are not significantly different based on LSD ($P = 0.05$). Data presented in (A) are modified from Li and Kremer (2000). Site codes are listed in Table 1.

obic microbial activity (Linn and Doran, 1984). Increased water-stable aggregation has been related also to increased substrate availability under certain crop rotations, cover crops, grasslands, and organic amendments (Fraser et al., 1988).

Organic carbon inputs can affect microbial activity by providing suitable microhabitats within the soil profile (Islam and Weil, 2000). Thus, the study of soil aggregates in conjunction with soil enzyme activity may provide an insight into the relationships between soil microbial communities and the soil types they colonize.

3.4. Weed seedling bioassays

Bioassays of soil bacterial isolates showed a variety of effects on root growth in green foxtail and field bindweed seedlings. Seedling root responses to bacterial inoculants ranged from growth inhibition, to no effect, to growth stimulation. Phytotoxic activity of bacteria from among the different cropping systems varied from 5–21 to 1–16% of the total isolates recovered for green foxtail and field bindweed, respectively (Fig. 1B). Bioassays on green foxtail and ivyleaf morning glory were included for comparative purposes (Li and Kremer, 2000) (Fig. 1A). Growth-suppressive bacteria were defined as those that caused 70% root inhibition, based on our experience in previous studies (Kremer et al., 1990; Li and Kremer, 2000). Symptoms of root damage included necroses, blackened root tips, discoloration of root surfaces, stunted lateral root development, and reduced root hair development.

In general the highest number of soil bacteria phytotoxic to green foxtail were recovered from soils under the integrated crop management systems (CS-5), corn-wheat-red clover rotation (SF-26), organic farming (OF) systems, and the native prairie (TP). The highest number of bacteria phytotoxic to field bindweed were detected in OF, TP, CS-5, cool-season pasture (CS-6), and continuous corn (SF-6). In contrast, the lowest number of bacteria phytotoxic to green foxtail were detected among isolates recovered from continuous corn (SF-6), continuous soybean (SF-39), and chemical-intensive (CS-1) cropping systems, which, except for SF-6, also had the lowest number of isolates phytotoxic to field bindweed. Interestingly, the relative distribution of phytotoxic isolates was similar for each soil management sys-

tem, regardless of whether the soil originated from the rhizosphere or bulk soil (Fig. 1A and B).

Comparisons of the uncultivated prairie (TP) and the cool-season pasture (CS-6), which may be considered similar in terms of general vegetation type (permanent grassland), yielded dramatically different numbers of bacteria that suppressed green foxtail (Fig. 1). We suggest that such variations may be related to differences in soil organic matter content and soil pH. Similarly, differences in the frequency of weed-suppressive bacteria associated with different weed species may also be influenced by differences in soil topography (Ibekwe and Kennedy, 1999).

The higher incidence of weed-suppressive bacteria from the organic farming system seems to confirm the concept that regular additions of organic amendments enhance the development of high population densities of weed-suppressive bacteria in weed rhizospheres. Similar findings were reported for compost-amended soils planted to winter wheat, which exhibited 29 and 78% reductions in broadleaf and grassy weed densities, respectively, compared to field soils receiving inorganic fertilizer or no supplementary nutrient sources (Carpenter-Boggs et al., 2000b). We found that populations of weed-suppressive bacteria seemed to be associated with management systems characterized by high levels of biological activity.

4. Conclusions

Management of the microbial components of agroecosystems for natural weed suppression is a theme of many recent reports (Boyetchko, 1996; Gallandt et al., 1999; Kennedy, 1999). In the present study total bacterial numbers (rhizosphere and bulk soil) did not differ greatly for most management systems, however, a population subset comprising fluorescent pseudomonads was found to increase in the sustainably managed soils (data not shown). Increased levels of soil enzymatic activity observed in uncultivated prairie, organic farming, integrated cropping (CS-5), and crop rotation (SF-26) systems were generally associated with higher proportions of weed-inhibiting bacteria. The improvement in soil quality as measured by water-stable aggregates was evident in soils containing high levels of organic matter (i.e., TP, OF, CS-5, CS-6) and from which generally higher

numbers of potentially weed-suppressive bacteria were recovered. Soil and crop management systems that increase organic matter in the soil surface provide a source of readily available carbon substrates that can support increased microbial activity. We suggest that microbial competition in soils, as demonstrated by greater enzymatic activity, may influence the proliferation of weed-suppressive bacteria. We concur with previous studies that practices enhancing certain aspects of soil quality may also favor the creation of weed-suppressive soils (Parr et al., 1992; Horwath et al., 1998; Gallandt et al., 1999).

An outcome of this research is that simple soil and crop management tactics might be used to manipulate the soil environment to enhance the development of weed suppression. Community-specific soil and rhizosphere bacteria develop as a result of specific crop and soil management practices and these can be detected using biological indicators of soil quality including relatively simple tests for selected soil enzyme activities. Our results confirm previous observations that elevated levels of soil enzyme activity associated with disease-suppressive soils (Hoitink and Boehm, 1999) can also be related to weed-suppressive activity.

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References

- Angers, D.A., Mehuys, G.R., 1993. Aggregate stability to water. In: Carter, M.R. (Ed.), *Soil Sampling and Methods of Analysis*. Canadian Society of Soil Science, Lewis Publishers, Boca Raton, FL, pp. 651–657.
- Araújo, M.A.V., Mendonça-Hagler, L.C., Hagler, A.N., van Elsas, J.D., 1996. Selection of rhizosphere-competent *Pseudomonas* strains as biocontrol agents in tropical soils. *World J. Microbiol. Biotech.* 12, 589–593.
- Boyetchko, S.M., 1996. Impact of soil microorganisms on weed biology and ecology. *Phytoprotection* 77, 41–56.
- Carpenter-Boggs, L., Kennedy, A.D., Reganold, J.P., 2000a. Organic and biodynamic management: effects on soil biology. *Soil Sci. Soc. Am. J.* 64, 1651–1659.
- Carpenter-Boggs, L., Reganold, J.P., Kennedy, A.C., 2000b. Biodynamic preparations: short-term effects on crops, soils, and weed populations. *Am. J. Altern. Agric.* 15, 110–118.
- Casida Jr., L.E., 1977. Microbial metabolic activity in soil as measured by dehydrogenase determinations. *Appl. Environ. Microbiol.* 34, 630–636.
- Dick, R.P., 1997. Soil enzyme activities as integrative indicators of soil health. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R. (Eds.), *Biological Indicators of Soil Health*. CAB International, Oxford, UK, pp. 121–156.
- Dick, R.P., Rasmussen, P.E., Kere, E.A., 1988. Influence of long-term residue management on soil enzyme activity in relation to soil chemical properties of a wheat fallow system. *Biol. Fert. Soils* 6, 159–164.
- Doran, J.W., 1980. Soil microbial and biochemical changes associated with reduced tillage. *Soil Sci. Soc. Am. J.* 44, 765–771.
- Doran, J.W., Parkin, T.B., 1994. Defining and assessing soil quality. In: Doran, J.W., Molina, J.A.E., Harris, R.F. (Eds.), *Defining Soil Quality for a Sustainable Environment*. Soil Science Society of America, Madison, WI, pp. 3–21.
- Frankenberger, W.T., Dick, W.A., 1983. Relationships between enzyme activities and microbial growth and activity indices in soil. *Soil Sci. Soc. Am. J.* 47, 945–951.
- Fraser, D.G., Doran, J.W., Sahts, W.W., Lesoing, G.W., 1988. Soil microbial populations and activities under conventional and organic management. *J. Environ. Qual.* 17, 585–590.
- Gallandt, E.R., Liebman, M., Huggins, D.R., 1999. Improving soil quality: implications for weed management. *J. Crop Prod.* 2, 95–121.
- Hoitink, H.A.J., Boehm, M.J., 1999. Biocontrol within the context of soil microbial communities: a substrate-dependent phenomenon. *Annu. Rev. Phytopathol.* 37, 427–446.
- Horwath, W.R., Elliott, L.F., Lynch, J.M., 1998. Influence of soil quality on the function of inhibitory rhizobacteria. *Lett. Appl. Microbiol.* 26, 87–92.
- Ibekwe, A.M., Kennedy, A.C., 1999. Fatty acid methyl ester (FAME) profiles as a tool to investigate community structure of two agricultural soils. *Plant Soil* 206, 151–161.
- Islam, K.R., Weil, R.R., 2000. Soil quality indicator properties in mid-Atlantic soils as influenced by conservation management. *J. Soil Water Conserv.* 55, 69–78.
- Jordan, D., Kremer, R.J., Bergfield, W.A., Kim, K.Y., Cacio, V.N., 1995. Evaluation of microbial methods as potential indicators of soil quality in historical agricultural fields. *Biol. Fert. Soil* 19, 297–302.
- Karlen, D.L., Stott, D.E., 1994. A framework for evaluating chemical and physical indicators of soil quality. In: Doran, J.W., Molina, J.A.E., Harris, R.F. (Eds.), *Defining Soil Quality for a Sustainable Environment*. Soil Science Society of America, Madison, WI, pp. 53–72.
- Kemper, W.D., Rosenau, R.C., 1986. Aggregate stability and size distribution. In: Klute, A. (Ed.), *Methods of Soil Analysis*.

- Part 1, 2nd ed. American Society of Agronomy, Madison, WI, pp. 425–442.
- Kennedy, A.C., 1999. Soil microorganisms for weed management. *J. Crop Prod.* 2, 123–138.
- Kirchner, M.J., Wollum II, A.G., King, L.D., 1993. Soil microbial populations and activities in reduced chemical input agroecosystems. *Soil Sci. Soc. Am. J.* 57, 1289–1295.
- Koul, O., Dhaliwal, G.S. (Eds.), 2002. Microbial biopesticides: an introduction. In: *Microbial Biopesticides*. Taylor & Francis, London, pp. 1–11.
- Kremer, R.J., Kennedy, A.C., 1996. Rhizobacteria as biocontrol agents of weeds. *Weed Technol.* 10, 601–609.
- Kremer, R.J., Begonia, M.F.T., Stanley, L., Lanham, E.T., 1990. Characterization of rhizobacteria associated with weed seedlings. *Appl. Environ. Microbiol.* 56, 1649–1655.
- Li, J., Kremer, R.J., 2000. Rhizobacteria associated with weed seedlings in different cropping systems. *Weed Sci.* 48, 734–741.
- Linn, D.M., Doran, J.W., 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. *Soil Sci. Soc. Am. J.* 48, 1267–1272.
- Martens, D.A., Johanson, J.B., Frankenburger Jr., W.T., 1992. Production and persistence of soil enzymes with repeated additions of organic residues. *Soil Sci.* 153, 53–61.
- Newman, R.M., Thompson, D.C., Richman, D.B., 1998. Conservation strategies for the biological control of weeds. In: Barbosa, P. (Ed.), *Conservation Biological Control*. Academic Press, San Diego, pp. 371–396.
- Pankhurst, C.E., Lynch, J.M., 1994. The role of the soil biota in sustainable agriculture. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R., Grace, P.R. (Eds.) *Soil Biota: Management in Sustainable Farming Systems*. CSIRO, East Melbourne, Australia, pp. 3–9.
- Parr, J.F., Papendiek, R.I., Hornick, S.B., Meyer, R.E., 1992. Soil quality: attributes and relationship to alternative and sustainable agriculture. *Am. J. Altern. Agric.* 7, 5–11.
- Roper, M.M., Ophel-Keller, K.M., 1997. Soil microflora as bioindicators of soil health. In: Pankhurst, C.E., Doube, B.M., Gupta, V.V.S.R. (Eds.), *Biological Indicators of Soil Health*. CAB International, Oxford, UK, pp. 157–177.
- Schnlirer, J.S., Rosswall, T., 1982. Fluorescein diacetate hydrolysis as a measure of total microbial activity in soil and litter. *Appl. Environ. Microbiol.* 43, 1256–1261.
- Smibert, R.M., Krieg, N.R., 1994. Phenotypic characterization. In: Gerhardt, P., Murray, R.G.E., Wood, W.A., Krieg, N.R. (Eds.), *Methods for General and Molecular Bacteriology*. American Society for Microbiology, Washington, pp. 607–654.
- Tabatabai, M.A., 1994. Soil enzymes. In: Weaver, R.W., Angle, J.S., Bottomley, P.S. (Eds.), *Methods of Soil Analysis, Part 2*, 2nd ed. American Society of Agronomy, Madison, WI, pp. 775–883.
- Turco, R.F., Kennedy, A.C., Jawson, M.D., 1994. Microbial indicators of soil quality. In: Doran, J.W., Molina, J.A.E., Harris, R.F. (Eds.), *Defining Soil Quality for a Sustainable Environment*. Soil Science Society of America, Madison, WI, pp. 73–90.
- Zablotowicz, R.M., Locke, M.A., Smeda, R.J., 1998. Degradation of 2,4-D and fluometuron in cover crop residues. *Chemosphere* 37, 87–101.