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Enzyme activities and microbial community structure in semiarid agricultural soils

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Abstract This study investigated the effect of management on β -glucosidase, β -glucosaminidase, alkaline phosphatase, and arylsulfatase activities and the microbial community structure in semiarid soils from West Texas, USA. Surface samples (0–5 cm) were taken from a fine sandy loam, sandy clay loam, and loam that were under continuous cotton (*Gossypium hirsutum* L.) or in cotton rotated with peanut (*Arachis hypogaea* L.), sorghum (*Sorghum bicolor* L.), rye (*Secale cereale*) or wheat (*Triticum aestivum* L.), and had different water management (irrigated or dryland), and tillage (conservation or conventional). The enzyme activities were higher in the loam and sandy clay loam than in the fine sandy loam. Soil pH was not affected by management, but the soil organic C and total N contents were generally affected by the different crop rotations and tillage practices studied. The trends of the enzyme activities as affected by management depended on the soil, but in general crop rotations and conservation tillage increased the enzyme activities in comparison to continuous cotton and conventional tillage. The soil enzyme activities were significantly correlated with the soil organic C (r -values up to 0.90, $P < 0.001$), and were correlated among each other (r -

values up to 0.90, $P < 0.001$). There were differences in the fatty acid methyl ester profiles between the fine sandy loam and the sandy clay loam and loam, and they reflected the differences in the enzyme activities found among the soils. For example, a 15:0 ranged from $1.61 \pm 0.25\%$ in cotton-peanut/irrigated/no-till in the fine sandy loam to $3.86 \pm 0.48\%$ in cotton-sorghum/dryland/conservation tillage in the sandy clay loam. There were no differences due to management within the same soil.

Keywords Fatty acid methyl ester · Tillage · Dryland · Cropping systems · Soil management

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Introduction

Over 20% of the USA cotton (*Gossypium hirsutum*) crop is produced in the Texas High Plains. Most of this cotton is produced in monoculture systems that contribute to wind-induced soil erosion and reduce the organic matter of semiarid soils. Recent efforts to protect the semiarid soils and enhance environmental quality favor conservation tillage practices and crop rotations. It has been well documented that soil management impacts on different biological attributes of soils, related to organic matter cycling, such as organic C and N, microbial biomass, mineralizable C and N, enzyme activities, and the soil fauna and flora (Gregorich et al. 1997). Studies on humid soils have reported that multi-cropping systems, compared to monoculture systems, have increased soil organic C, the potential cumulative N mineralized, microbial biomass C and N, and enzyme activities of soils (Klose et al. 1999; Deng and Tabatabai 2000; Klose and Tabatabai 2000; Moore et al. 2000; Ekenler and Tabatabai 2002). Soils under long-term practices showed that no-tillage and mulch (corn stalks added) treatments increased the soil organic C content and enzyme activities including the amidohydrolases (L-asparaginase, L-glutaminase, amidase, and urease), glycosidases (β -glucosidase, α -glucosidase, β -galactosidase, and α -galactosidase), phosphatases (alkaline phosphatase, acid phosphatase, and

phosphodiesterase), arylsulfatase (Deng and Tabatabai 1996a, 1996b, 1997), and arylamidase (Acosta-Martínez and Tabatabai 2001). Little information, however, is available about the effects of different crop rotations and tillage practices on soil biological attributes such as the enzyme activities and the microbial community structure of semiarid soils in West Texas, USA, in comparison to the typical practice of continuous cotton under conventional tillage.

Enzyme activities are involved in processes important to soil function such as organic matter decomposition and synthesis, nutrient cycling, and decomposition of xenobiotics. The overall activity of a single enzyme may depend on enzymes in different locations including intracellular enzymes from viable proliferating cells, and accumulated or extracellular enzymes stabilized in clay minerals and/or complexed with humic colloids (Burns 1982; Tabatabai 1994; Nannipieri et al. 2002). Even though an assessment of several enzyme activities is needed in order to provide a better picture of the status of soil processes as affected by management, there are particular enzyme activities, which are involved in key reactions of important metabolic processes of soils (i.e., organic matter decomposition, nutrient cycling) that have been shown to be sensitive to management and require a simple assay procedures. For example, β -glucosidase activity is involved in the final step of cellulose degradation that provides simple sugars for microorganisms in soils, and it has shown to be sensitive to residue management (Acosta-Martínez et al. 1999; Bandick and Dick 1999). β -glucosaminidase activity is involved in the hydrolysis of the *N*-acetyl- β -D-glucosamine residue from the terminal non-reducing ends of chito-oligosaccharides. This hydrolysis is considered to be important in C and N cycling in soils because it participates in the processes whereby chitin is converted to amino sugars, which are one of the major sources of mineralizable N in soil (Stevenson 1994; Ekenler and Tabatabai 2002). The β -glucosaminidase activity was affected by cropping systems and fertilization, and significantly correlated to the cumulative N mineralized in soils (Ekenler and Tabatabai 2002). Arylsulfatase activity is involved in the processes whereby soil organic S is mineralized (Tabatabai 1994), and its total, intracellular, and extracellular activity are affected by soil management (Bandick and Dick 1999; Klose et al. 1999; Ndiaye et al. 2000). Alkaline and acid phosphatase activities catalyze the hydrolysis of both organic P esters and anhydrides of phosphoric acid into inorganic P (Schmidt and Laskowski 1961), but alkaline phosphatase activity is induced in high pH soils.

According to Kandeler et al. (1996) the microbial composition of a soil determines its potential for substrate catalysis since most of the processes in soil are mediated by microorganisms and carried out by enzymes. Recently, the potential of fatty acid methyl ester (FAME) analysis for the characterization of the soil microbial community structure has been suggested (Turco et al. 1994; Kennedy 1999; Schutter et al. 2001). The interpretation of FAME profiles from whole soil communities can be difficult

because many fatty acids are extracted from soils and are common to different microorganisms (Cavigelli et al. 1995). Nevertheless, several studies have found changes in FAME profiles due to cropping systems and management (Klug and Tiedje 1993; Ibekwe and Kennedy 1999; Schutter et al. 2001).

The objectives of this study were to: (1) investigate the impacts of soil management on β -glucosidase, β -glucosaminidase, arylsulfatase and alkaline phosphatase activities, and the microbial community structure in semiarid soils, and (2) assess the relationship between these enzyme activities and organic C and total N contents in the soils.

Materials and methods

Soil sampling and sites description

Samples were taken in January 1996, after the growing season, from commercial grower fields and research plots in West Texas (west and south of Lubbock, Texas), USA. The surface soils in this region generally have a high (45–95%) sand content (Lee et al. 1994). After removing the upper 2 cm of the soil surface, to avoid contamination from sediments recently deposited by wind, the consecutive 5-cm soil depth was collected. Three different sites were sampled for each treatment studied. Each sample was a composite mixture from five points taken on a diamond-grid pattern near the center of each site to better represent the treatment studied. After sampling, soils were sieved through a 2-mm-mesh screen and stored at 4°C until FAME analysis was performed the same year.

The classification, management, and selected chemical properties of the soils studied are described in Table 1. Soils with different textures were selected, e.g., a fine sandy loam, a sandy clay loam (fine-loamy, mixed, thermic, superactive, Aridic Paleustalfs), and a loam (fine-loamy, mixed, thermic, superactive, Aridic Paleustolls). Each treatment studied consists of the crop rotation, water management, and tillage used for at least 2 years prior to the time of sampling. Rotations were continuous cotton (*Gossypium hirsutum* L.) or cotton rotated with peanut (*Arachis hypogaea* L.), sorghum (*Sorghum bicolor* L.), rye (*Secale cereale*) or wheat (*Triticum aestivum* L.) in different combinations. The fields were either dryland or irrigated. In the conventional tilled soils, the stalks of the first crop in the rotation were shredded and disked in December, moldboard (fine sandy loam and sandy clay loam) or deep chisel (loam) plowed in February, herbicide incorporated with a spring-tooth chisel followed by listing (creates 20- to 30-cm-high planting beds) in March, rod-weeding before planting in early May. After planting in May, a rotary hoe was used for wind erosion control and to break the crust in May and June. Field cultivation was done twice, in June and July. The conservation tillage, which may also be specified as reduced or no-tillage, was applied as follows:

1. Continuous cotton (Ct-Ct), irrigated (Irrig) or dryland (Dry), reduced tillage (Red): cotton stalks were shredded, preplant herbicide was added to the old rows and cultivated as needed for weed control.
2. Terminated (^T; refers to herbicide treatment to kill vegetation) rye (^R) or wheat (^W)-cotton (^W-Ct), Irrig or Dry, no-tillage (No-t): rye or wheat planted into cotton stalks following harvest and chemically treated 2–4 weeks prior to cotton planting, and cotton then planted into the rye or wheat residue.
3. Sorghum-cotton (Ct-Sr), Irrig or Dry, conservation tillage (Cs) system: cotton planted into previous sorghum.
4. Wheat-cotton (W-Ct), Irrig or Dry, conservation tillage (Cs) system: wheat grown for grain, the wheat stubble left standing and cotton planted into wheat stubble the following year.

Table 1 Classification, management, and chemical properties of the three semiarid agricultural soils studied. *Ct* Cotton, *Sr* sorghum, *W* wheat, *Wi* wheat interseed, ^T*W* terminated wheat, ^T*r* terminated rye, *Pt* peanut, *Irrig* irrigated, *Dry* dryland, *Cv* conventional tillage,

Cs conservation tillage, *Red* reduced tillage, *N-t* no-tillage, *b. h.* before harvest, *a. h.* after harvest, *LSD* least significant difference (among the treatments for each soil)

| Soil | | | Treatment abbreviation | Soil management | | | Chemical properties | | |
|----------|--------------------|-----------------|----------------------------------|------------------------------|----------------------|----------------------|---------------------|---------------------------------|-------------------------------|
| Series | Subgroup | Texture | | Rotation ^a | Water management | Tillage | pH | Organic C (g kg ⁻¹) | Total N (g kg ⁻¹) |
| Amarillo | Aridic Paleustalfs | Fine sandy loam | Ct-Ct/Irrig/Cv | Cotton-cotton | Irrigated | Conventional | 7.7 | 2.06 | 0.19 |
| | | | Ct-Ct/Irrig/Red | | Irrigated | Reduced | 7.4 | 2.64 | 0.23 |
| | | | Ct-Ct/Dry/Cv | | Dryland | Conventional | 7.4 | 1.71 | 0.13 |
| | | | Ct-Ct/Dry/Red | | Dryland | Reduced | 7.1 | 1.85 | 0.19 |
| | | | Ct-W/Dry/N-t | Cotton-wheat | Dryland | No tillage | 7.4 | 2.41 | 0.20 |
| | | | Ct-Wi/Dry/Cv | Cotton-wheat interseed | Dryland | Conventional | 7.8 | 2.02 | 0.21 |
| | | | Ct-Pt/Irrig/N-t | Cotton-peanut | Irrigated | No tillage | 7.7 | 1.64 | 0.15 |
| | | | ^T W-Ct/Irrig/N-t | Terminated | Irrigated | No tillage | 7.8 | 2.80 | 0.24 |
| | | | ^T W-Ct/Dry/N-t | wheat-cotton | Dryland | No tillage | 7.4 | 1.36 | 0.15 |
| | | | | (LSD <i>P</i> <0.05) | 0.3 | 0.45 | 0.04 | | |
| | | Sandy clay loam | Ct-Ct/Dry/Cv | Cotton-cotton | Dryland | Conventional | 7.7 | 6.14 | 0.66 |
| | Ct-Ct/Dry/Red | | | Dryland | Reduced | 7.8 | 6.36 | 0.71 | |
| | Ct-W/Dry/Cs | | Cotton-wheat | Dryland | Conservation | 7.6 | 7.77 | 0.81 | |
| | W-Ct/Dry/Cs | | Wheat-cotton | Dryland | Conservation | 7.8 | 7.61 | 0.79 | |
| | Ct-Sr/Dry/Cv | | Cotton-sorghum | Dryland | Conventional | 7.6 | 7.17 | 0.71 | |
| | Ct-Sr/Dry/Cs | | | Dryland | Conservation | 7.6 | 8.27 | 0.80 | |
| | Sr-Ct/Dry/Cv | | Sorghum-cotton | Dryland | Conventional | 7.6 | 9.54 | 1.07 | |
| | Sr-Ct/Dry/Cs | | | Dryland | Conservation | 7.6 | 9.62 | 1.03 | |
| | | | | | (LSD <i>P</i> <0.05) | 0.2 | 1.55 | 0.19 | |
| Acuff | Aridic Paleustolls | Loam | Ct-Ct/Irrig/Cv | Cotton-cotton | Irrigated | Conventional | 8.3 | 8.95 | 1.03 |
| | | | Ct-Ct/Irrig/Red | | Irrigated | Reduced | 8.2 | 10.00 | 1.10 |
| | | | Ct-W/Irrig/Cv | Cotton-wheat | Irrigated | Conventional | 8.2 | 10.27 | 1.11 |
| | | | Ct-W/Irrig/Cs | | Irrigated | Conservation | 8.1 | 11.99 | 1.25 |
| | | | W-Ct/Irrig/Cv | Wheat-cotton | Irrigated | Conventional | 8.2 | 9.02 | 1.01 |
| | | | W-Ct/Irrig/Cs | | Irrigated | Conservation | 8.0 | 12.16 | 1.24 |
| | | | Ct-Sr/Irrig/Cv | Cotton-sorghum | Irrigated | Conventional | 8.0 | 9.96 | 1.05 |
| | | | Ct-Sr/Irrig/Cs | | Irrigated | Conservation | 8.0 | 11.69 | 1.19 |
| | | | Sr-Ct/Irrig/Cv | Sorghum-cotton | Irrigated | Conventional | 8.1 | 9.31 | 1.02 |
| | | | Sr-Ct/Irrig/Cs | | Irrigated | Conservation | 8.0 | 10.64 | 1.15 |
| | | | ^T W-r/Irrig/N-t | Terminated rye/cotton b.h. | Irrigated | No tillage | 7.9 | 10.51 | 1.09 |
| | | | ^T W-Ct/Irrig/N-t b.h. | Terminated wheat/cotton b.h. | Irrigated | No tillage | 7.9 | 9.95 | 1.05 |
| | | | ^T W-Ct/Irrig/N-t a.h. | Terminated wheat/cotton a.h. | Irrigated | No tillage | 7.9 | 10.20 | 1.10 |
| | | | | | | (LSD <i>P</i> <0.05) | 0.2 | 1.54 | 0.12 |

^a Samples always taken during the first crop indicated

Soil analyses

The pH values were measured in air-dried soil (<2 mm) by using a glass combination electrode (soil: water ratio, 1:2.5) (Table 1). The β -glucosidase, alkaline phosphatase, arylsulfatase, and β -glucosaminidase activities were assayed (<2 mm air-dried soil) at their optimal pH values in duplicates including one control. The results are expressed in milligrams of *p*-nitrophenol (PN) released per kilogram soil (moisture-free basis) per hour. The assay procedures for β -glucosidase, arylsulfatase, and alkaline phosphatase activities are described in Tabatabai (1994) and the assay procedure for β -glucosaminidase activity is described in Parham and Deng (2000). From the enzyme activities values and organic C contents, the specific activities were calculated and are expressed in g PN released kg⁻¹ organic C. Soil subsamples (air-dried) were ground to pass an 80-mesh (180 μ m) sieve for total C and N analyses in the Vario Max-ELEMENTAR CN analyzer (Hanau, Germany).

Microbial community analysis

Field-moist soil (1 g, <2 mm) was treated with 1 ml NaOH [15% (wt/vol)] in 50% methanol to promote mild-alkaline cell hydrolysis and saponified at 100°C in a water bath for 30 min. The sample was cooled, acidified to a pH below 1.5, methylated with 2 ml of HCl in aqueous methanol (92 ml MeOH/108 ml 6.0 N HCl), and placed in an 80°C waterbath for 10 min. After cooling, the FAME were extracted with 1:1 hexane:methyl-*tert*-butyl-ether (H/MTBE) by mixing end-over-end for 10 min. The tube was centrifuged (1,000 *g* for 1 min) to separate the phases, and the organic phase (top phase) was added a second volume of H/MTBE. The combined organic phases were washed with diluted NaOH (2.4 g NaOH in 200 ml d₁ H₂O) and the phases were allowed to separate. The organic phase (top phase), containing FAME, was analyzed in a 5890 GC series II (Hewlett Packard, Wilmington, Del.) equipped with a flame ionization detector and 25 m \times 0.2-mm fused silica capillary column using ultra high purity hydrogen as the carrier gas. The temperature program was ramped from 170°C to 250°C at 5°C min⁻¹.

The Eukary method of the Microbial Identification System (Microbial ID, Newark, Del.) was used to develop a fatty acid profile by calibrating retention times of fatty acids ranging from 9–

30 carbons. Each sample peak was compared to standard fatty acids (Microbial ID) and interpolation of retention time was done using the equivalent chain length method. A pattern recognition program was used to identify similarities and differences among the fatty acid fingerprints (Sasser 1990).

FAMES are described by the number of C atoms, followed by a colon, the number of double bonds and then by the position of the first double bond from the methyl (ω) end of molecules, and *cis* and *trans* isomers are indicated by *c* and *t*, respectively. Branched fatty acids are indicated by the prefixes *i* and *a* for iso and anteiso, respectively. Other notations are Me for methyl, OH for hydroxy, cy for cyclopropane and G for ganglioside.

Statistical analyses

Statistical analyses, including ANOVA and mean separation by least significant differences, were performed for each soil (fine sandy loam, sandy clay loam, and loam) by using the general linear model procedure of the SAS system (1999) to determine significant effects of the different systems studied (each system includes the crop rotation, water management, and tillage practice treatments). Multivariate analysis of variance was done for each soil to compare the continuous cotton and crop rotation treatments, and the conventional tillage and conservation tillage treatments using at least three of the enzyme activities investigated (β -glucosaminidase, β -glucosidase and arylsulfatase activities).

In the FAME analysis, the principal component analyses (PCA) was used to demonstrate the similarities and differences in the FAME profiles among samples due to soil type by including all the fatty acids extracted. Each PC extracts a portion of the variance in the original data, with the greatest amount of variance for the first PC, and as much of the remaining variability as possible for each succeeding PC.

Results and discussion

Soil enzyme activities

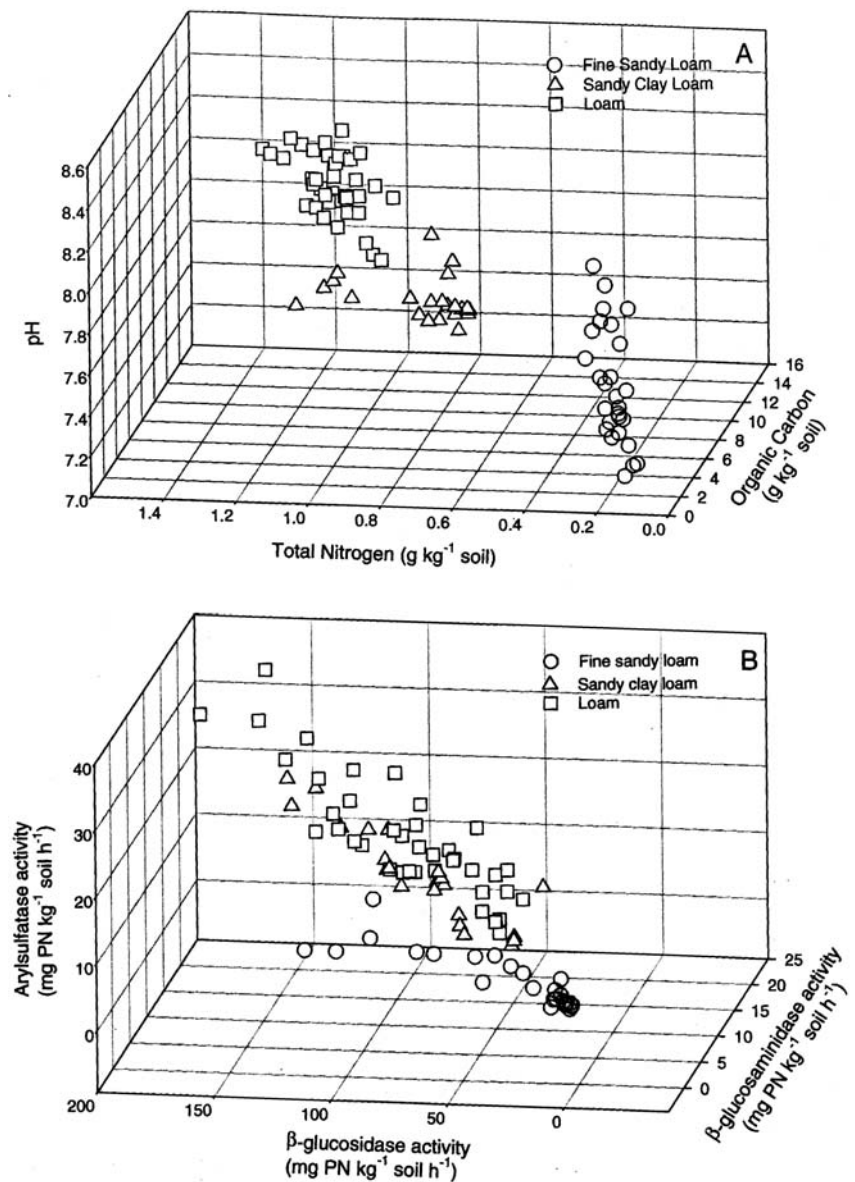
A plot of the activities of β -glucosidase, β -glucosaminidase, and arylsulfatase activities showed there were greater activities in the loam and sandy clay loam than in the fine sandy loam reflecting the differences in the chemical properties among the soils (Fig. 1a, b). Another plot showed that alkaline phosphatase activity ranged from 72 (Ct-Ct/Irrig/Cv) to 170 (^TW-Ct/Irrig/N-t, after harvest), 58 (Ct-Ct/Dry/Cv) to 122 (Ct-Sr/Dry/Cs), and from 8 (Ct-Ct/Dry/Cv) to 70 mg PN kg⁻¹ soil h⁻¹ (^TW-Ct/Irrig/N-t) in the loam, sandy clay loam, and fine sandy loam, respectively (Fig. 2). The differences in enzyme activities among the soils are related to the higher organic C and total N contents of the loam and sandy clay loam compared to the fine sandy loam (Table 1). It is known that a particular enzyme has many different sources (i.e., microorganisms, plant roots, animals) and states (i.e., active microbial biomass, enzyme stabilized in soil surfaces and cell fragments) (Skujins 1976), and that soil organic matter affects enzyme activities (Tabatabai 1994). Although the sandy clay loam may have the highest clay content (20–35%) among the soils, a typical loam will contain a slightly lower clay content (7–27%) but a measurably lower sand content (23–52%) than the other soils (43–85%). Generally, greater microbial biomass C, and thus enzyme activities can be sustained in finer-

textured soils, compared to coarser-textured soils under similar land use (Ladd et al. 1996; Sparling 1997). Thus, the texture, combined with a high organic C content (>8.95 g kg⁻¹ soil), may result in more available surfaces for the microbial biomass and enzyme stabilization in the loam.

Alkaline phosphatase and β -glucosidase activities were higher than arylsulfatase and β -glucosaminidase activities in the semiarid soils studied (Fig. 2). Alkaline phosphatase and β -glucosidase activities in Ct-Ct/Irrig/Cv in the loam were 58 and 43 mg PN kg⁻¹ soil h⁻¹, respectively, which is more than 5 times greater than arylsulfatase (9 mg PN kg⁻¹ soil h⁻¹) and β -glucosaminidase activities (8 mg PN kg⁻¹ soil h⁻¹). Other studies have also found alkaline phosphatase and β -glucosidase activities are predominant in soils from other regions (Bandick and Dick 1999; Acosta-Martínez and Tabatabai 2000). These findings indicate that even though enzyme activities are affected by soil properties, the predominance and ecological role among enzymes do not change in different soils and vegetation.

The soil pH did not show a particular trend related to soil management. At the soil depth evaluated, the organic C content, and in most cases the total N were generally greatest in soils under crop rotations and conservation tillage practices than under the typical practice of continuous cotton under conventional tillage (Table 1). The impact of crop rotations on the enzyme activities investigated differed among the fine sandy loam, sandy clay loam, and loam soils and with the type of enzyme studied (Fig. 2). The enzyme activities were not impacted by the cotton-peanut rotation [Ct-peanut (Pt)/Irrig/No-t] in comparison to continuous cotton (Ct-Ct/Irrig/Red or Ct-Ct/Irrig/Cv) in the fine sandy loam (Fig. 2). There was generally a significant ($P < 0.05$) increase in the enzyme activities in cotton rotated with wheat or sorghum compared to continuous cotton in the sandy clay loam and loam (Fig. 2). A plot of arylsulfatase, β -glucosaminidase and β -glucosidase activities showed a significant ($P < 0.05$) increase in the enzyme activities due to crop rotations in comparison to continuous cotton in the three soils (Fig. 3A). These results are due to the little residue cover during the winter and spring periods in soils under continuous cotton, which makes the soil more susceptible to wind and water erosion, and reduces the soil organic matter content. Generally, under crop rotation each residue provides C, N, and other elements in different amounts and available forms. In comparison to monoculture, the amounts and type of residue left in soils by different crops affect differently soil organic matter content and the microbial populations and, thus the amounts of enzymes produced and stabilized in soils. Studies in humid environments have reported greater microbial biomass (Moore et al. 2000) and enzyme activities (Klose et al. 1999; Klose and Tabatabai 2000; Ekenler and Tabatabai 2002) in soils under other crop rotations including corn (*Zea mays* L.) in rotations with meadow (alfalfa) (*Medicago sativa* L.), soybean (*Glycine*

Fig. 1 Three-dimensional plot of the soil pH, organic C, and total N contents (A); and of the β -glucosidase, β -glucosaminidase and arylsulfatase activities (B) in the three semiarid agricultural soils. *PN p* -Nitrophenol



max L.) and oats (*Avena sativa* L.) than under continuous corn.

There was not a general trend of enzyme activities as affected by irrigation in the fine sandy loam, which was under both water management treatments (irrigated and dryland) (Fig. 2). For example, β -glucosaminidase, arylsulfatase, and β -glucosidase activities were higher in irrigated continuous cotton under reduced tillage practices compared to the corresponding system in dryland, but continuous cotton under conventional tillage was not impacted by irrigation. The differences in the enzyme activities could be attributed to the combination of irrigation and conservation tillage practices, and the impacts of tillage on the soil organic matter (Table 1). Previous studies have found that soil C and N conservation is greater with no-tillage because of less soil disturbance (Dick 1984; Deng and Tabatabai 1996a, 1996b, 1997).

Studies in humid environments reported that arylsulfatase, alkaline phosphatase, and acid phosphatase activities, as well as other enzyme activities, were increased in reduced or no-tillage systems compared to conventional tillage (Dick 1984; Deng and Tabatabai 1996a, 1996b; 1997; Kandeler et al. 1999; Acosta-Martínez and Tabatabai 2001). In this study, β -glucosidase, β -glucosaminidase and alkaline phosphatase activities were increased by conservation tillage in continuous cotton under the same water management in the fine sandy loam (Fig. 2). In the sandy clay loam, the plot of β -glucosidase, β -glucosaminidase and arylsulfatase activities showed no differences in these enzyme activities due to tillage practices (Fig. 3B). In the loam, the enzyme activities were generally increased by conservation tillage practices in the different cotton and sorghum or wheat rotations studied (Fig. 3B). For example, β -glucosidase activity was three times higher in W-Ct/Irrig/Cs (168 mg PN kg⁻¹

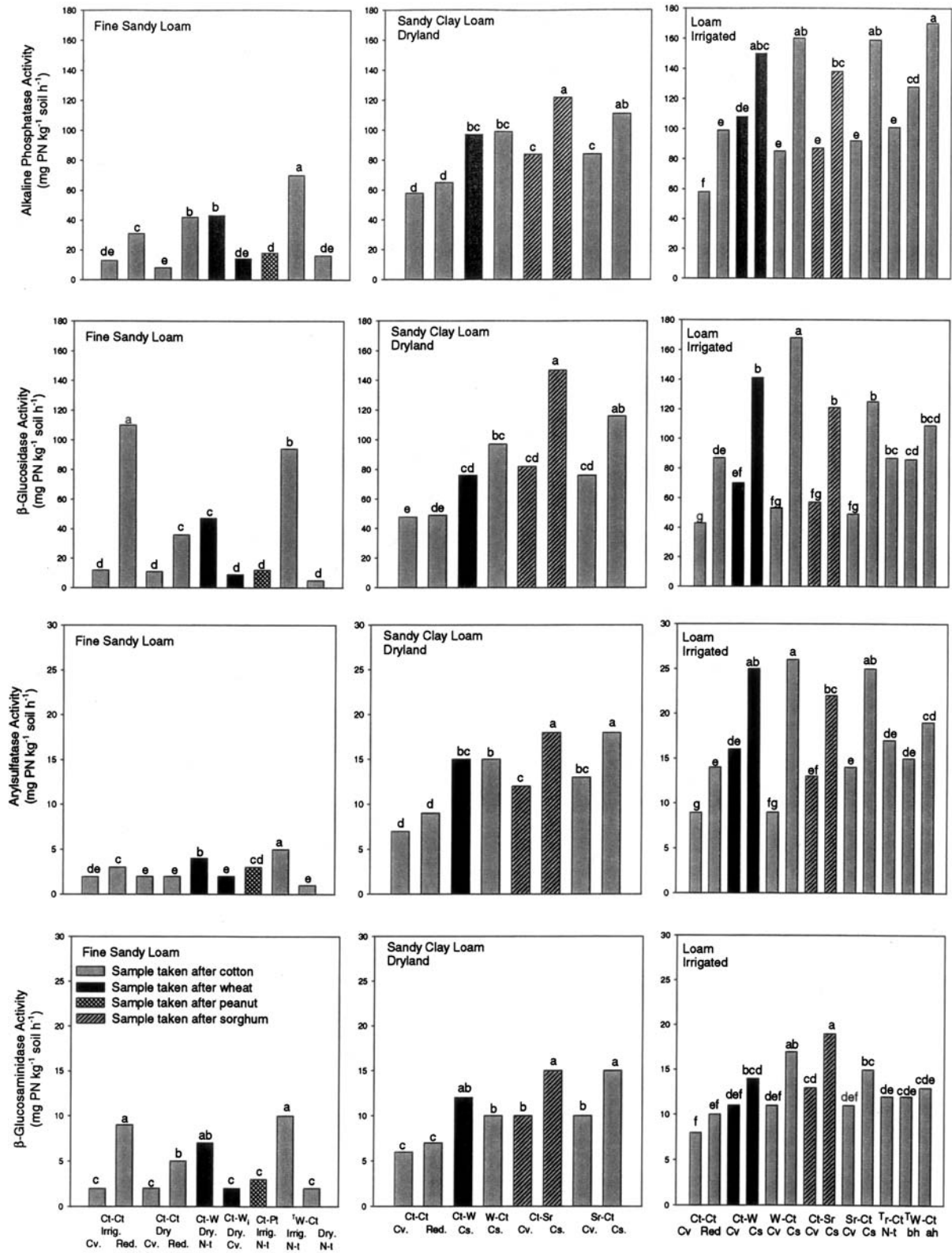


Fig. 2 Enzyme activities in the semiarid agricultural soils studied. Bars with different letters are significantly ($P < 0.05$) different. Ct Cotton, Sr sorghum, W wheat, W i wheat interseed, T_r terminated wheat, Pt peanut, Irrig irrigated, Dry dryland, Cv conventional, Cs conservation, Red reduced, N-t no-tillage, b. h. before harvest, a. h. after harvest

Fig. 3 Three-dimensional plot of β -glucosidase, β -glucosaminidase and arylsulfatase activities as affected by crop rotations (**A**) and tillage practices (**B**) in the semiarid agricultural soils studied

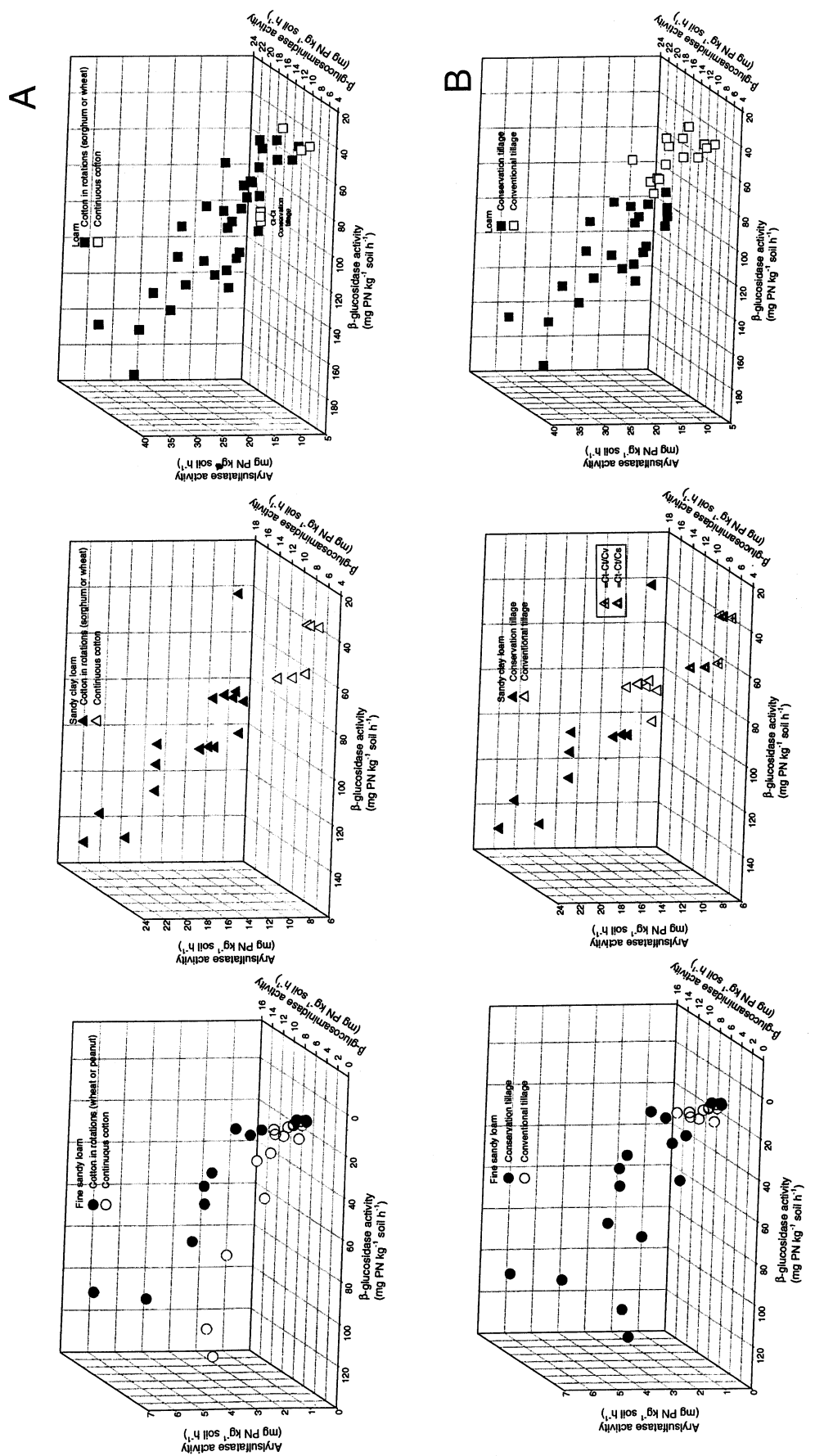


Table 2 Specific activities of the enzymes investigated in the three semiarid soils studied. *PN p* -Nitrophenol; for other abbreviations, see Table 1

| Soil and management | Specific activities | | | |
|------------------------------------|--|--------------------------|----------------------|---------------|
| | β -Glucosidase | β -Glucosaminidase | Alkaline phosphatase | Arylsulfatase |
| | (g PN released kg ⁻¹ organic C) | | | |
| Fine sandy loam | | | | |
| Ct-Ct/Irrig/Cv | 5.6 | 1.1 | 6.4 | 0.9 |
| Ct-Ct/Irrig/Red | 42.0 | 3.4 | 11.8 | 1.1 |
| Ct-Ct/Dry/Cv | 6.1 | 0.9 | 4.5 | 0.9 |
| Ct-Ct/Dry/Red | 21.3 | 3.2 | 24.1 | 1.1 |
| Ct-W/Dry/N-t | 19.4 | 2.9 | 18.0 | 1.5 |
| Ct-Wi/Dry/Cv | 4.3 | 1.0 | 7.1 | 0.9 |
| Ct-Pt/Irrig/N-t | 7.1 | 1.8 | 11.5 | 1.6 |
| ^T W-Ct/Irrig/N-t | 33.8 | 3.5 | 25.2 | 1.9 |
| ^T W-Ct/Dry/N-t | 4.1 | 1.1 | 11.5 | 1.0 |
| LSD (<i>P</i> <0.05) _b | 6.2 | 1.1 | 3.5 | 0.4 |
| Sandy clay loam | | | | |
| Ct-Ct/Dry/Cv | 7.1 | 1.0 | 9.5 | 1.2 |
| Ct-Ct/Dry/Red | 8.3 | 1.1 | 10.3 | 1.4 |
| Ct-W/Dry/Cs | 9.6 | 1.6 | 12.4 | 1.9 |
| W-Ct/Dry/Cs | 12.8 | 1.4 | 13.0 | 2.0 |
| Ct-Sr/Dry/Cv | 11.0 | 1.5 | 11.7 | 1.7 |
| Ct-Sr/Dry/Cs | 15.8 | 1.8 | 14.7 | 2.2 |
| Sr-Ct/Dry/Cv | 8.0 | 1.1 | 7.4 | 1.3 |
| Sr-Ct/Dry/Cs | 12.2 | 1.6 | 11.3 | 2.0 |
| LSD (<i>P</i> <0.05) | 5.1 | 0.4 | 3.3 | 0.4 |
| Loam | | | | |
| Ct-Ct/Irrig/Cv | 4.8 | 0.9 | 8.1 | 1.0 |
| Ct-Ct/Irrig/Red | 8.7 | 1.0 | 10.7 | 1.4 |
| Ct-W/Irrig/Cv | 6.8 | 1.1 | 11.5 | 1.6 |
| Ct-W/Irrig/Cs | 10.0 | 1.1 | 12.4 | 2.0 |
| W-Ct/Irrig/Cv | 5.9 | 1.2 | 8.7 | 1.0 |
| W-Ct/Irrig/Cs | 12.8 | 1.4 | 12.5 | 2.2 |
| Ct-Sr/Irrig/Cv | 5.9 | 1.3 | 8.7 | 1.3 |
| Ct-Sr/Irrig/Cs | 10.3 | 1.7 | 11.7 | 1.8 |
| Sr-Ct/Irrig/Cv | 6.4 | 1.1 | 9.9 | 1.5 |
| Sr-Ct/Irrig/Cs | 10.8 | 1.4 | 15.0 | 2.3 |
| ^T W-r/Irrig/N-t | 11.0 | 1.1 | 9.6 | 1.6 |
| ^T W-Ct/Irrig/N-t b.h | 9.5 | 1.2 | 12.8 | 1.6 |
| ^T W-Ct/Irrig/N-t a.h. | 10.2 | 1.2 | 16.1 | 1.8 |
| LSD (<i>P</i> <0.05) | 2.1 | 0.3 | 4.6 | 0.3 |

soil h⁻¹) than in W-Ct/Irrig/Cv (53 mg PN kg⁻¹ soil h⁻¹) in the loam (Fig. 2).

The results showed that in the sandy clay loam and loam, the application of both crop rotations and conservation tillage significantly increased the enzyme activities studied in comparison to continuous cotton under conventional tillage (Figs. 2, 3a, b). For example, the enzyme activities were up to twofold higher in ^Tr-Ct/Irrig/N-t and ^TW-Ct/Irrig/N-t (before or after harvest) in comparison to Ct-Ct/Irrig/Cv (Fig. 2).

Because organic C content and the enzyme activities were both affected by the soil management, the specific activities were calculated to account for the enzyme activity due to the organic C content of the soil (Table 2). According to Ekenler and Tabatabai (2002), the specific activity values could be used as indexes of organic C quality. In general, there were significantly higher specific activities under the combination of crop rotations and conservation tillage practices in comparison to continuous cotton and conventional tillage. There were also significant increases in the specific activities in

systems that still were not showing significant differences in the organic C content in comparison to continuous cotton and conventional tillage. Therefore, the enzyme activities reflected the differences in soil organic matter quality and quantity developed under alternative systems to continuous cotton and conventional tillage.

Linear regression analyses demonstrated that the response of the organic C content to soil management was correlated to the soil enzyme activities (Table 3). The correlation between the enzyme activities and organic C ranged from $r=0.45$ ($P<0.01$) (relationship of organic C and alkaline phosphatase activity in the loam) to $r=0.90$ ($P<0.001$) (relationship between organic C and arylsulfatase activity in the loam). The correlation between total N and the enzyme activities were not always significant, but the significant relationships ranged from $r=0.39$ ($P<0.05$) (total N and β -glucosaminidase activity in the fine sandy loam) to $r=0.86$ ($P<0.001$) (total N and arylsulfatase activity in the loam).

Table 3 Correlations (r) between the chemical and biochemical parameters investigated. The correlations were computed for each soil individually, and for the three soils (*All soils*). *FSL* Fine sandy loam, *SCL* sandy clay loam, *L* loam

| Soil parameters | Semiarid soils studied | | | |
|---------------------------------------|--|---------|---------|-----------|
| | FSL | SCL | L | All soils |
| | Correlation coefficient (r) values | | | |
| Organic C and | | | | |
| β -Glucosidase activity | 0.79*** | 0.63*** | 0.87*** | 0.71*** |
| β -Glucosaminidase activity | 0.80*** | 0.72*** | 0.76*** | 0.83*** |
| Alkaline phosphatase activity | 0.67*** | 0.47* | 0.45** | 0.84*** |
| Arylsulfatase activity | 0.75*** | 0.72*** | 0.90*** | 0.91*** |
| Total N and | | | | |
| β -Glucosidase activity | 0.37 | 0.43* | 0.80*** | 0.64*** |
| β -Glucosaminidase activity | 0.39* | 0.51* | 0.69** | 0.78*** |
| Alkaline phosphatase activity | 0.31 | 0.26 | 0.40* | 0.81*** |
| Arylsulfatase activity | 0.48* | 0.53* | 0.86*** | 0.87*** |
| β -Glucosidase activity and | | | | |
| β -Glucosaminidase activity | 0.88*** | 0.90*** | 0.72*** | 0.87*** |
| Alkaline phosphatase activity | 0.73*** | 0.88*** | 0.58** | 0.83*** |
| Arylsulfatase activity | 0.69*** | 0.90*** | 0.90*** | 0.76*** |
| β -Glucosaminidase activity and | | | | |
| Alkaline phosphatase activity | 0.82*** | 0.86*** | 0.33* | 0.87*** |
| Arylsulfatase activity | 0.77*** | 0.92*** | 0.75*** | 0.79*** |
| Alkaline phosphatase activity and | | | | |
| Arylsulfatase activity | 0.82*** | 0.83*** | 0.59** | 0.86*** |

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Microbial community structure

In order to better understand the relationship between enzyme activities and the composition of the microflora of semiarid soils, it is also important to investigate the effects of soil management on the microbial community structure responsible for the biochemical reactions studied. Seventy fatty acids were extracted from the fine sandy loam, sandy clay loam, and loam studied. The fatty acids present in the three semiarid soils studied are also common in other soils and vegetation types (Cavigelli et al. 1995, Ibekwe and Kennedy 1999, Schutter et al. 2001). Of those 70 fatty acids, only 28 were present in most of the soil samples including *a* 15:0, 16:0, *i* 16:0, *a* 17:0, *i* 17:0, *i* 15:0 20:0, 22:0, 17:1 ω 8c, 18:1 ω 9c, 18:2 ω 6c, and 18:3 ω 6c. While these fatty acids were present in most of the samples they did not occur in the same proportion in the three soils (Table 4). For example, the levels of *a* 15:0 ranged from 1.61 \pm 0.25% in Ct-Pt/Irrig/N-t (fine sandy loam) to 3.86 \pm 0.48% in Ct-Sr/Dry/Cs (sandy clay loam) and the levels of 18:1 ω 9c ranged from 5.05 \pm 0.32 in Ct-Ct/Irrig/Cv in the fine sandy loam to 10.92 \pm 2.11% in Ct-Sr/Irrig/Cs in the loam. Palmitic acid (16:0) showed the highest area percent and together with the other common fatty acids made up about 50% of total fatty acid content.

The PCA developed using all the fatty acids present in the samples showed a trend of differentiation in the FAME profiles of the fine sandy loam compared to the loam and sandy clay loam (Fig. 4). The PCA contained 22% of the variability in PC1 and 18% in PC2 (Fig. 4). Differences in the microbial community structure among the soils are due to the combined effects of different texture, pH, organic C and total N contents, and soil management (Table 1). The trend of different FAME

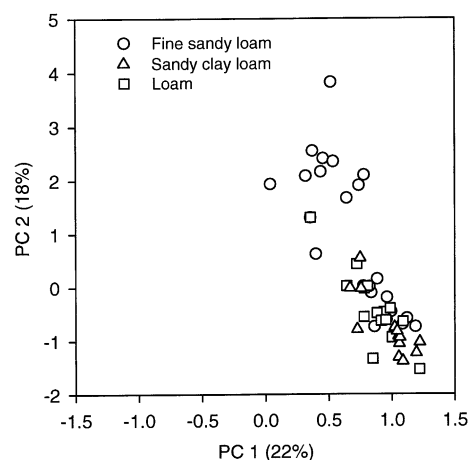


Fig. 4 Principal component analysis (PCA) of microbial community fatty acid methyl ester profiles of the semiarid agricultural soils studied. Percent of variance explained by each principal component (PC) is shown in parentheses

profiles in the fine sandy loam in comparison to the sandy clay loam and loam soils is in agreement with the lower enzyme activities in the fine sandy loam compared to the other two soils. This may be an indication that the differences in enzyme activities among the soils are due to the differences in the microbial community structure (Fig. 2).

Previous studies have reported that soil management impacts FAME profiles and these changes have been correlated to changes in the microbial community structure (Zelles et al. 1995; Cavigelli et al. 1995; Schutter et al. 2001). In this study, however, there were no significant differences in FAME profiles due to management within

Table 4 Fatty acids present in the semiarid agricultural soils studied. Numbers in parentheses are the SDs for the replicates of the treatment specified; where no SD is given, only one replicate was analyzed

| Soil and management | Fatty acids extracted from semiarid soils | | | | | | | | | | | |
|----------------------|---|--------------|-------------|-------------|-------------|-------------|-------------|-------------|----------------|--------------|---------------|--------------|
| | A15:0 | 16:0 | i 16:0 | a 17:0 | I 17:0 | i15:0 | 20:0 | 22:0 | 17:1 ω8c | 18:1 ω9c | 18:2 ω6c | 18:3 ω6c |
| Area percent | | | | | | | | | | | | |
| Fine sandy loam | | | | | | | | | | | | |
| Ct-Ct/Dry/Cv | 2.78 (0.59) | 21.32 (5.58) | 2.95 (0.34) | 1.96 (0.24) | 2.15 (0.20) | 4.27 (0.51) | 2.21 (0.32) | 1.58 (0.32) | 0.60 (1.05) | 8.63 (2.39) | 3.98 (1.470) | 1.88 (0.26) |
| Ct-Ct/Dry/Red | 3.31 (0.49) | 17.04 (3.29) | 3.00 (0.31) | 1.71 (0.26) | 2.00 (0.66) | 4.01 (0.75) | 2.14 (0.25) | 1.57 (1.37) | 1.74 (0.70) | 10.36 (1.30) | 4.98 (1.17) | 1.09 (1.30) |
| Ct-Ct/Irrig/Cv | 2.19 (0.69) | 20.88 (5.28) | 2.25 (0.31) | 2.06 (0.33) | 1.99 (0.55) | 3.24 (1.35) | 1.00 (0.88) | 0.98 (0.85) | - ^a | 5.05 (0.32) | 3.14 (0.46) | 3.35 (3.270) |
| Ct-Ct/Irrig/Red | 3.08 (0.74) | 20.41 (2.43) | 2.10 (0.22) | 1.17 (0.10) | 1.22 (0.23) | 2.44 (0.14) | 1.52 (0.32) | 1.83 (0.09) | 2.03 (0.32) | 9.87 (2.85) | 8.14 (2.49) | 0.74 (0.73) |
| Ct-Pt/Irrig/N-t | 1.61 (0.25) | 23.90 (3.04) | 1.80 (0.53) | 0.23 (0.40) | 1.19 (0.06) | 2.81 (0.43) | 1.65 (0.29) | 1.55 (0.50) | 0.22 (0.38) | 8.31 (4.36) | 3.52 (0.94) | 2.33 (0.45) |
| Ct-W/Dry/N-t | 2.70 (0.82) | 15.65 (2.50) | 3.00 (0.58) | 1.56 (0.22) | 1.57 (1.58) | 3.87 (1.29) | 1.13 (0.98) | 1.08 (1.02) | 1.53 (0.86) | 10.90 (3.81) | 8.58 (1.54) | 1.24 (1.09) |
| TW-Ct/Dry/N-t | 2.06 (1.43) | 19.07 (5.04) | 2.31 (0.64) | 1.54 (0.93) | 0.85 (0.43) | 3.07 (1.29) | 1.97 (0.71) | 3.34 (1.32) | - | 7.24 (6.51) | 3.34 (4.29) | 1.09 (1.89) |
| TW-Ct/Irrig/N-t | 3.15 (0.40) | 17.95 (2.04) | 2.27 (0.26) | 1.50 (0.22) | 1.47 (0.13) | 3.31 (0.15) | 1.60 (0.07) | 0.52 (0.91) | 1.94 (0.13) | 9.10 (1.17) | 7.61 (2.40) | 1.09 (1.43) |
| Sandy clay loam | | | | | | | | | | | | |
| Ct-Ct/Dry/Cv | 3.29 (0.87) | 15.42 (2.72) | 3.52 (0.82) | 1.85 (0.26) | 2.30 (0.51) | 4.84 (1.15) | 2.07 (0.71) | 1.17 (1.13) | 2.41 (0.71) | 9.14 (3.13) | 4.24 (1.72) | 0.41 (0.56) |
| Ct-Ct/Dry/Red | 3.15 (0.76) | 16.60 (3.78) | 3.49 (0.36) | 2.08 (-) | 2.28 (0.19) | 4.64 (0.80) | 1.00 (1.41) | 1.97 (2.78) | 3.15 (0.68) | 10.00 (1.38) | 4.48 (1.12) | - |
| Ct-Sr/Dry/Cs | 3.86 (0.48) | 14.45 (0.75) | 3.79 (0.24) | 1.84 (0.08) | 1.88 (0.03) | 4.77 (0.51) | 1.61 (0.33) | 0.47 (0.82) | 3.09 (0.18) | 10.66 (1.28) | 5.16 (0.40) | - |
| Ct-W/Dry/Cv | 3.11 (0.20) | 15.23 (0.18) | 3.12 (0.17) | 1.59 (0.03) | 1.58 (0.07) | 4.55 (0.11) | 1.41 (0.08) | 0.91 (1.29) | 2.57 (0.33) | 9.45 (0.73) | 5.21 (0.42) | - |
| Sr-Ct/Dry/Cs | 3.24 (0.80) | 15.96 (0.43) | 2.86 (0.60) | 1.55 (0.20) | 1.49 (0.17) | 4.10 (0.68) | 1.46 (0.45) | 1.06 (0.97) | 2.53 (0.37) | 11.81 (0.80) | 14.14 (10.00) | - |
| Loam | | | | | | | | | | | | |
| Ct-Ct/Irrig/Cv | 3.35 (0.99) | 17.09 (2.48) | 2.39 (0.35) | 1.35 (0.20) | 1.49 (0.36) | 3.53 (0.86) | 0.81 (0.70) | 0.83 (0.71) | 2.28 (0.49) | 7.59 (1.15) | 4.91 (0.46) | 2.55 (0.33) |
| Ct-Ct/Irrig/Red | 3.85 (-) | 16.53 (-) | 2.88 (-) | 1.82 (-) | 1.57 (-) | 4.40 (-) | - | - | 3.45 (-) | 9.57 (-) | 5.52 (-) | 3.81 (-) |
| Ct-Sr/Irrig/Cs | 3.18 (1.64) | 17.65 (2.80) | 2.21 (-) | 1.57 (0.74) | 1.44 (0.29) | 3.50 (1.51) | 0.91 (0.79) | 0.93 (0.91) | 2.21 (1.35) | 10.92 (2.11) | 6.23 (2.33) | 1.98 (0.21) |
| Ct-Sr/Irrig/Cv | 2.28 (-) | 18.65 (-) | 1.71 (-) | 2.14 (-) | 1.26 (-) | 3.14 (-) | 1.07 (-) | 1.71 (-) | 1.20 (-) | 13.68 (-) | 4.01 (-) | - |
| Ct-W/Irrig/Cs | 2.69 (-) | 10.43 (-) | 1.94 (-) | 1.32 (-) | 1.29 (-) | 3.75 (-) | 0.64 (-) | - | 2.47 (-) | 7.41 (-) | 6.55 (-) | 3.21 (-) |
| Ct-W/Irrig/Cv | 2.35 (-) | 13.81 (-) | 2.24 (-) | 1.14 (-) | 1.41 (-) | 3.38 (-) | 0.93 (-) | 0.95 (-) | 1.55 (-) | 6.65 (-) | 5.86 (-) | 1.58 (-) |
| Sr-Ct/Irrig/Cs | 3.82 (0.06) | 15.51 (-) | 2.68 (-) | 1.75 (-) | 2.03 (-) | 5.38 (-) | - | - | 2.24 (-) | 8.89 (-) | 7.47 (-) | 2.52 (-) |
| Sr-Ct/Irrig/Cv | 3.86 (-) | 17.85 (1.21) | 3.11 (0.05) | 0.92 (1.32) | 0.85 (1.20) | 4.06 (0.11) | - | - | 2.51 (0.60) | 9.73 (0.25) | 6.87 (1.56) | 4.03 (0.21) |
| TW-Ct/Irrig/N-t a.h. | 3.48 (-) | 15.38 (-) | 2.31 (-) | 1.96 (-) | 2.17 (-) | 4.35 (-) | 1.46 (-) | 2.15 (-) | 3.08 (-) | 9.09 (-) | 5.89 (-) | 2.74 (-) |
| TW-Ct/Irrig/N-t b.h. | 3.17 (-) | 12.07 (-) | 2.24 (-) | 1.14 (-) | 1.1 (-) | 3.75 (-) | 0.75 (-) | 1.49 (-) | 2.24 (-) | 6.96 (-) | 4.50 (-) | 3.00 (-) |

^a Below detection limit for gas chromatography

the same soil (Table 4). This may be because: (1) the microbial community structure was more affected by sudden changes in environmental parameters typical for these regions (i.e., high winds, low precipitation with sudden rain events, high temperature); (2) the combined effects of the crop rotations, tillage, and water management treatments masked each other; and/or (3) the fact that in FAME analysis many fatty acids are extracted from each sample which are common to different microorganisms, which is a disadvantage of the technique (Cavigelli et al. 1995).

Although the size and the composition of the microbial community control the production of enzymes, the enzyme activities studied and the FAME profiles did not respond simultaneously to soil management. Enzyme activities are often closely related to soil physical properties, organic matter, and to microbial biomass and activity (Dick et al. 1996). However, enzyme activity measurements do not provide information on the enzyme pool being measured, and the contribution of the intracellular and extracellular enzyme pools to the overall activity may differ depending on the enzyme and the soil properties. For example, the activity of arylsulfatase from the microbial biomass ranged from 39.6 to 73.1% and the remaining extracellular activity from 26.9 to 60.4% in soils under a wide range of organic C, sand, and clay contents (Klose et al. 1999). Because air-dried soils were used for the measurement of soil enzyme activities by a short-term assay, it could be assumed that mainly extracellular activities were detected. This enzyme pool may remain active, even if the conditions are unfavorable for microbial populations in soils. The fatty acids detected by FAME analysis were extracted from field-moist soils, where more active microorganisms are expected than in air-dried soils. Because our findings indicated that the two parameters investigated varied in the rate they responded to management, samples taken over >1 year and analyzed by FAME may be needed for evaluating the impacts of management on the microbial community structure in these semiarid soils, and we suggest that enzyme activities should be measured in field-moist samples.

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