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Bacterial and fungal abundance and biomass in conventional and no-tillage agroecosystems along two climatic gradients

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Abstract

Microbial community composition may be an important determinant of soil organic matter (SOM) decomposition rates and nutrient turnover and availability in agricultural soils. Soil samples were collected from six long-term tillage comparison experiments located along two climatic gradients to examine the effects of no-tillage (NT) and conventional tillage (CT) management on bacterial and fungal abundance and biomass and to examine potential controls on the relative abundances of bacteria and fungi in these two systems. Samples were divided into 0–5 and 5–20 cm depth increments and analyzed for bacterial and fungal abundance and biomass, total C and N, particulate organic matter C and N (POM-C and N), soil water content, texture, pH, and water-stable aggregate distributions. Soil moisture, which varied by tillage treatment and geographically with climate, ranged from 0.05 to 0.35 g g^{-1} dry soil in the surface 0–5 cm and 0.15 to 0.28 g g^{-1} dry soil at 5–20 cm. Measured organic matter C and N fractions and mean weight diameter (MWD) of water-stable aggregates were significantly higher in NT relative to CT at three of the six sites. Fungal hyphal length ranged from 19 to 292 m g^{-1} soil and was 1.9 to 2.5 times higher in NT compared to CT surface soil across all sites. Few significant tillage treatment differences in soil physical and chemical properties or in fungal abundance and biomass were observed at 5–20 cm. Bacterial abundance and biomass were not consistently influenced by tillage treatment or site location at either depth. The proportion of the total biomass composed of fungi ranged from 10 to 60% and was significantly higher in NT compared to CT surface soil at five of six sites. Proportional fungal biomass was not strongly related to soil texture, pH, aggregation, or organic C and N fractions, but was positively related to soil moisture ($r = 0.67$; $P < 0.001$). The relationship between soil moisture and the degree of fungal dominance was due to the positive response of fungal biomass and the lack of response of bacterial biomass to increasing soil moisture across the range of measured soil water contents. Tillage treatment effects on fungal biomass and proportional fungal abundance were not significant when the data were analyzed by analysis of covariance with soil moisture as the covariate. These results suggest that observed tillage treatment and climate gradient effects on fungi are related to differences in soil moisture. Further research is needed, however, to determine how tillage-induced changes in the soil environment shape microbial community composition in agroecosystems.

Keywords: Bacteria; Fungi; Microbial community composition; Tillage; Soil organic matter

1. Introduction

Tillage-induced shifts in the relative abundances of bacteria and fungi may influence the rate of soil organic matter (SOM) decomposition and nutrient availability in agroecosystems. The soil microbial community has not been well characterized in agroecosystems (Wardle, 1995), particularly in conventional tillage (CT) and no-tillage (NT) systems which are the predominant management practices in U.S. agriculture. The abundances of bacteria and fungi in NT and CT soils have been quantified using plate counts (Norstadt and McCalla, 1969; Doran, 1980; Linn and Doran, 1984). However, these data do not allow quantitative comparison of the relative amounts of bacterial and fungal biomass, a critical requirement when linking community composition to nutrient dynamics. We know of only one study site, the long-term tillage comparison experiment in Horseshoe Bend, GA, where microbial community composition in NT and CT systems has been quantitatively examined (Hendrix et al., 1986; Neely et al., 1991; Beare et al., 1992, 1993; Beare,

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1997). At this site, the proportion of the microbial biomass composed of fungi is greater in NT compared with CT soil (Beare, 1997). Since it is not known whether this pattern is generalizable to other NT and CT systems, our primary objective was to determine the effects of NT and CT management on the relative amounts of bacterial and fungal biomass at sites representing a wide range of climatic conditions.

Our second objective was to examine potential controls on microbial community composition. Several hypotheses have been proposed to explain tillage treatment differences in relative bacterial and fungal abundance. Fungi may be favored in NT systems because (1) reduced disturbance in NT facilitates establishment and maintenance of extensive hyphal networks (Wardle, 1995), (2) fungi, with their mycelial growth form, can bridge the soil–residue interface and utilize the spatially separated C and N resources by translocating N from the soil inorganic N pool into the C-rich surface residues (Holland and Coleman, 1987; Beare et al., 1992), and (3) fungi, unlike bacteria, can maintain activity in the dry surface litter environment encountered in NT systems (Hendrix et al., 1986; Holland and Coleman, 1987; Beare et al., 1992). These hypotheses remain largely untested.

We have examined correlations between several soil physical and chemical characteristics and relative bacterial and fungal biomass. In particular, our goal was to assess the relationship between climate- and tillage-controlled soil moisture and the degree of fungal dominance. To address our objectives we collected soil samples from six long-term tillage comparison experiments for which average soil moisture varies within each experimental site as a function of tillage treatment and across sites due to geographic differences in annual temperature and precipitation patterns.

2. Materials and methods

2.1. Site characteristics

Soil and surface residue samples were collected from NT and CT plots at six long-term field experiments in May and June, 1996 (Table 1). Four sites located in the Great Plains (Mandan, ND; Sidney, NE; Stratton, CO; and Bushland, TX) represent a temperature gradient. Mean annual precipitation is relatively constant (380–473 mm) across these sites while mean annual temperature ranges from 5.0°C at Mandan, ND, to 12.7°C at Bushland, TX. Annual open pan evaporation ranges from 940 mm at Mandan, ND, to 1762 mm at Bushland, TX. An additional two experiments were sampled at sites located on tallgrass prairie (Manhattan, KS) and forest-derived (Lexington, KY) soils. These two sites, along with Bushland, TX, represent a precipitation gradient. Mean annual temperature at these three sites is similar (~13°C) but mean annual precipitation varies from 473 mm at Bushland, TX, to 1140 mm at Lexington, KY. Our sampling schedule was such that each site was sampled at a similar time in the growing season.

Tillage treatments at all sites, except Stratton, CO, are arranged in a randomized complete block design with three to four replications. At Stratton, CO, conventional tillage is not included as a treatment in the experiment; therefore, samples were collected from an adjacent farmer's field that has been under continuous CT cultivation for at least 50 y. There are two replications at this site. Wheat-fallow rotations were sampled at each of the Great Plains sites, while soybean-wheat and continuous corn rotations were sampled at Manhattan, KS, and Lexington, KY, respectively. All samples were collected in the fallow phase of the rotation except at Manhattan, KS, and Lexington, KY, where cropping is continuous. In the latter two cases, samples were collected in newly planted plots. At

Table 1
Site characteristics

Site	Experiment duration (y)	Previous management	Soil classification	MAP[a] (mm)	MAT (°C)	OPE (mm)	Sampling date (1996)
Mandan, ND[b]	12	>60 y CT wheat-fallow[c]	fine-loamy, mixed, Typic Argiborolls	402	5.0	940[d]	June 24
Sidney, NE[e]	26	uncultivated native sod	fine-silty, mixed, mesic Pachic Haplustoll	380	8.5	1120[d]	June 17
Stratton, CO[f]	11	50+ y CT wheat-fallow	fine-silty, mixed, mesic Aridic Argiustoll	410	10.7	1270	June 3
Bushland, TX[g]	15	30+ y CT wheat-fallow	fine, mixed, thermic Torrertic Paleustoll	473	12.7	1762	May 13
Manhattan, KS[h]	22	60+ y CT annual cropping	fine-silty, mixed, mesic Cumulic Haplustoll	835	12.8	1200[d]	May 20
Lexington, KY[i]	26	50 y bluegrass sod	fine, mixed, mesic Typic Paleudalfs	1140	13.0	899[j]	June 10

[a] Abbreviations: MAP = mean annual precipitation, MAT = mean annual temperature, OPE = open pan evaporation for the growing season, April–September. [b]Site information obtained from Black and Tanaka (1997). [c]Ardell Halvorson (pers. comm.). [d]Data obtained from the National Climate Data Center database. [e]Site information obtained from Lyon et al. (1997). [f]Site information obtained from Peterson and Westfall (1997). [g]Site information obtained from Jones et al. (1997). [h]Site information obtained from Havlin and Kissel (1997). [i]Site information obtained from Frye and Blevins (1997). [j]Data obtained from Farnsworth and Thompson (1982).

Manhattan, KS, soybeans had not germinated at the time of sampling. At Lexington, KY, the corn plants in sampled plots were approximately 2 weeks old. Additional information regarding management history and current management practices at these sites can be found in the references listed in Table 1.

2.2. Sample collection and processing

Six 5.6 cm dia soil cores were collected from each treatment replicate and divided into 0–5 and 5–20 cm depth increments. In addition to soil samples, surface residues were collected from each NT plot. All samples were transported to the laboratory on ice and subsequently stored at 4°C for no longer than 72 h prior to analysis. Soil cores for each treatment replicate were composited by depth increment, gently broken apart, sieved (8 mm), thoroughly mixed and subsampled for soil water content determined gravimetrically by drying for 24 h at 105°C. A 500 g subsample was taken and used for the microbiological analyses described below. The remainder of the soil was immediately air dried. No-tillage surface residue samples were placed on a 250 μm sieve to facilitate removal of unassociated soil particles. Large rocks and soil aggregates remaining on the sieve were removed by hand.

2.3. Physical and chemical analyses

Physical and chemical analyses were conducted on air-dried samples from which crop residues, root fragments and rocks larger than 2 mm had been removed. Total organic C (TOC) and N (TON) were determined on finely ground subsamples using a Leco CHN-1000 analyzer. Soil pH was determined in a 2:1 water:soil (vol/wt) suspension. Texture and particulate organic matter C and N (POM-C and N) were determined by a modified version of the POM isolation method of Cambardella and Elliott (1992). Briefly, 30 g soil was dispersed by shaking for 18 h in 100 ml 0.5% sodium hexametaphosphate. This suspension was passed through a 53 μm sieve and the sand plus POM fraction remaining on the sieve was thoroughly rinsed with deionized water, dried at 50°C, finely ground, and analyzed for total C and N as described above. The soil suspension that passed through the sieve (silt plus clay) was transferred to a 1 l sedimentation cylinder and the silt and clay contents were determined by the hydrometer method (Gee and Bauder, 1986). Soil physical characteristics are given in Table 2.

The size distribution of water-stable aggregates was measured according to the method described by Cambardella and Elliott (1993). Briefly, a 100 g

Table 2
Soil physical characteristics

	Depth increment									
	0–5 cm					5–20 cm				
Site[a]	sand content (g kg^{-1})	clay content (g kg^{-1})	pH	water content (g g^{-1})	MWD[b] (mm)	sand content (g kg^{-1})	clay content (g kg^{-1})	pH	water content (g g^{-1})	MWD (mm)
Mandan, ND										
NT	180	260	6.2	0.23	0.29	180	280	6.3	0.23	0.29
CT	200	280	6.2	0.20	0.23	190	310	6.4	0.23	0.32
Sidney, NE										
NT	150*	310*	6.5*	0.31*	0.49*	350	210	7.0	0.23*	0.54*
CT	360	210	6.8	0.16	0.32	370	210	6.8	0.20	0.32
Stratton, CO										
NT	220	330	7.4*	0.27*	0.22	190	360	7.9	0.26*	0.37
CT	280	240	8.1	0.19	0.26	270	260	8.3	0.22	0.35
Bushland, TX										
NT	170	330	5.6	0.06	0.25	140	380	6.5	0.18*	0.40
CT	170	310	5.8	0.05	0.20	140	380	6.6	0.15	0.36
Manhattan, KS										
NT	60	210	5.2	0.23*	0.28*	50	270	5.5	0.22	0.24
CT	60	210	5.2	0.14	0.16	50	260	5.6	0.21	0.22
Lexington, KY										
NT	80	300	6.1	0.34*	1.86*	80	310	6.6	0.28*	1.03*
CT	70	320	6.0	0.23	0.61	70	320	6.3	0.25	0.66

[a] The sites are listed according to the climatic gradient along which they are located, with Mandan, ND, Sidney, NE, Stratton, CO, and Bushland, TX, located along the north–south temperature gradient and Bushland, TX, Manhattan, KS, and Lexington, KY, located from west to east along the precipitation gradient. [b]MWD = mean weight diameter of water-stable aggregates. *Treatment means within a site and depth increment are significantly different at the 0.05 probability level.

subsample of air-dried soil was wet sieved through a series of three sieves to obtain the following aggregate size fractions: >2000 μm, 250–2000 μm, 53–250 μm and <53 μm. Soil remaining on each sieve was backwashed into an aluminum pan, dried overnight at 50°C, and weighed. The amount of soil in each aggregate size class was used to calculate the mean weight diameter (MWD) for each treatment replicate and depth increment (Kemper and Rosenau, 1986). MWD was used as an aggregation index for comparison across treatments.

2.4. Bacterial and fungal abundance and biomass

Bacterial abundance and fungal hyphal lengths were determined on field moist subsamples from each treatment replicate and depth increment. Ten g soil was suspended in 90 ml filter (0.2 μm) sterilized water and blended in a Waring blender at high speed for 1 min (Babiuk and Paul, 1970). The blended suspension was allowed to settle for 30 s and a 10 ml subsample was collected and used to prepare dilutions. Two sets of soil smears, one each for bacterial and fungal staining, were prepared by pipetting 10 μl of the appropriate soil dilution (1:50 or 1:100) onto microscope slides containing 6 mm dia wells. The smears were thoroughly air-dried and heat-fixed prior to staining. Residue samples were treated similarly except that 0.5 g residue material was blended in 100 ml of filter sterilized water. After blending, 10 μl of this suspension was pipetted directly into a well on a microscope slide and dried.

Bacteria were counted from soil smears stained with DTAF (5-(4, 6-dichlorotriazin-2-yl)aminofluorescein) (Bloem et al., 1995). The smears were observed under a Zeiss Axiophot epifluorescence microscope at 1000× magnification using a Zeiss filter set for blue light (BP 450–490 nm exciter filter, 510 nm beam splitter and LP 520 nm barrier filter). Bacteria were manually counted from images of each microscope field that were captured using an Optronics cooled CCD camera (model DEI-470) and Adobe Photoshop image capturing software. Camera resolution was 470 TV lines horizontal and 450 TV lines vertical (PAL). Five to 20 images were randomly collected from each smear, depending on the number of cells observed in each image. In no case were fewer than 200 individual cells enumerated. Widths and lengths of individual cells, in pixels, were manually measured on a random subset of the collected images using the mouse and IPLab Spectrum image analysis software (Signal Analytics Corporation, Vienna, VA). The number of pixels for each width or length measurement was converted to μm using a conversion factor obtained from measurements of an image of a stage micrometer. Twenty to 30 cells were measured for each treatment replicate and depth increment for a total of 1557 cell measurements. Bacterial biovolumes per cell (V) were calculated from average widths (W) and lengths (L) using the equation $V = \pi/4 \times W^2 \times (L - W/3)$ (Bloem et al., 1995). There were no significant differences in bacterial biovolume across treatment or depth within a site; however, biovolume did vary across sites. The following biovolume values were used for conversion of bacterial abundance to biomass: Mandan, 0.30 μm^3; Sidney, 0.28 μm^3; Stratton, 0.25 μm^3; Bushland, 0.16 μm^3; Manhattan, 0.24 μm^3; Lexington, 0.20 μm^3. Bacterial biomass C was estimated by assuming a specific carbon content of 0.22 mg C cm^{-3} (Bratbak and Dundas, 1984).

Fungal hyphae were stained with calcifluor M2R fluorescence brightener (Bloem et al., 1995) and observed at 400× magnification using the filter set for UV illumination (BP 340–380 nm exciter filter, 400 nm beam splitter and LP 430 nm barrier filter). Thirty images were randomly collected from each smear. In a preliminary experiment, we found that collection of 30 images was necessary to obtain acceptable levels of variability in the estimation of fungal hyphal length from a given soil smear (Fig. 1). Fungal hyphal lengths and widths were measured as described for bacteria. The image analysis software used allows for measurement of irregularly shaped objects. Fungal hyphae, which are often curved, were measured by outlining the entire hyphal length using the mouse. There were no significant differences in hyphal width across treatment or depth, but hyphal width did vary across sites. The following width values were used for conversion of fungal length to biovolume: Mandan, 1.49 μm;

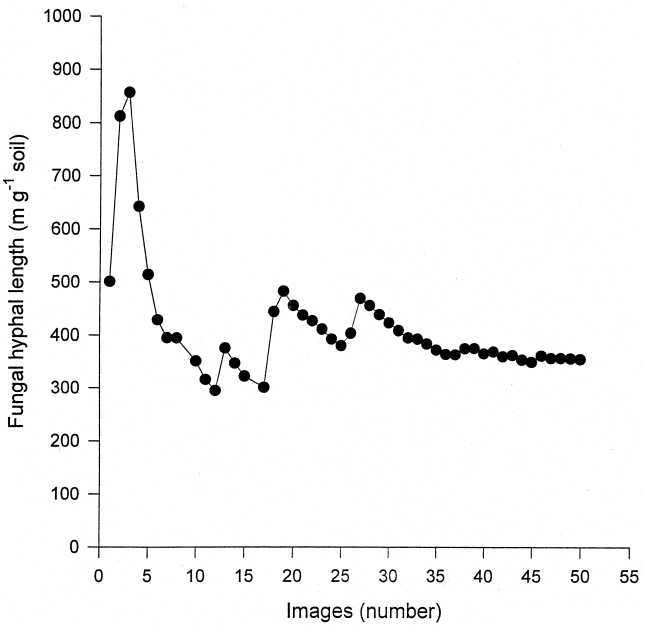

Fig. 1. Fungal abundance as a function of the number of microscope fields from which fungal hyphal length measurements were made.

Sidney, 1.27 μm; Stratton, 1.48 μm; Bushland, 1.20 μm; Manhattan, 1.27 μm; Lexington, 1.58 μm. Fungal biomass C was estimated by multiplying biovolumes by 0.33 g cm^{-3} and assuming 40% C (van Veen and Paul, 1979). Our biomass estimates represent total fungal biomass as calcifluor does not differentiate between empty and cytoplasm-filled hyphae.

2.5. Statistical analyses

Analysis of variance for determining tillage effects on soil physical, chemical and microbiological characteristics was performed using the SAS general linear models procedure (PROC GLM, SAS Institute, 1990). Analysis of covariance was performed with soil moisture as the covariate to examine whether soil moisture could explain observed tillage differences in fungal biomass and relative fungal abundance. The assumption of analysis of covariance, that the slope of the covariate by independent variable was the same for all levels of the independent variable, was verified by testing for heterogeneity of slopes (Cody and Smith, 1997). All abundance and biomass data were log transformed and proportions were arcsine-square-root transformed prior to analysis in order to meet normality and homogeneity of variance assumptions for ANOVA and ANCOVA (Sokal and Rohlf, 1981). The SAS correlation procedure was used for determining correlation coefficients among soil physical, chemical and microbiological properties. Linear and curvilinear regressions and coefficients of determination (r^2) were computed using SigmaPlot for Windows 1.02 (Jandel Scientific).

3. Results and discussion

3.1. Soil physical and chemical characteristics

Intact soil cores were collected for bulk density measurements since it is often preferable to express soil C and N fractions and water content on a volumetric basis. However, it was often difficult to get intact cores in recently plowed CT plots and at sites, particularly Bushland, TX, where the surface soil was dry. Therefore, we were unable to obtain accurate bulk density values for all treatment replicates. By making volumetric calculations for the sites where intact cores were collected, we found that expression of the data on a volumetric basis did not significantly change our results. Therefore, all C and N data are expressed on a concentration basis. Likewise, gravimetric water content is reported rather than volumetric water content or % water-filled pore space.

The extent to which soil water content at the time of sampling reflected across-site differences in mean annual temperature and precipitation depended on the gradient along which the sites were located (Tables 1 and 2). Soil water content at 0–5 cm for sites located along the precipitation gradient was positively related to mean annual precipitation ($r = 0.90$, $n = 18$, $P < 0.001$) and negatively related to annual open pan evaporation ($r = -0.89$, $n = 18$, $P < 0.001$). Soil water content across the temperature gradient was negatively related to mean annual temperature ($r = -0.61$, $n = 22$, $P < 0.001$) and open pan evaporation ($r = -0.79$, $n = 22$, $P < 0.001$). Soil moisture was significantly higher in NT compared to CT at four of six sites for the 0–5 cm depth increment. Treatment and across-site differences for the 5–20 cm depth increment were less pronounced.

Although NT systems generally show higher amounts of SOM (Doran, 1980, 1987; Paustian et al., 1997) and aggregate stability (Cambardella and Elliott, 1993; Beare et al., 1994), only three of the six sites showed treatment differences for these soil characteristics (Tables 2 and 3). No-till soil at the Sidney, NE, Manhattan, KS, and Lexington, KY, sites had significantly higher TOC and N, POM-C and N and MWD of water-stable aggregates compared to CT. Greater accumulations of microbial aminosugars (muramic acid and glucosamine) have also been observed in NT soil for these three sites (Guggenberger, personal communication). Most treatment differences were observed in the top 0–5 cm. Total organic C and N showed the greatest differences at Sidney, NE, and Lexington, KY, sites which were uncultivated prior to experiment establishment. The Nebraska site was established on virgin prairie sod, while the Kentucky site had been in bluegrass sod for at least 50 y. Our results are consistent with previous studies at these sites (Doran, 1980, 1987).

Few significant treatment differences were observed at either depth increment at the Mandan, ND, Stratton, CO, and Bushland, TX, sites. These sites were established on previously cultivated and highly degraded soil. Soil organic matter accumulation coupled with a reduction in further SOM losses in the NT plots would be necessary for the development of observable treatment differences under such soil conditions. Several factors may limit SOM accumulation at these Great Plains sites. Since NT was implemented 12–15 y prior to our sampling, as opposed to the 22–26 y for the other sites, there has been less time for significant accumulation to occur. Additionally, and perhaps most importantly, C inputs are low in wheat-fallow systems, particularly in low rainfall areas (Peterson et al., 1998) and decomposition rates, while potentially water-limited during the summer, can be high during the warm, moist spring (Coleman et al., 1990).

Table 3
Total organic and particulate organic matter (POM) C and N (g kg^{-1} soil)

	Depth increment							
	0–5 cm				5–20 cm			
Site	total organic C	total organic N	POM-C	POM-N	total organic C	total organic N	POM-C	POM-N
Mandan, ND								
NT	19.5	2.00	2.55	0.19	18.3*	1.77*	0.98	0.08
CT	22.1	2.00	2.63	0.18	21.5	2.07	1.29	0.08
Sidney, NE								
NT	23.0*	2.33*	4.36*	0.38*	13.1	1.40	1.06	0.12
CT	12.7	1.33	1.42	0.12	13.0	1.33	1.29	0.10
Stratton, CO								
NT	10.5	1.10	2.66	0.19	8.1	0.75	0.68*	0.05
CT	9.9	1.10	2.09	0.18	9.5	0.90	1.22	0.07
Bushland, TX								
NT	9.7	1.17	1.28	0.10	8.0	0.87	0.40	0.04
CT	10.1	1.07	1.32	0.09	8.8	1.00	0.50	0.04
Manhattan, KS								
NT	18.2*	1.87*	4.00*	0.33*	13.9	1.20	0.81	0.06
CT	11.7	1.17	2.27	0.17	11.7	1.17	1.08	0.08
Lexington, KY								
NT	24.9*	2.73*	3.19*	0.21*	13.8	1.60	1.55	0.11
CT	12.1	1.20	1.74	0.13	12.4	1.47	1.61	0.12

*Treatment means within a site and depth increment are significantly different at the 0.05 probability level.

3.2. Bacterial and fungal abundance and biomass

Bacterial abundance for the 0–5 cm depth increment ranged from $5.6 \times 10^8 \pm 1.4 \times 10^7$ bacteria g^{-1} soil in NT at Bushland, TX, to $1.6 \times 10^9 \pm 1.4 \times 10^8$ bacteria g^{-1} soil in NT at Manhattan, KS. There were no significant treatment differences at four of the six sites (Fig. 2A). Bacterial abundance was significantly higher in NT relative to CT at Sidney, NE, and Manhattan, KS. There was a trend of increasing bacterial abundance in CT relative to NT at 5–20 cm for the four Great Plains sites (Fig. 2B); however, these differences were only significant at the Mandan, ND, and Stratton, CO, sites. This trend was not altogether unexpected since we frequently observed a concentration of crop residues at 10–20 cm while sampling. This observation is supported by the trend toward increased amounts of POM-C in CT compared to NT at 5–20 cm (Table 3).

Fungal abundance in surface soil (0–5 cm) was significantly higher in NT than in CT at all sites (Fig. 2C). Fungal hyphal length in NT ranged from 46 m g^{-1} soil at Bushland, TX, to 292 m g^{-1} soil at Lexington, KY, and was 1.9–2.5 times greater in NT relative to CT across all sites. Hyphal lengths in CT ranged from a low of 19 m g^{-1} soil at Bushland, TX, to a high of 128 m g^{-1} soil at Lexington, KY. When we compared sites located along the temperature gradient, we observed that fungal hyphal length in NT increased from 72 m g^{-1} soil at Mandan, ND, the coldest site on average, to 203 m g^{-1} soil at Stratton, CO, and declined to a low of 46 m g^{-1} soil at Bushland, TX, the warmest site. Fungal abundance in surface soil at sites along the precipitation gradient increased from the dryest (Bushland, TX) to wettest (Lexington, KY) site. Fungal abundance in CT followed the same patterns, although the trends were less pronounced. No significant treatment differences in fungal hyphal length at 5–20 cm were observed; however, the across-site trends discussed above for the 0–5 cm depth were also evident at the lower depth (Fig. 2D). Our fungal abundance estimates are well within the wide range of 3.0 to 500 m g^{-1} soil reported for other intensively cultivated systems (Holland and Coleman, 1987; Gupta and Germida, 1988; Beare et al., 1993). An even wider range is obtained if the bacterially-dominated polder soils of The Netherlands (Brussaard et al., 1990; Bloem et al., 1994) and the fungally-dominated forest-derived soils from Sweden (Schnürer et al., 1985, 1986) are considered.

Fungi were more strongly influenced by tillage than were bacteria in our study. These results are in contrast to previous studies where abundances of both bacteria and fungi in surface soil (0–7.5 cm) were observed to be higher in NT compared to CT (Doran, 1980; Linn and Doran, 1984), but are in agreement with the idea that fungi are more susceptible than are bacteria to disturbance caused by plowing (Wardle, 1995). Holland and Coleman (1987) observed significantly higher fungal hyphal lengths in the surface

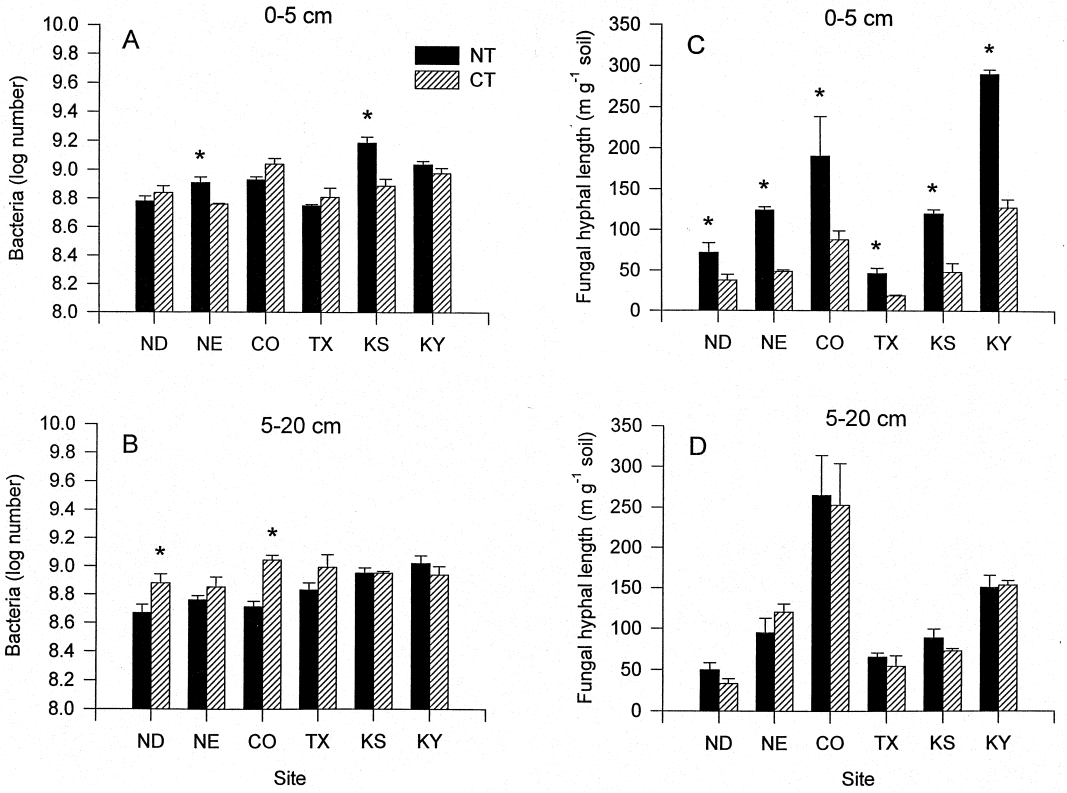

Fig. 2. Average abundances for bacteria (A and B) and fungi (C and D) in the 0–5 cm and 5–20 cm depth increment, respectively. Site abbreviations are: ND = Mandan, ND; NE = Sidney, NE; CO = Stratton, CO; TX = Bushland, TX; KS = Manhattan, KS; KY = Lexington, KY. Sites are arranged according to their location along gradients of increasing temperature (ND to TX) and precipitation (TX to KY). An asterisk indicates a statistically significant difference ($P < 0.05$) between tillage treatments within a site and depth increment. Bars represent standard errors.

0–5 cm of plowed soil when wheat residues were surface applied rather than directly incorporated into the soil, suggesting that higher fungal biomass in NT systems is related to the presence of surface residues.

To examine the relative contributions of bacteria and fungi to the microbial community, it was necessary to convert the abundance data to biomass. Since there were no significant differences in bacterial biovolumes and fungal widths between treatments within a site, absolute amounts of bacterial and fungal biomass C followed the same trends as the abundance data, except that across-site differences were more pronounced (Table 4). Bacterial biomass C was significantly higher in NT compared to CT at only two sites (Sidney, NE, and Manhattan, KS) for the 0–5 cm depth increment. Fungal biomass C was significantly higher in NT compared to CT in surface soil for all sites. Total microbial biomass C (bacteria + fungi) in surface soil showed treatment differences at three of the six sites (Sidney, NE; Manhattan, KS; Lexington, KY), the same sites that showed treatment differences in TOC and N, POM-C and N and in MWD of water stable aggregates (Tables 2 and 3). Total biomass was not significantly higher in NT at three of the Great Plains sites (ND, CO, TX) because significant differences in fungal biomass were offset by increases in bacterial biomass in CT. No significant treatment differences in total microbial biomass C were observed for the 5–20 cm depth increment at any of the sites.

The amount of microbial biomass present in a system is often related to SOM contents (Schnürer et al., 1985; Wardle, 1992). Changes in microbial biomass may also be indicative of future changes in amounts of SOM since the microbial community responds rapidly to disturbance or altered residue inputs (Gupta et al., 1994). In our study, total microbial biomass was higher in NT compared to CT only at those sites showing significantly higher SOM levels under NT; however, fungal biomass responded positively to NT management at all sites, suggesting that the fungal component of the microbial biomass may be a sensitive indicator of long-term change in these systems.

The relative contributions of bacteria and fungi to the total microbial biomass were significantly influenced by tillage (Fig. 3), especially at 0–5 cm. Fungal biomass made up a significantly higher proportion of the total biomass in surface soil of NT compared to CT at five of six sites even though bacterial biomass was greater than fungal biomass under both tillage treatments in most cases (Fig. 3A). Our data agree

Table 4
Bacterial, fungal and total microbial biomass C

	Microbial biomass C (μg C g^{-1} soil)					
	0–5 cm			5–20 cm		
Site	bacteria	fungi	total biomass[a]	bacteria	fungi	total biomass
Mandan, ND						
NT	39.7	16.3*	56.0	31.5*	11.3	42.8
CT	44.8	8.5	54.9	50.9	7.5	58.4
Sidney, NE						
NT	50.8*	20.4*	71.2*	35.3	15.7	50.9
CT	35.5	8.0	43.5	45.1	19.8	64.9
Stratton, CO						
NT	46.6	42.5*	89.1	28.5*	59.3	87.7
CT	60.2	19.6	79.8	60.3	56.7	117.0
Bushland, TX						
NT	19.9	6.8*	26.7	24.3	9.7	34.0
CT	23.4	2.8	26.2	35.9	8.0	43.9
Manhattan, KS						
NT	82.6*	19.8*	102.0*	47.1	14.7	61.8
CT	41.2	7.9	49.1	47.6	12.1	59.7
Lexington, KY						
NT	48.3	74.3*	123.0*	47.2	38.9	86.1
CT	42.2	32.7	74.9	39.4	39.6	78.9

[a] Total microbial biomass is calculated here as bacterial biomass C plus fungal biomass C.*Treatment means within a site and depth increment are significantly different at the 0.05 probability level.

with the work of Beare et al. (1992) and Beare (1997) who observed higher fungal to bacterial ratios in NT compared to CT residues and soil at their site in Horseshoe Bend, GA. Our results indicate that fungi are a relatively more important component of the microbial biomass in NT compared to CT surface soil across a wide range of climates.

In general, proportional fungal biomass, when calculated over the whole plow layer (0–20 cm), was higher in NT compared to CT (data not shown). However, most significant treatment differences in fungal biomass and proportional fungal biomass were observed in the 0–5 cm depth (Figs. 2 and 3). Thus a shift in microbial community composition in NT systems will be most critical for residue decomposition and nutrient cycling processes occurring near the soil surface.

Expressed as a percentage of TOC, total microbial biomass (bacterial + fungal C) ranged from 0.3 to 0.8%. There were no differences between CT and NT soils for this variable. The observed values are at the low end of the range of 0.3 to 3.1% reported for bacterial and fungal biomass estimates made by direct counts (Schnürer et al., 1985; Paustian et al., 1990; Bloem et al., 1994) and are lower than most estimates using microbial biomass C values as measured by chloroform-fumigation methods (Hassink et al., 1991; Gupta et al., 1994). Discrepancies between the two methods for microbial biomass estimation have been reported (Holland and Coleman, 1987; Ingham and Horton, 1987; Bloem et al., 1994). In particular, microbial biomass C estimates obtained by chloroform fumigation are often significantly higher than those obtained by direct microscopic enumeration.

While chloroform fumigation methods may result in overestimation of microbial biomass C (Ingham and Horton, 1987; Bloem et al., 1994), direct count methods may give underestimates. Reasons cited for this underestimation include (1) masking of microbes, especially bacteria, by soil particles, (2) weakly stained bacterial cells and non-fluorescent hyphae (Scheu and Parkinson, 1994), (3) difficulty in detaching microorganisms, especially fungi, from plant residues, and (4) inaccurately assumed or measured biovolumes. Additionally, a wide range of factors are reported for conversion of biovolume to biomass, especially for bacteria. To minimize these problems, we made tests to determine the amount of dilution required to minimize masking and maximize cell counts. We also made careful biovolume measurements rather than assume a literature value for all cells. Our bacterial biovolume (0.16–0.30 μm^3) and hyphal width (1.20–1.49 μm) estimates appear reasonable when compared with reported values. As for conversion factors, we selected the most widely used and accepted conversion factor for fungal biomass (van Veen and Paul, 1979) and selected an intermediate value from the published range for conversion of bacterial biovolume to biomass (Bratbak and Dundas, 1984). Although our direct count methods may have underestimated bacterial and fungal

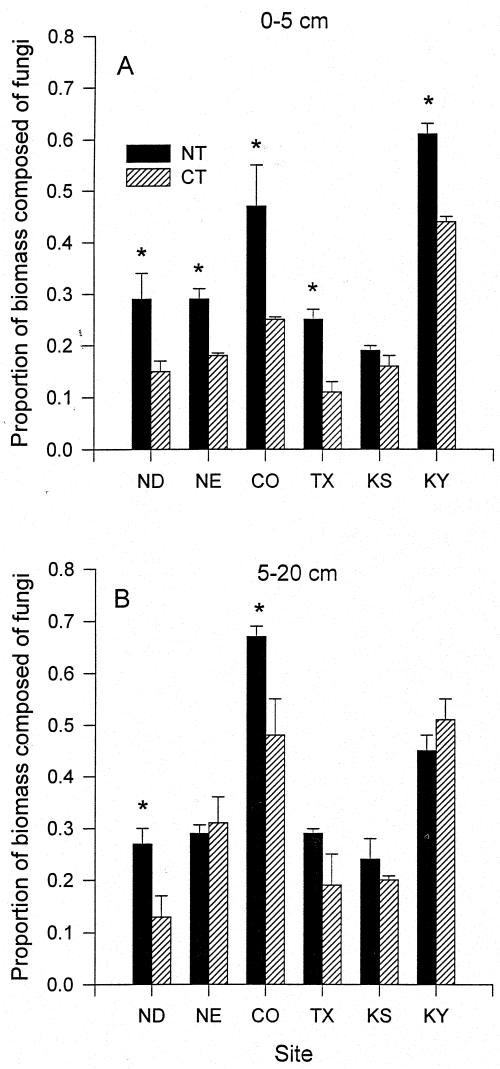

Fig. 3. The proportion of total microbial biomass C composed of fungi for the 0–5 cm (A) and 5–20 cm (B) depth increments. Abbreviations and symbols are as in Fig. 2.

biomass, the relative differences between treatments and sites were not affected.

3.3. Relationships among soil characteristics and bacterial and fungal biomass

Bacterial and fungal biomass in surface soil of NT and CT were not strongly related to soil texture or pH but were positively correlated with measured soil C and N fractions (Table 5). Cause and effect relationships are difficult to assess, however, since these fractions, like bacterial and fungal biomass C, were also positively related to soil water content with correlation coefficients of 0.74, 0.73, 0.71, and 0.64 for TOC, TON, POM-C and POM-N, respectively ($n = 34$, $P < 0.001$ for all comparisons). Mean weight diameter was significantly correlated with fungal biomass ($r = 0.66$, $P < 0.001$); however, this relationship was due to the high MWD values observed at the Lexington, KY, site. When the KY data were excluded from the analysis, this relationship was no longer significant ($r = 0.34$, $P > 0.05$). There were no significant correlations between sand, silt or clay content and soil moisture. Correlation analysis for the 5–20 cm depth increment is not presented since few differences in soil physical, chemical or microbiological characteristics were observed. Bacterial and fungal biomass and proportional fungal abundance associated with NT surface residues showed no significant correlations with residue or soil moisture (data not shown).

Table 5
Correlation coefficients among soil physical and chemical characteristics, bacterial biomass, fungal biomass, and the proportion of total biomass composed of fungi (%Fungi) for the 0–5 cm depth increment

Soil characteristic	Bacterial biomass C (μg g^{-1} soil)	Fungal biomass C (μg g^{-1} soil)	%Fungi
Sand (g kg^{-1})	NS	NS	NS
Silt (g kg^{-1})	0.42*	NS	NS
Clay (g kg^{-1})	–0.39*	NS	0.40*
pH	NS	NS	NS
Water content (g g^{-1} dry soil)	0.67***	0.85***	0.67***
Total organic C (mg g^{-1} soil)	0.44**	0.45**	NS
Total organic N (mg g^{-1} soil)	0.40**	0.51*	0.42*
POM C (mg g^{-1} soil)	0.65***	0.49**	NS
POM N (mg g^{-1} soil)	0.65***	0.41*	NS

*, **, ***Significant at the 0.05, 0.01, and 0.001 probability levels, respectively; NS = not significant.

Soil water content measured at the time of sampling accounted for the highest proportion of the variation in both bacterial and fungal biomass data (Table 5, Fig. 4A). Both bacterial and fungal biomass were positively related to water content. A curvilinear function best described the relationship for bacteria ($r^2 = 0.62$, $n = 34$, $P < 0.001$). Bacterial biomass increased linearly from water contents of 0.05 g g^{-1} dry soil to approximately 0.15 g g^{-1} dry soil and then remained relatively constant above that value. Fungal biomass was linearly related to soil moisture across the entire range of water contents measured ($r^2 = 0.72$, $n = 34$, $P < 0.001$). Due to the differential response of bacteria and fungi to soil moisture, proportional fungal abundance was curvilinearly related to soil moisture (Fig. 4B; $r^2 = 0.54$, $n = 34$, $P < 0.001$). Since bacterial and fungal biomass responded similarly to water contents below 0.15 g g^{-1} dry soil, proportional fungal abundance was not related to water content below this value. Above 0.15 g g^{-1} dry soil, however, fungi composed an increasing percentage of the total biomass as water content increased, ranging from approximately

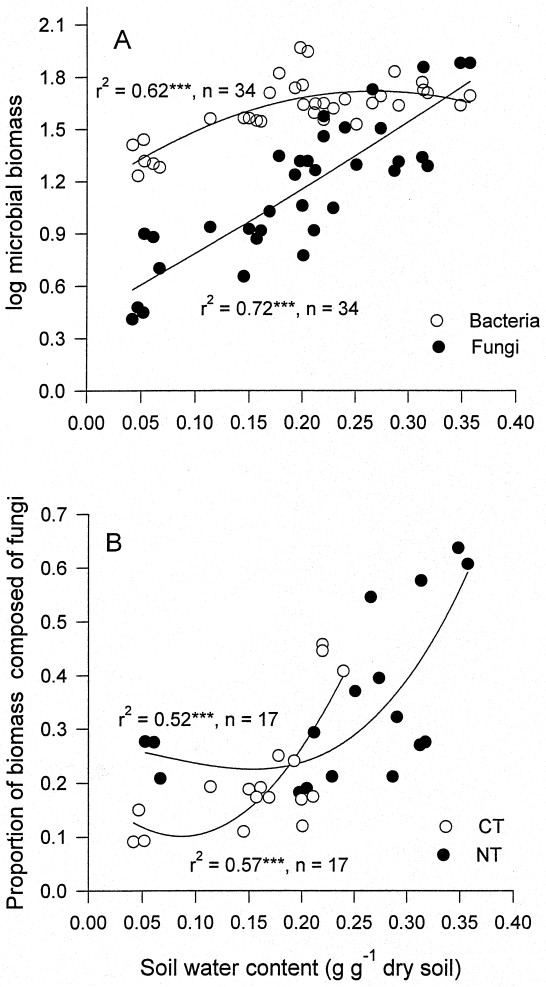

Fig. 4. Relationships between soil water content of the 0–5 cm depth increment and (A) bacterial and fungal biomass C and (B) the proportion of total microbial biomass composed of fungi; data from all sites, both tillage treatments (A only) and all field replicates are combined.

20% at 0.15 g g^{-1} dry soil to 60% at 0.35 g g^{-1} dry soil.

3.4. Soil moisture as a control on microbial community composition

Our results suggest that soil moisture may be an important control on microbial community structure, not only across sites varying in soil moisture as a result of varying precipitation and temperature regimes, but also between tillage treatments within a site. This idea is supported further by our examination of the data by analysis of covariance using soil moisture as the covariate (Sokal and Rohlf, 1981). This analysis allowed us to determine whether treatment differences in our measured dependent variables would exist if soil moisture were held constant across tillage treatments. When the data were adjusted for soil moisture, significant tillage treatment effects on fungal biomass and the proportion of the microbial biomass composed of fungi were not observed (Table 6). We also ran the covariance analysis of variance with MWD, TOC and POM-C as covariates and found that when the data were adjusted for these variables the tillage effects on fungal parameters were still significant (data not shown). These results lead us to hypothesize that treatment-induced differences in soil moisture account, at least in part, for the observed shifts in microbial community structure in NT agroecosystems.

Other hypotheses have been proposed to explain tillage treatment differences in microbial community composition. It has been suggested that fungi are relatively more abundant than bacteria in NT compared to CT systems because they are physiologically capable of growth and activity at much lower water potentials than are bacteria and thus have an advantage over bacteria in the dry environment encountered in NT surface residues (Hendrix et al., 1986; Holland and Coleman, 1987; Beare et al., 1992). This hypothesis, based on studies in which the responses of bacteria and fungi to drying have been examined (Griffin, 1972; Wilson and Griffin, 1975; Schnürer et al., 1986), predicts that the degree of fungal dominance in NT surface residues will be inversely related to soil moisture (Hendrix et al., 1986). While total microbial biomass tends to decline in response to drying (Wardle, 1992), there is often a differential effect of drying on the biomass and activity of bacteria and fungi. Griffin (1972, 1981) reviewed the data on microbial growth over a range of soil water potentials. Bacterial abundance and activity decline rapidly as soil water content falls below field capacity and bacterial respiration and bacterially mediated transformations are negligible at potentials below −1.5 MPa (Wilson and Griffin, 1975; Griffin, 1981). Many fungi are active at considerably lower water potentials. Schnürer et al. (1986) found that both bacterial numbers and active fungal hyphae

Table 6
Results of analysis of variance (ANOVA) and analysis of covariance (ANCOVA) showing the F value and level of significance for each variation source associated with total fungal biomass and the proportion of the total biomass composed of fungi (n = 34)

Analysis, dependent variable	Sources of variation[a]	
	tillage	moisture
ANOVA		
Total fungal biomass	8.97**	N/A
Fungi as proportion of total biomass	8.72**	N/A
ANCOVA with moisture as covariate		
Total fungal biomass	1.09 NS	59.78***
Fungi as proportion of total biomass	1.93 NS	16.78***

[a] N/A = not applicable, NS = not significant.** and *** indicate significance at the 0.01 and 0.001 probability level, respectively.

declined rapidly as a field soil dried; however, active hyphal dynamics paralleled O_2 consumption and thus the majority of microbial respiration was attributed to fungi.

The above explanation, though widely accepted, cannot account for the increased fungal abundance observed in NT soils. Firstly, previous studies have shown that fungi are the dominant decomposers of NT surface residues (Neely et al., 1991; Beare et al., 1992). However, we estimate, based on measurements of bacterial and fungal biomass on surface residues and average residue loading data obtained from long-term site records (Peterson et al., 1998), that bacterial and fungal biomass associated with NT surface residues represents less than 1% of the total microbial biomass present in the system to a soil depth of 20 cm. Therefore, relative fungal dominance in NT surface residues cannot explain the increased fungal abundance in NT systems as a whole. Secondly, our data do not support the prediction that relative fungal dominance is inversely related to soil moisture since we found no correlation between our residue biomass estimates and soil water content. Finally, if we applied to soil the argument that fungi have an advantage over bacteria under dry conditions, we would predict higher relative fungal abundance in CT rather than NT since CT soil, in general, is drier than adjacent NT soil where the presence of surface residues reduces evaporative water loss.

While many fungi are physiologically capable of growth under dry conditions that otherwise would limit bacterial activity, this trait does not explain our observation of increasing proportional fungal abundance with increasing soil moisture. Although bacteria and fungi have different low-end water potential limits for growth, most microorganisms attain maximum growth rates at or above −0.1 MPa and therefore under moister conditions, relative differences in bacteria and fungi are likely due to factors other than direct effects of water potential on growth, such as pH, aeration, nutrient availability and microbivory (Cook and Baker, 1983). In our study, fungal biomass increased linearly, while bacterial biomass was relatively constant across most of the observed range in soil water content. Schnürer et al. (1986) observed, in irrigated field plots kept continuously moist, that both bacterial and fungal biomass were relatively constant; however, observations of cell sizes and populations of grazers suggested that fungal growth was promoted to a greater degree than bacterial growth. Schnürer et al. (1986) suggested that bacteria become substrate limited under continuously moist conditions as available labile C sources are utilized, while fungi remain active by utilizing more recalcitrant SOM. Alternatively, the germination and proliferation of 'sugar fungi' may be promoted by the soluble compounds released when dry soil is wetted following an irrigation or precipitation event.

In summary, different agricultural tillage practices can strongly influence the abundance and biomass of soil microorganisms. In this study, fungal biomass and the proportion of the total biomass composed of fungi increased in surface soil in response to reduced tillage and across a gradient of increasing soil moisture, while bacterial biomass was not strongly affected by tillage and remained relatively constant in response to changing soil moisture above a water content of approximately 0.15 g g^{-1} dry soil. Soil moisture may differentially influence bacteria and fungi either by directly affecting survival and growth or indirectly through shifts in substrate availability or microbivore populations. We caution, however, that altering the tillage regime affects the soil environment in complex, interactive ways. No-till soils, in addition to being moister, tend to have higher SOM contents, higher bulk densities and lower temperatures. Further research, especially controlled experimentation, is needed to elucidate the role that tillage-induced changes in the soil environment play in shaping microbial community composition.

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