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Soil Food Webs and Carbon Dynamics in Response to Conservation Tillage in California

H. Minoshima
L.E. Jackson*
Dep. of Land, Air, and Water Resources
Univ. of California
Davis, CA 95616

T.R. Cavagnaro
School of Biological Sciences
Monash University
Clayton, Victoria
3800 Australia

S. Sánchez-Moreno
H. Ferris
Dep. of Nematology
Univ. of California
Davis, CA 95616

S.R. Temple
S. Goyal
J.P. Mitchell
Dep. of Plant Sciences
Univ. of California
Davis, CA 95616

Reducing disturbance by tillage and addition of crop residues affects soil biota and their role in soil C storage. For 1 yr in a field station trial in Davis, CA, these treatments were compared: no-tillage + continuous cropping, no-tillage + fallow, standard tillage + continuous cropping, and standard tillage + fallow. The continuous cropping treatment consisted of tomato (*Lycopersicon esculentum* Mill.)/sorghum–sudangrass [*Sorghum bicolor* (L.) Moench]/garbanzo (*Cicer arietinum* L.)/cowpea cover crop [*Vigna unguiculata* (L.) Walpers ssp. *unguiculata*]. The fallow rotation omitted the sorghum–sudangrass and cowpea cover crops. No-tillage + continuous cropping resulted in significant changes in the surface layer (0–5 cm): higher microbial biomass C, more fungi as indicated by ergosterol and phospholipid fatty acid analysis, and higher soil NO_3^- in summer, and higher pH, soluble K^+, and Olsen P at the end of the experiment. At lower depths (5–15 and 15–30 cm), few differences were observed. Total soil C (at 0–30 cm) was least with standard tillage + fallow, the typical management practice in the region. The soil food web, as indicated by the nematodes, did not become more complex with no-tillage + continuous cropping, contrary to expectations, possibly because higher trophic level nematodes had been eliminated after decades of cultivation. The bacterial decomposition pathway dominated the surface layer in all treatments, but, with no-tillage, opportunistic (colonizer-persistent Group 1) bacterial feeders greatly decreased with depth. Plant productivity, except for weeds, was reduced by no-tillage, especially in the garbanzo crop. By decreasing disturbance and increasing fungi, no-tillage + continuous cropping appears to have accelerated soil C storage but management alterations are needed to produce higher crop biomass in this Mediterranean-type climate.

Abbreviations: CA, correspondence analysis; cp, colonizer-persistent; MBC, microbial biomass carbon; PLFA, phospholipid fatty acid; SOM, soil organic matter; WFPS, water-filled pore space.

Recent concerns about global climate change have encouraged the development of agricultural systems that sequester soil C (Cole et al., 1997; Ogle et al., 2003). Sequestration of C is a function of the difference between C inputs, primarily from plant biomass, and C losses due to the activity of soil organisms; it is impacted by agricultural management. Loss of soil C in agricultural systems has been attributed primarily to oxidation following soil cultivation (Schlesinger, 1984). Agricultural systems that use no-tillage along with rotations that provide continuous C inputs via litter and root activity may be most likely to store soil C (Kay and VandenBygaart, 2002; Deen and Kataki, 2003; Carter, 2005; Puget and Lal, 2005). Specific groups of soil biota may be associated with an increase in soil C, particularly in the surface soil, where C accumulation occurs most rapidly in no-tillage systems (Six et al., 2006).

The *soil food web* refers to the community of organisms in the soil that are interdependent for sources of C and energy (Phillips et al., 2003). The ecological functions performed by the soil food web are determined by the identity, abundance, and interactions of its components (Ferris, 2005). Carbon enters soil food webs in the form of plant litter and root exudates (Coleman et al., 1976), and consumption and incorporation of plant-derived C by food web organisms leads, via biological transformation, to formation of molecules that are more resistant to degradation (Wardle et al., 2004).

Soil food webs are made up of a hierarchy of organisms spanning a range of taxa and trophic levels. The flow of C from plants and soil organic matter (SOM) into the soil food web is initiated by organisms at the entry level: microbiota (fungi and bacteria) and herbivores (plant-feeding nematodes and arthropods). At the next trophic level, microfauna (e.g., protozoa and some nematodes) and mesofauna (some microarthropods) consume the primary decomposers, which, in turn, are consumed by both specialist and generalist predators of the mesofauna (e.g., some nematodes and arthropods). Macrofauna may also play an important role in direct plant herbivory. Soil food webs dominated by organisms at the entry level tend to have greater C loss due to their rapid turnover and decomposition rates (Beare et al., 1992; Blagodatskaya and Anderson, 1998). Greater retention of C has been hypothesized to

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*Corresponding author (lejackson@ucdavis.edu).

occur when soil organisms at higher trophic levels are more abundant, due to greater C conserved in biomass, gradual transformation to more recalcitrant forms of C, and protection in smaller aggregate size fractions (Fu et al., 2000).

Different biota may contribute in different ways to soil C sequestration. Fungi have a higher C/N ratio than bacteria, produce compounds that are more degradation resistant (Kogel-Knabner, 2002), and increase aggregate formation, which physically protects and retains plant-derived C in the soil (Six et al., 2006). Quantifying bacterial and fungal communities or biomass in soil is successfully achieved by indicators, such as PLFA markers (Bossio et al., 1998, Drijber et al., 2000) or compounds such as ergosterol, which is thought to be mainly fungal derived (Djajakirana et al., 1996). In contrast, for higher trophic levels, significant advances have been made through study of multifunctional taxonomic groups. For example, soil nematodes are sufficiently abundant and functionally diverse to provide excellent indicators of food web structure and functioning (Bongers and Ferris, 1999; Ferris et al., 2001; Neher, 2001; Ferris, 2005).

Food web dynamics are complex and reflect the integration of many factors, including plant community composition (Viketoft et al., 2005), plant succession or crop sequence (Gunapala et al., 1998), edaphic conditions (Yeates, 1994), and soil management (Ferris et al., 2001). In highly disturbed soils, the soil food web typically consists almost exclusively of metabolically active primary decomposers and herbivores adapted to such conditions (Beare et al., 1992; Frey et al., 1999). Organisms at higher trophic levels are more sensitive to soil disturbance, compaction, frequent wet–dry cycles, pesticide application, and mineral fertilizers (Ferris et al., 2004; Berkelmans et al., 2003).

Lack of disturbance and reliable C inputs via continuous cropping are, thus, hypothesized to increase fungi, soil food web complexity, and the abundance of organisms at higher trophic levels, thus increasing the sequestration of soil C.

The objectives of this study were to compare the effects of disturbance, i.e., tillage vs. no-tillage, and crop rotation, i.e., continuous cropping vs. intermittent fallowing, on: (i) the size and composition of soil food webs; (ii) total soil C, microbial biomass C, inorganic N, and nutrients; and (iii) crop yields and weeds. A year-round legume–vegetable system in California was the context for this research.

MATERIALS AND METHODS

Field Site

This research was conducted in 2003 and 2004 in companion plots to the main experiment at the Long Term Research in Agricultural Systems site at the University of California Davis (ltras.ucdavis.edu/ [verified 9 Feb. 2007]). The plot area (0.5 ha) had been conventionally farmed for many decades, with oat (*Oryza sativa* L.)–hay crops, including the 2002/2003 season. The soil is classified as Rincon silty clay loam (fine, montmorillonitic, thermic Mollic Haploxeralf). Monthly average air temperatures were 9.2°C in winter 2003/2004 and 22.7 and 23.4°C in summer 2003 and 2004, respectively. Annual rainfall was 420 and 368 mm in 2003 and 2004, respectively. Rainfall only occurred from October 2003 through April 2004.

Tillage Regime and Crop Rotations

Two levels of tillage intensity, no-tillage and standard tillage, were used. For no-tillage plots, permanent beds were prepared in May 2003 and there were no further tillage operations for the duration of the experiment, except for the clearing of furrows in midsummer. All crop residues were flail-mowed and distributed on the bed tops. For standard tillage plots, crop residues were incorporated to the 20-cm depth and beds were shaped between each cropping season with the Sundance system (Sundance Farms, Coolidge, AZ), which consists of disks and lister bottoms. After disking, a ring roller was used to smooth the beds before planting.

In 2003, the continuous cropping treatment consisted of a late spring planting of tomato, a late summer planting of sorghum–sudangrass Sweeter-n-honey hybrid cover crop, and a late fall planting of garbanzo, a winter legume also known as chickpea, and in 2004, a summer planting of cowpea. This sequence included more crops and cover crops, more continuous plant cover, and more crop diversity than the typical 2-yr tomato/wheat (*Triticum aestivum* L.)–fallow rotation of the local region. The fallow rotation omitted the sorghum–sudangrass and cowpea cover crops. It consisted of tomato followed by garbanzo, with a fall and summer fallow. Of these crops, tomato and garbanzo were harvested, and sorghum–sudangrass and cowpea were used as cover crops.

The combination of rotation and tillage level provided four treatments: no-tillage + continuous cropping, no-tillage + fallow, standard tillage + continuous cropping, and standard tillage + fallow. The experiment was a randomized complete block design with three blocks, four plots per block, and three beds per plot. Each plot was 306 m^2 (67 m long and 4.57 m wide), i.e., three 152-cm (60″) wide beds.

Mineral fertilizers (112.0 kg P ha^{-1} as a starter fertilizer, 50.4 kg N, P, and K ha^{-1}, and 67.2 kg N ha^{-1} as sidedressings) were applied in the summer of 2003, before this experiment started. No fertilizers were applied during the experiment so as to evaluate responses of the systems to the nutrient demands and supplies of both cash and cover crops. Herbicide applications occurred in December 2003 (0.14 kg oxyfluorfen [2-chloro-1-(3-ethoxy-4-nitrophenoxy)-4-(trifluoromethyl)benzene]+ 1.1 kg pendimethalin [*N*-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine]) ha^{-1}) on all plots, and in June 2004 on the continuously cropped plots (2.7 kg pendimethalin ha^{-1}). Glyphosate [*N*-(phosphonomethyl)glycine] was applied with a backpack sprayer. In the standard tillage plots, weeds were cultivated in mid-March 2004. No-tillage plots were hand weeded in May and July 2004. Surface furrow irrigation occurred on 14 Apr. and 18 May 2004 for the garbanzo, and for the cowpea on 8, 9, and 29 July, 9, 17, and 25 Aug., and 5 and 16 Sept. 2004.

Plant Sampling and Analysis

Aboveground biomass was clipped from 2-m^2 plots in the sorghum–sudangrass cover crop, and from 1-m^2 plots in the garbanzo and cowpea crops, then separated into crop harvestable yield when appropriate. Weed aboveground biomass was collected from the same plots as the garbanzo samples.

Soil Sampling

Soil was sampled for biota and nutrients on December 2003, and June, September (only continuous cropping treatments), and December 2004. Soil cores were taken at randomly selected locations at 0 to 5, 5 to 15, and 15 to 30 cm from three points across the center bed of each of four plots in each block, and were stored on ice. Inorganic N (NO_3^- and NH_4^+) was extracted within 1 d. Soil samples for soil microbial biomass C (MBC) and nematodes were stored at 4°C and processed within 2 and 7 d after sampling, respectively (see below). Within 12 h, samples for soil ergosterol were stored at −20°C, as were samples for PLFA analysis on the last sampling date.

Table 1. Aboveground biomass of the sorghum–sudangrass cover crop, the garbanzo crop including beans, weeds at harvest of the garbanzo crop, and the cowpea cover crop, and garbanzo bean dry yields. Statistical comparisons were conducted on power transformed data, but non-transformed means and standard errors are provided.

Cropping and tillage system†	Sorghum–sudangrass cover crop	Garbanzo crop aboveground biomass	Weeds at harvest of garbanzo crop	Garbanzo bean dry yield	Cowpea cover crop	Sum of total plant biomass‡
	g dry wt. m^{-2}					
Harvest date	31 Oct. 2003	28 June 2004	28 June 2004	28 June 2004	7 Oct. 2004	
NTCC	116 ± 25 a§	121 ± 16 b	122 ± 42 a	25 ± 6 b	482 ± 30 b	840 ± 41 b
NTF		432 ± 47 a	33 ± 15 a	138 ± 11 a		464 ± 50 c
STCC	126 ± 6 a	486 ± 50 a	20 ± 14 a	193 ± 65 a	756 ± 22 a	1389 ± 56 a
STF		538 ± 130 a	108 ± 14 a	233 ± 87 a		646 ± 134 bc

† NT, no-tillage; ST, standard tillage; CC, continuous cropping; F, fallow.

‡ Garbanzo bean yields are not included in the summed total plant biomass.

§ Means ± SE. Means followed by the same letter are not significantly different at the $P < 0.05$ level.

Subsamples for analysis of bulk soil chemical properties were dried at 60°C for 2 to 3 d. Samples for bulk density were taken in February 2005 by gently tapping rings (8.2-cm diam.) of known volume into the soil, and measuring soil dry mass.

Soil Analysis

Duplicate subsamples from each soil sample (25 g moist soil) were analyzed for MBC by the fumigation extraction method (Vance et al., 1987). Soil samples (10 g moist soil) were extracted with 2 *M* KCl, and inorganic N content determined colorimetrically using a modification of Miranda et al. (2001) for NO_3^- (plus NO_2^-, which can generally be assumed to be negligible in these soils) and Forster (1995) for NH_4^+. Ergosterol, a fungal biomarker, was measured (2 g moist soil) using a modification (Cavagnaro et al., 2006) of the method of Djajakirana et al. (1996).

Phospholipid fatty acids were extracted from 5 g of moist soil according to the method of Bossio et al. (1998) and measured by gas chromatography. Total mass of PLFAs, an indicator of total microbial biomass, was compared with MBC data. The biomass of bacteria was determined using the combined weights of fatty acids *iso* 15:0, *anteiso* 15:0, 15:0, *iso* 16:0, 16:1ω5c, *iso* 17:0, *anteiso* 17:0, 17:0cy, 17:0, and 19:0cy. That of fungi was determined as the sum of 18:2ω 6 and 18:2ω 9c (Bossio et al., 1998; Mikola and Setala, 1998).

Nematodes were extracted from 350 g of soil using a combination of decanting and sieving and Baermann funnel methods (Barker, 1985). Nematodes were counted under a dissecting microscope, and a subsample (minimum of 100) was identified to the genus or family level at higher magnification. The actual abundance of each taxon was adjusted according to the total number of nematodes in the sample.

Nematode taxa were classified into four feeding habits (bacterial feeders, fungal feeders, plant feeders, and predators or omnivores) (Yeates et al., 1993), and into colonizer-persistent (cp) groups (Bongers, 1990). The cp scale classifies nematode families in five groups from cp1 (short life cycles, large number of eggs, resistant to environmental perturbation, r-strategists) to cp5 (long life cycles, low number of eggs, sensitive to environmental perturbation, k-strategists). The combination of both classifications results in 16 nematode functional guilds (Bongers and Bongers, 1998), not all of which were represented here.

Nematode faunal analysis, based on functional group abundances, generated indices of food web structure, status, function, and resource availability (Ferris, 2006; Ferris et al., 2001; Ferris and Matute, 2003). Values of the Enrichment Index, the Structure Index, the Channel Index, and the Basal Index were calculated as described by Ferris et al. (2001). To calculate food web indices and sizes of trophic and cp groups, nematode abundances were expressed on a soil mass basis by correcting for bulk density. Nematode biomass C was calculated by multiplying the abundance of each taxon by their calculated fresh weight (Andrássy, 1956), and conversion assuming 20% of wet weight is dry weight of nematodes (Persson et al., 1980) and that C content is 52% of dry weight (Persson, 1983).

Soil chemical analysis, soil total C, soil total N, soil pH, K, and plant-available Olsen P were determined by the DANR Analytical Laboratory, University of California, Davis. Briefly, total soil C and N were measured by combustion (Nelson and Sommers, 1982), soil K and pH were measured by the saturated paste method (Thomas, 1996; Soltanpour et al., 1982), and P was measured according to Olsen and Sommers (1982).

Statistical Analysis

The data other than PLFA profiles were subjected to analysis of variance according to the GLM procedures of SAS Version 9.1 (SAS Institute, Cary, NC). Means and interactions were separated by Tukey's multiple range test and significant effects were expressed at $P < 0.05$. For plant data, which was highly variable among plots within some treatments, statistical comparisons were conducted on power-transformed data, but untransformed means and standard errors are provided (Table 1). The PLFA data, expressed in moles, were analyzed using correspondence analysis (CA) and the first two principal components were used to express the total sample variance. The CANOCO 4.5 (Microcomputer Power, Ithaca, NY) software was used to generate biplots.

RESULTS

Aboveground Plant Biomass

Total aboveground plant biomass, including crop yields and weeds, serves as an indicator of the amount of C produced by each treatment throughout the study. Summed across all crops and cover crops, it was highest with the standard tillage + continuous cropping and lowest with no-tillage + fallow treatments (Table 1). The aboveground biomass production in the fallow treatments was approximately half that of the continuous cropping treatments. With continuous cropping, aboveground biomass was higher with standard tillage than no-tillage. Although the aboveground biomass of sorghum–sudangrass did not differ among treatments, garbanzo and cowpea aboveground biomass was higher with standard tillage than with no-tillage. In treatments with fallow periods, total aboveground plant biomass also tended to be higher with standard tillage.

Crop yields were much lower with no-tillage + continuous cropping than any of the other three treatments, which were not different from one another (Table 1). Garbanzo bean yields in no-

Table 2. Analysis of variance statistical significance of treatments, depth, and sampling date on soil microbial biomass C (MBC), ergosterol, and nematode number, biomass C, and various indices: Nematode Enrichment Index, Structure Index, Basal Index, and Channel Index are based on nematode number kg^{-1} dry soil for three sampling dates.

Parameter	Treatment	Depth	Date	Treatment × date	Treatment × depth	Depth × date	Treatment × depth × date
MBC, mg C kg^{-1} dry soil	***	***	***	NS	***	NS	*
Ergosterol, μg kg^{-1} dry soil	***	***	***	***	***	***	***
Nematode number kg^{-1} dry soil	***	***	***	NS	NS	NS	NS
Nematode biomass C, mg C kg^{-1} dry soil	NS†	***	***	NS	NS	NS	NS
Enrichment Index	**	***	***	NS	NS	NS	NS
Structure Index	**	NS	NS	NS	NS	NS	NS
Basal Index	*	***	***	NS	NS	NS	NS
Channel Index	***	***	***	NS	NS	NS	NS

* Statistically significant at $P < 0.05$.

** Statistically significant at $P < 0.01$.

*** Statistically significant at $P < 0.001$.

† NS = not statistically significant.

tillage + continuous cropping were 10 to 20% of the other treatments, probably due to high weed pressure in those plots. Cowpea aboveground biomass in no-tillage + continuous cropping was 60% of that in standard tillage + continuous cropping.

Microbial Biomass Carbon, Phospholipid Fatty Acids, and Soil Ergosterol

Soil MBC, expressed as milligrams of C per kilogram of dry soil, was different by treatment, depth, and sampling date, and also in the interactions between treatment and depth and between treatment, depth, and date (Table 2). Microbial biomass C was greatest in the 0- to 5-cm layer and decreased with soil depth among all treatments (Fig. 1A). In particular, differences in MBC between the 0- to 5-cm and lower layers were relatively large under no-tillage compared with standard tillage, and the difference between the layers was greatest with no-tillage + continuous cropping.

To show the impact of treatments on MBC during the entire period, MBC was expressed as grams of C per square meter at the end of the experiment in December 2004 (Fig. 2A). In the 0- to 5-cm layer, grams MBC per square meter was higher with no-tillage + continuous cropping than the other treatments. In contrast, below the 5-cm depth, MBC with

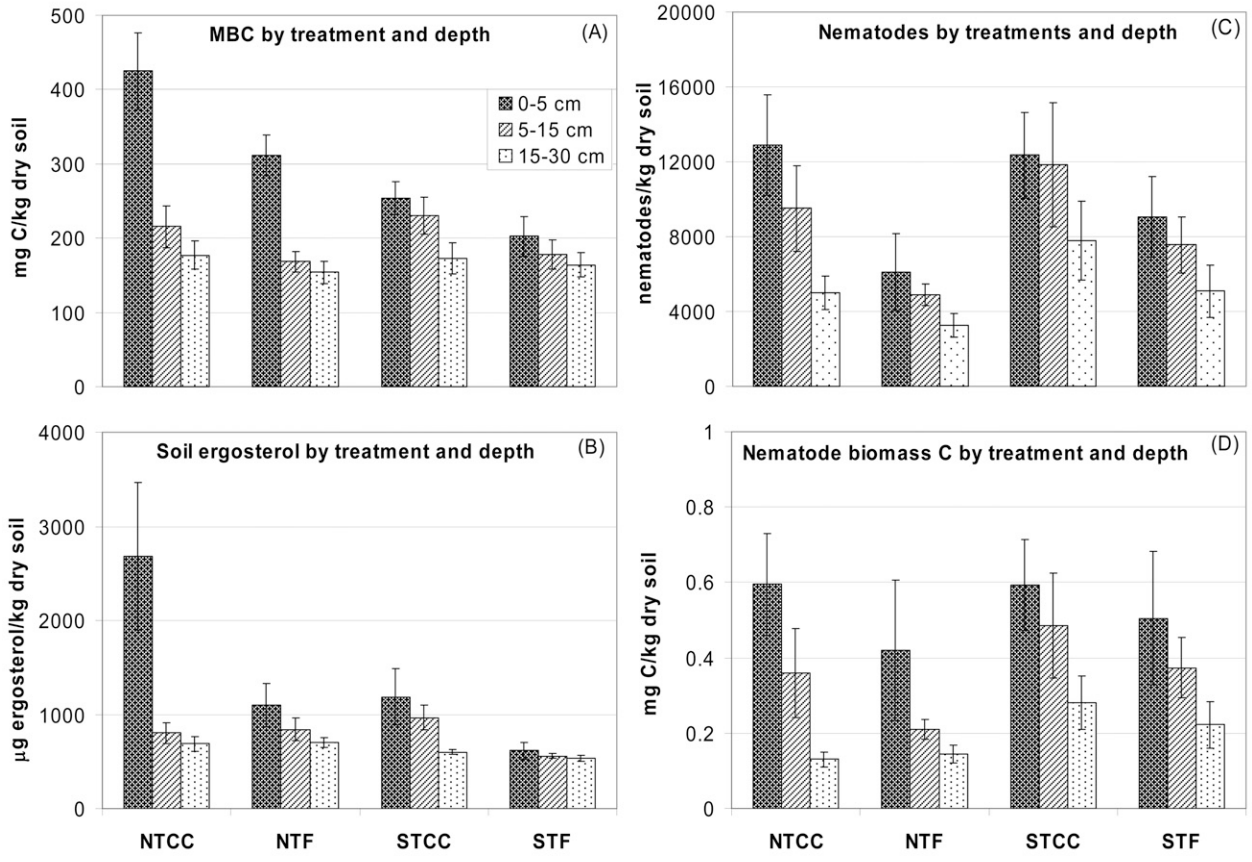

Fig. 1. (A) Soil microbial biomass C, (B) soil ergosterol, (C) nematodes kg^{-1} dry soil, and (D) nematode biomass C by treatment and depth across three sampling dates. NT = no-tillage; ST = standard tillage; CC = continuous cropping; and F = fallow. Data are means ± SE.

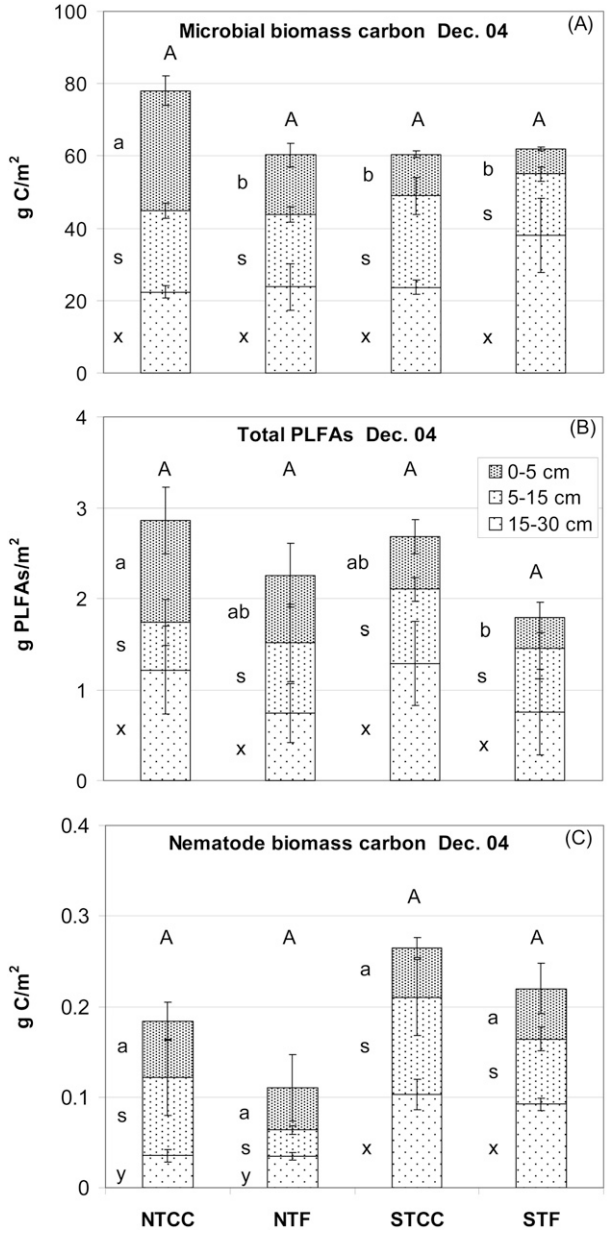

Fig. 2. (A) Soil microbial biomass C, (B) total phospholipid fatty acids (PLFAs), and (C) nematode biomass C in the top 30-cm layer in December 2004 at the end of the field station trial. NT = no-tillage; ST = standard tillage; CC = continuous cropping; and F = fallow. Data are means ± SE. Means followed by the same letter are not significantly different at the *P* < 0.05 level. Uppercase letters compare treatments in the top 0- to 30-cm layer; lowercase letters compare treatments for each depth.

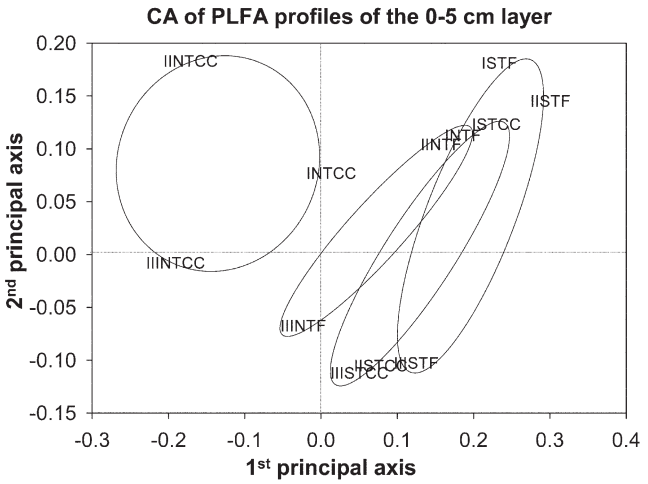

Fig. 3. Correspondence analysis (CA) of phospholipid fatty acid (PLFA) profiles of the 0- to 5-cm layer in December 2004 at the end of the field station trial. NT = no-tillage; ST = standard tillage; CC = continuous cropping; and F = fallow. I, II, and III refer to Block I, Block II, and Block III, respectively.

standard tillage was similar to that in no-tillage plots. Overall, there were no significant differences in MBC in the entire 0- to 30-cm layer among the treatments. Although MBC (g C m^{-2}) was not different among treatments in the 0- to 30-cm layer on the last sampling date, when compared across all three sampling dates, it was higher for no-tillage + continuous cropping compared with standard tillage + fallow (data not shown). This was also true for the 0- to 5-cm layer (data not shown).

At the end of the study, the trends for total PLFA were slightly different from those for MBC, and were more variable. Like MBC, total PLFA (0–30-cm depth) was similar in all treatments (Fig. 2A and 2B). In the 0- to 5-cm layer, however, statistical differences were less pronounced than those for MBC; the only differences were between no-tillage + continuous cropping and standard tillage + fallow.

In the 0- to 5-cm layer, PLFA profiles in no-tillage + continuous cropping clearly separated in the CA biplot from the other treatments, which were similar (Fig. 3). The first two principal components accounted for 48.1 and 23.6% of the total sample variance, respectively. Phospholipid fatty acids of bacterial biomarkers (micrograms per kilogram of soil) in the 0- to 5-cm layer were higher in no-tillage + continuous cropping than standard tillage + fallow and those below 5-cm depth were similar in all treatments (Fig. 4A). Phospholipid fatty acids of fungal biomarkers (micrograms per kilogram of soil) in the 0- to 5-cm layer were also higher in the no-tillage + continuous cropping treatment than in other treatments. Those below 5-cm depth were similar in all treatments (Fig. 4B).

Soil ergosterol, a fungal marker, differed by treatment, depth, date, and their interactions across three sampling dates (Table 2). Specifically, soil ergosterol was much higher in the 0- to 5-cm layer in no-tillage + continuous cropping than in other treatments and depths across the three sampling dates (Fig. 1B), resulting in significant interactions. In December 2004, soil ergosterol was positively correlated with PLFA of fungal biomarkers (r^2 = 0.71, P < 0.0001, data not shown).

Nematode Faunal Analysis

Total nematode abundance was lower in no-tillage + fallow than under continuous cropping treatments; it was highest in upper soil layers (Table 2). By the end of the experiment, nematode numbers in the 15- to 30-cm layer were higher in standard tillage + continuous cropping than either of the no-tillage treatments but did not differ among treatments in the 0- to 5- and 5- to 15-cm layers (Fig. 5A, 5B, and 5C). Both nematode abundance and biomass tended to be greater in the 0- to 15-cm layers than in the 15- to 30-cm layer, but were more evenly distributed across the 0- to 30-cm profile in standard tillage than no-tillage (Fig. 1C and 1D). In December 2004, nematode biomass mirrored nematode abundance. In the entire 0- to 30-cm profile, nematode biomass was similar among all treatments

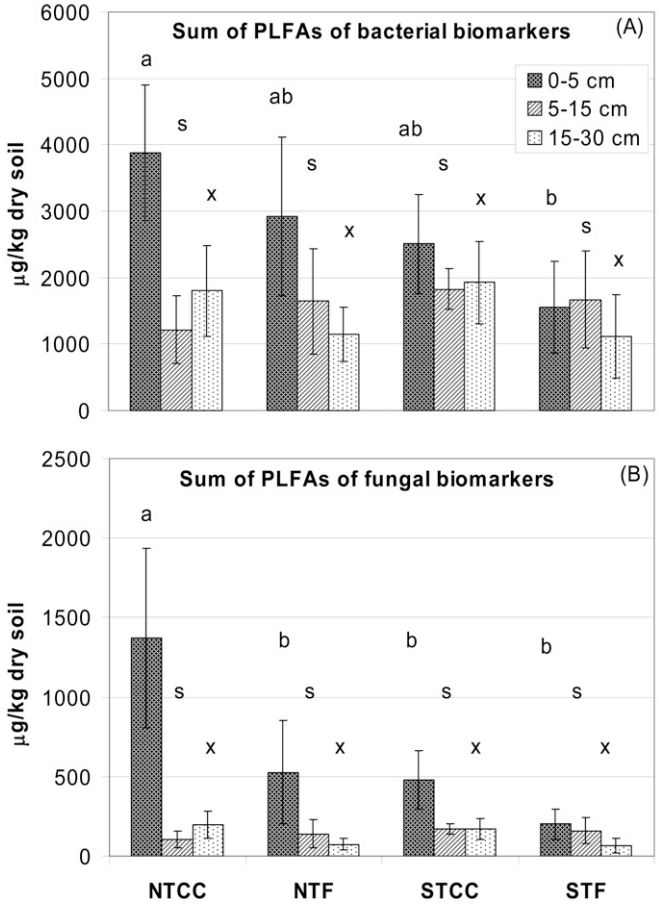

Fig. 4. Sum of phospholipid fatty acids (PLFAs) of (A) bacterial and (B) fungal biomarkers by treatment in December 2004 at the end of the field station trial. NT = no-tillage; ST = standard tillage; CC = continuous cropping; and F = fallow. Data are means ± SE. Means followed by the same letter are not significantly different at the *P* < 0.05 level. Differences indicated by a and b (0–5-cm layer), and s and x (5–15 and 15–30 cm, respectively).

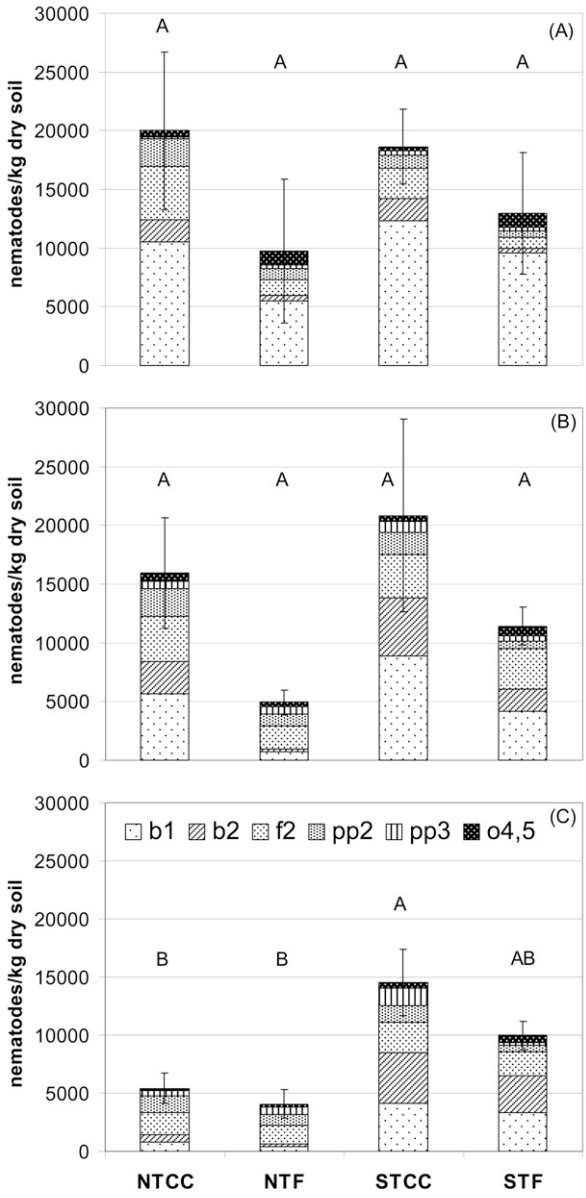

Fig. 5. Nematodes by functional groups in the (A) 0–5 cm, (B) 5–15 cm, and (C) 15–30 cm soil layers: b1, bacterial-feeding nematode and colonizer-persister (cp) 1; b2, bacterial-feeding nematode cp 2; f2, fungal-feeding nematode cp 2; pp2, plant parasitic nematode cp 2; pp3, plant parasitic nematode cp 3; o4,5, omnivorous nematodes cp 4 or 5. Data are means ± SE. Means followed by the same letter are not significantly different at the *P* < 0.05 level. Uppercase letters compare treatments for the entire nematode population at each depth. Standard errors are shown by error bars. NT = no-tillage; ST = standard tillage; CC = continuous cropping; and F = fallow. In the 0- to 5- and 5- to 15-cm soil layers, no treatment effects occurred for any functional group, while in the 15- to 30-cm layer, b1 in STCC was significantly higher than in NTCC or NTF.

but, it should be noted, had much lower values in no-tillage + fallow than in standard tillage + continuous cropping, although this difference was not statistically significant (Fig. 2C).

Detailed nematode faunal analyses at the end of the experiment reflected the cumulative effects of the management treatments. In the 0- to 5-cm layer, the community was comprised largely of cp1 bacteria feeders (Fig. 5A, see b1 and b2). These opportunistic species decreased with depth in all treatments, particularly under no-tillage (Fig. 5A, 5B, and 5C). Their abundance was correlated with PLFA bacterial biomarkers at the December 2004 sampling. Bacterial feeders of cp2 showed similar, but less pronounced, trends. Fungal feeders of cp2 were in greatest abundance in the 5- to 15-cm layer on all three sampling dates (data not shown) but were not correlated with PLFA fungal biomarkers at the December 2004 sampling (data not shown). In all treatments, cp2 bacterial and fungal feeders were the major component of the nematode community below 5-cm depth while cp1 bacteria lfeeders predominated in the 0- to 5-cm layer. Plant-parasitic and omnivorous nematodes were in low abundance in all treatments and depths, except that one cp3 plant-parasitic species increased with depth with standard tillage + continuous cropping.

Values of the Enrichment, Basal, and Channel indices (EI, BI, and CI), based on nematode functional guilds, differed by treatment, depth, and date (Table 2). The EI value, indicating opportunistic bacterial- and fungal-feeding species that respond rapidly to resource changes, was higher with standard tillage + continuous cropping than in either no-tillage treatments; it was higher in the 0- to 5-cm layer than below 5 cm, and increased during the course of the experiment (data not shown). The BI value, indicating abundance of general opportunists adapted to surviving adverse conditions, was higher in the continuous cropping treatments under no-tillage than

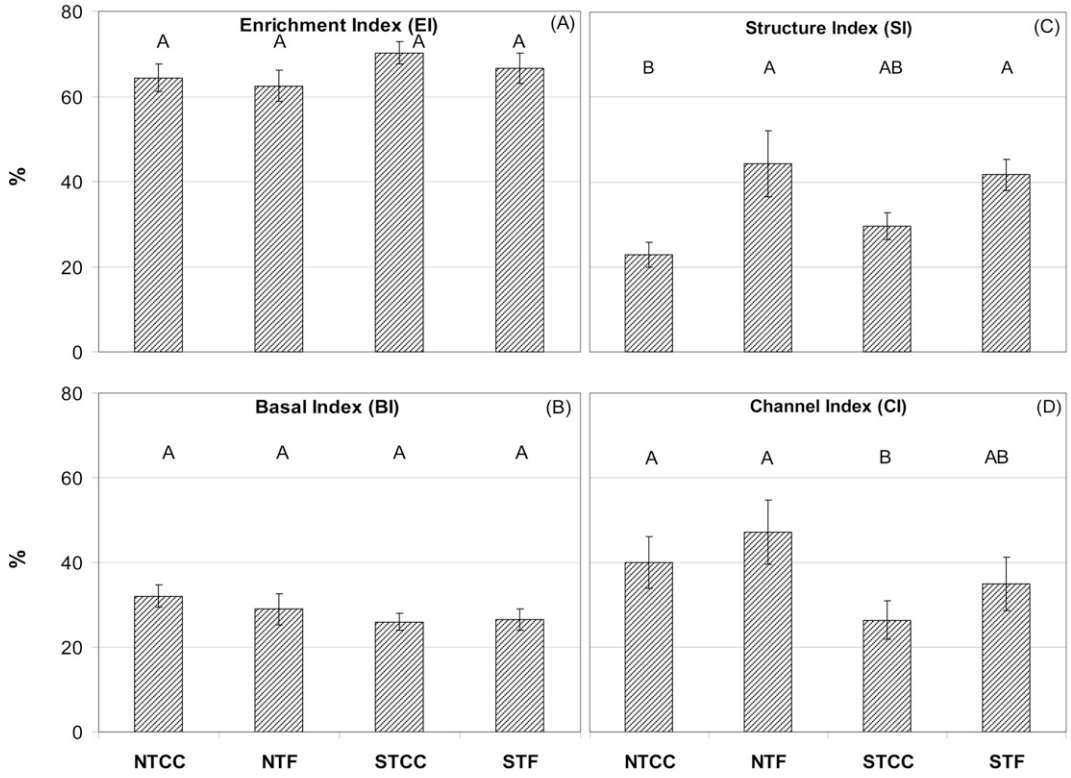

Fig. 6. (A) Nematode Enrichment Index, (B) Basal Index, (C) Structure Index, and (D) Channel Index in the 0- to 30-cm soil layer for nematodes across three sampling dates from the field station trial. NT = no-tillage; ST = standard tillage; CC = continuous cropping; and F = fallow. Data are means ± SE. Means followed by the same letter are not significantly different at the $P < 0.05$ level.

standard tillage, greater below 5-cm depth, and decreased with time (data not shown). When EI and BI values were calculated for the entire soil column (0–30 cm), however, weighted by soil mass, there were no differences between treatments (Fig. 6A and 6B).

The value of the Structure Index (SI), indicating complexity and connectance of the food web, differed by treatment but not by depth and date (Table 2). The SI value was higher in fallow than in continuous cropping treatments (data not shown). The SI value (0–30 cm) in both fallow treatments was higher than in no-tillage + continuous cropping (Fig. 6C). The CI value, indicating the degree of fungal participation in the primary decomposition channels, was lower in standard tillage + continuous cropping than in either of the no-tillage treatments, lower in the 0- to 5-cm layer than that below 5 cm, and decreased with time. The CI value (0–30 cm) was significantly higher in both no-tillage treatments than with standard tillage + continuous cropping (Fig. 6D).

Total Soil Carbon and Nitrogen, and Soil Physical and Chemical Properties

By December 2004, the total C per kilogram of soil was significantly higher in no-tillage + continuous cropping than with standard tillage + fallow in the 0- to 5-cm layer, but no differences occurred among the treatments below 5 cm (Table 3). There were no differences in total soil N per kilogram of

Table 3. Chemical and physical properties of soils in December 2004 at the end of the field station trial.

Depth	Treatment†	Total C	Total N	pH	K	P	Bulk density‡
cm		g C kg^{-1} soil	g N kg^{-1} soil		mg L^{-1}	mg kg^{-1} soil	g cm^{-3}
0–5	NTCC	11.9 ± 0.4 a§	1.22 ± 0.07 a	7.27 ± 0.07 a	12.9 ± 1.3 a	27.1 ± 1.8 a	1.31 ± 0.03 a
	NTF	10.9 ± 0.3 ab	1.10 ± 0.00 a	7.03 ± 0.03 ab	10.3 ± 0.8 ab	18.9 ± 0.5 b	1.33 ± 0.08 a
	STCC	10.9 ± 0.1 ab	1.23 ± 0.03 a	7.13 ± 0.03 ab	7.70 ± 0.2 bc	18.6 ± 0.5 b	1.19 ± 0.02 a
	STF	9.9 ± 0.2 b	1.22 ± 0.04 a	6.90 ± 0.06 b	6.00 ± 0.3 c	15.6 ± 0.3 b	1.21 ± 0.05 a
5–15	NTCC	10.2 ± 0.1 s	1.13 ± 0.07 s	7.07 ± 0.03 s	5.90 ± 0.36 s	16.6 ± 0.8 s	1.33 ± 0.03 st
	NTF	9.9 ± 0.1 s	1.17 ± 0.03 s	6.90 ± 0.00 s	6.27 ± 0.47 s	14.6 ± 0.2 s	1.37 ± 0.00 s
	STCC	10.5 ± 0.5 s	1.17 ± 0.03 s	7.10 ± 0.06 s	6.97 ± 1.39 s	17.9 ± 1.9 s	1.26 ± 0.05 tu
	STF	10.2 ± 0.0 s	1.23 ± 0.03 s	6.90 ± 0.06 s	5.90 ± 0.21 s	16.2 ± 0.6 s	1.21 ± 0.02 u
15–30	NTCC	10.0 ± 0.4 x	1.20 ± 0.00 x	6.90 ± 0.06 xy	4.80 ± 0.38 y	13.5 ± 1.1 x	1.31 ± 0.05 x
	NTF	10.1 ± 0.4 x	1.20 ± 0.06 x	6.77 ± 0.03 y	5.50 ± 0.10 xy	14.4 ± 1.2 x	1.33 ± 0.03 x
	STCC	10.4 ± 0.7 x	1.20 ± 0.09 x	6.97 ± 0.03 x	6.33 ± 0.64 x	15.6 ± 1.7 x	1.31 ± 0.04 x
	STF	9.8 ± 0.3 x	1.13 ± 0.03 x	6.77 ± 0.03 y	5.87 ± 0.20 xy	15.6 ± 0.7 x	1.34 ± 0.03 x

† NT, no-tillage; ST, standard tillage; CC, continuous cropping; F, fallow.

‡ Samples of bulk density were taken in February 2005.

§ Means ± SE. Means followed by the same letter are not significantly different at the $P < 0.05$ level.

soil. Soil C in the 0- to 30-cm layer, expressed as kilograms of C per square meter, was higher in the no-tillage treatments than in standard tillage + fallow, but similar to standard tillage + continuous cropping (Fig. 7A). Soil C in the 0- to 5-cm layer was higher with no-tillage than standard tillage when there was continuous cropping. Soil N in each soil layer and the whole 0- to 30-cm profile was similar among treatments (Fig. 7B).

Nitrate concentrations varied in the soil surface layer among all treatments across the four sampling dates; they were much higher in the dry summer season and decreased during the rainy season in December (Table 4). Nitrate was significantly higher with no-tillage + continuous cropping than with standard tillage treatments in the 0- to 5-cm layer in June 2004, while it was significantly higher with standard tillage + continuous cropping than with either no-tillage treatment in the 15- to 30-cm layer in December 2004. Ammonium concentrations were lower in all treatments and depths and across all sampling dates compared with NO_3^-. The maximum and minimum NH_4^+ concentrations were 6.3 and 0.62 mg NH_4^+–N kg^{-1} soil, respectively, and the mean across all dates and sampling times was 1.6 ± 0.2 mg NH_4^+–N kg^{-1} soil.

Soil pH was always close to 7, but was significantly higher in no-tillage + continuous cropping than in standard tillage + fallow in the 0- to 5-cm layer on the last sampling date in December 2004 (Table 3). At 5 to 15 cm, pH was similar among treatments, but at 15 to 30 cm, it was slightly higher in continuous cropping treatments.

Higher concentrations of soluble K^+ were found in the no-tillage treatments in the surface layer (Table 3). The concentration of K^+ decreased with depth. It was higher in standard tillage than in no-tillage in the 15- to 30-cm layer. The P concentration was significantly higher with no-tillage + continuous cropping than in the other treatments in the 0- to 5-cm layer, and it was similar in all treatments below the 5-cm depth.

Bulk density was measured in February 2005. While there were no significant differences in the surface layer, the no-tillage treatments tended to be more compacted than standard tillage treatments. At 15 to 30 cm, bulk density was similar in all treatments (Table 3). Applying these bulk density values to the data for December 2004, water-filled pore space (WFPS) was higher in the no-tillage treatments in the upper two layers than with standard tillage (Table 4).

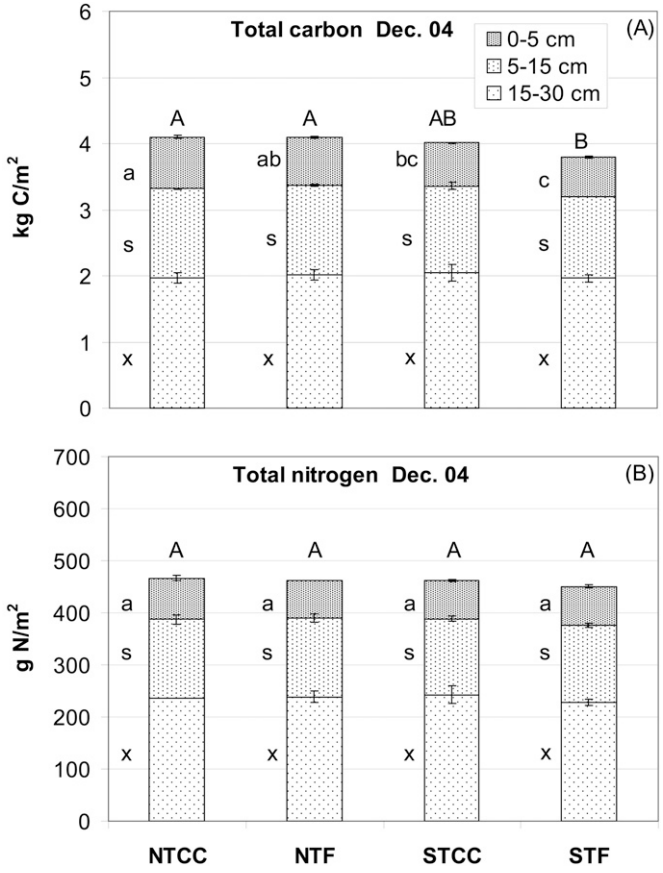

Fig. 7. Total soil (A) C and (B) N in the upper 30 cm in December 2004, at the end of the field station trial. NT = no-tillage; ST = standard tillage; CC = continuous cropping; and F = fallow. Data are means ± SE. Means followed by the same letter are not significantly different at the $P < 0.05$ level. Uppercase letters compare treatments in the top 0- to 30-cm layer; lowercase letters compare treatments for each depth.

DISCUSSION

Overall, this 1-yr study indicates that no-tillage + continuous cropping had a greater effect on surface layer biota and C pools than standard tillage. With no-tillage + continuous cropping, crop productivity decreased markedly in this Mediterranean-type climate, yet there was greater total soil C accumulation in the 0- to 30-cm profile, compared with the common practices of standard tillage with intermittent fallow periods. Changes in the composition and size of the

Table 4. Nitrate-N concentration of soils for four sampling dates and water-filled pore space (WFPS) on the last date. Soil samples were only taken from the continuous cropping treatments in September 2004.

Depth	Treatment†	Dec. 2003	June 2004	Sept. 2004	Dec. 2004	WFPS, Dec. 2004
cm						%
0–5	NTCC	2.3 ± 0.2 a‡	65.5 ± 7.1 a	79.4 ± 10.6 a	4.6 ± 1.6 a	72.5 a
	NTF	6.0 ± 2.5 a	48.7 ± 7.6 ab		8.1 ± 4.1 a	70.0 a
	STCC	0.4 ± 0.1 a	32.4 ± 2.4 b	74.4 ± 12.6 a	7.8 ± 0.5 a	56.3 b
	STF	0.4 ± 0.2 a	29.6 ± 0.8 b		5.0 ± 0.3 a	54.7 b
5–15	NTCC	2.2 ± 0.4 s	10.8 ± 1.3 s	4.8 ± 1.5 s	6.2 ± 2.7 s	70.2 t
	NTF	2.2 ± 0.8 s	7.0 ± 0.4 s		3.6 ± 1.6 s	74.4 s
	STCC	1.6 ± 0.5 s	9.4 ± 2.2 s	9.6 ± 4.0 s	11.2 ± 6.2 s	64.6 u
	STF	2.1 ± 0.7 s	8.1 ± 0.8 s		4.8 ± 0.3 s	58.5 v
15–30	NTCC	3.4 ± 0.8 x	10.3 ± 1.3 x	10.1 ± 3.8 x	2.9 ± 0.9 y	64.6 y
	NTF	6.8 ± 1.4 x	12.8 ± 1.9 x		4.8 ± 1.3 y	67.1 xy
	STCC	3.5 ± 0.5 x	12.2 ± 4.0 x	10.8 ± 0.3 x	17.1 ± 4.0 x	68.4 xy
	STF	8.8 ± 1.0 x	10.2 ± 1.1 x		9.6 ± 1.6 xy	69.2 x

† NT, no-tillage; ST, standard tillage; CC, continuous cropping; F, fallow.

‡ Means ± SE. Means followed by the same letter within each depth are not significantly different at the $P < 0.05$ level.

microbial community appear to be important for total C accumulation in the surface layer, as discussed below. The effects on higher trophic levels, as indicated by nematode soil food web analysis, are less clear. Although some nutrients accumulated in the surface layer with no-tillage, there may be greater propensity for NO_3^- loss, given that high NO_3^- concentrations, C availability, soil moisture, and bulk density all can increase the denitrification potential of soil. These outcomes suggest that there may be significant tradeoffs associated with conversions to no-tillage + continuous cropping in California cropping systems.

Crop Productivity and Management

As expected, lower aboveground biomass and yields occurred with no-tillage; they were particularly low with no-tillage + continuous cropping, probably due to higher accumulation of surface residue that impeded growth, as well as higher weed pressure. In temperate regions, no-tillage typically produces lower crop yields of corn (*Zea mays* L.) and wheat than standard tillage due to prolonged low temperatures during spring and poor stand establishment associated with the presence of large amounts of plant residue (Kiger and Grove, 1999; Kapusta et al., 1996). In California, where the climate is Mediterranean, tomato and cotton (*Gossypium hirsutum* L.) yields in conservation tillage plots with winter cover crops were lower than those with standard tillage with winter fallow because the accumulation of both crop and cover crop residues inhibit the early stages of crop growth (Mitchell et al., 2003).

Both lower garbanzo biomass and yields occurred with no-tillage, particularly with no-tillage + continuous cropping. In this treatment, accumulation of surface residue may have impeded growth, and there was more weed pressure. The garbanzo growth also might have been more inhibited by allelopathic chemicals from the sorghum–sudangrass cover crop than when the residue was incorporated with standard tillage (Mitchell et al., 2000). Lower aboveground cowpea cover crop biomass in no-tillage + continuous cropping compared with standard tillage + continuous cropping was associated with lower germination and stand establishment (personal observation). Poor garbanzo stand establishment led to serious weed problems in this treatment. The evenness of the bed tops, which is necessary for consistent sowing depth, good germination, and uniform furrow irrigation, deteriorated under no-tillage, especially with continuous cropping. For efficient irrigation, the furrows had to be tilled in midsummer. Further technological developments may be necessary to enhance yields in irrigated fields with crop residues on the soil surface, especially in no-tillage systems with cover crops.

Total Soil Carbon and Soil Microbes

Long term studies on no-tillage systems reveal that SOM becomes stratified in the surface layer and decreases with depth (Kay and VandenBygaart, 2002; Dick and Durkalski, 1998; Jarecki and Lal, 2005). McCarty et al. (1998) also reported that stratification occurred during the first 3 yr of converting from standard tillage to no-tillage. Higher SOM in the 0- to 5-cm layer with no-tillage was offset by lower SOM below 5 cm, however, and thus similar SOM content was observed in the total 0- to 30-cm profile with standard tillage and no-tillage (Dick, 1983; Needleman et al., 1999; Yang and Kay, 2001). These observations regarding C accumulation in the surface layer are consistent with our comparison of no-tillage + continuous cropping and standard tillage + continuous cropping, but not between comparisons of the no-tillage + fallow and standard tillage + fallow treatments.

Over the long term, tilling soils increases CO_2 release, soil respiration, and loss of soil C, partly because macroaggregates are disrupted by mechanical soil mixing and more C can be accessed by soil microbes (Lupwayi and Paustian, 1999; Six et al., 1999; Jackson et al., 2003). Because tillage moves residue deeper into the soil profile, however, more organic material can be adsorbed and stabilized in subsurface layers than when residues are deposited on the soil surface (Paustian et al., 1997). In our study, this assessment was complicated by the higher amounts of plant biomass in standard tillage than no-tillage. Yet, there was a strong trend toward lower total C in soils of the standard tillage treatments, despite higher plant biomass production. The amount of plant biomass entering the two fallow systems was similar, and thus the lower total soil C in standard tillage + fallow in the subsurface layer, and in the entire 0- to 30-cm soil profile, is best attributable to disturbance by tillage.

Changes in MBC reflect conditions affecting the accumulation of total C (Powlson et al., 1987; Sparling, 1997; Franzluebbers et al., 1999). A positive correlation between MBC and total soil C was observed in this study ($r^2 = 0.45$, $P < 0.0001$), as has been found previously (Liebig et al., 2004; Sherrod et al., 2005).

Not only the quality and quantity of residue, but also its placement and incorporation affect soil microbial community structure and size (Six et al., 2006). At the soil surface, MBC has been shown to be higher with no-tillage than standard tillage (Alvarez et al., 1995; Carter and Sanderson, 2001; Kisselle et al., 2001). In this study, MBC per square meter was higher in the soil surface layer in no-tillage + continuous cropping than other treatments and higher for the 0- to 30-cm profile than in standard tillage + fallow across all three sampling dates. Greater crop residue at the surface results in increased C substrate availability, increased infiltration, higher water holding capacity, and less fluctuation in moisture and temperature (Doran, 1980). Moisture content in the 0- to 5-cm layer with no-tillage + continuous cropping was significantly higher than in the other treatments at the last sampling date. A complex set of environmental changes thus could explain the marked shift in PLFA profiles and microbial composition observed in the no-tillage + continuous cropping system (Drijber et al., 2000; Calderón et al., 2000; Feng et al., 2003).

Higher fungal biomass in the soil surface layer, based on ergosterol and PLFA markers, as observed here with no-tillage, occurs when residue is left on the soil surface and soils are not disturbed by tillage. Residue decomposition by fungi increases due to the lack of disruption of hyphal networks (Beare et al., 1992; Frey et al., 1999; Fierer et al., 2003). Some researchers have found that soil fungi have higher microbial growth efficiency (MGE), which is defined as the amount of new biomass C produced per unit of substrate C metabolized, than bacteria (Sakamoto and Oba, 1994; Blagodatskaya and Anderson, 1998), but Thiet et al. (2005) reported no difference in MGE between fungal- and bacterial-dominated soils. Regardless of MGE, fungal substrates, biomass, and byproducts are more recalcitrant to decomposition, and more slowly degraded in soil, compared with those of bacteria (Martin and Haider, 1979; Kogel-Knabner, 2002). Moreover, the higher C/N ratio of fungi compared with that of bacteria implies that a greater proportion of C is retained in fungal biomass (Six et al., 2006).

Per amount of plant residue added to the soil, no-tillage had higher MBC than standard tillage. Despite much lower residue

additions, MBC (0–30 cm) was similar in the no-tillage and standard tillage under continuous cropping. Also, no-tillage + continuous cropping resulted in higher MBC in the 0- to 30-cm profile than standard tillage + fallow, despite similar C inputs. Fungal biomass, based on ergosterol and PLFA markers, was also higher, and may explain the higher recovery of C in microbes. Tillage of plant residue into soil causes rapid increases in MBC, followed by decreases to pre-incorporation levels, usually within a month after incorporation of plants (Kisselle et al., 2001; Lundquist et al., 1999; Jackson, 2000). Tillage also increases bacterial dominance of the microbial community (Hendrix et al., 1986; Holland and Coleman, 1987), leading to greater loss of CO_2, possibly due to the lower C/N ratio of the bacterial biomass and metabolic rates that may be higher than fungi (Six et al., 2006). The accumulation of MBC and total C in the surface layer with no-tillage + continuous cropping may thus be at least partially explained by the higher proportion of fungi in the microbial biomass.

Nematodes and the Soil Food Web

The positive correlation between nematode biomass in the 0- to 30-cm profile and total aboveground plant biomass was consistent with the idea that higher plant biomass entering systems leads to higher nematode populations across trophic levels (Ingham et al., 1985). Accumulation of residues at the soil surface in no-tillage leads to higher density of bacterial-feeding nematodes due to higher bacterial population size (Bouwman and Zwart, 1994; Lenz and Eisenbeis, 2000), as was observed here for cp 1 bacterial feeders. In contrast, fungal feeders were consistently highest in the 5- to 15-cm layer and were not correlated with fungal biomass. Levels of fungal feeders can reflect environmental conditions rather than a direct predator–prey relationship (Thornton and Matlack, 2002).

The increase of cp1 bacterial feeders in standard tillage + continuous cropping by the end of the experiment was consistent with observations that tillage and incorporation of residue favor organisms with r-selected characteristics (Ettema and Bongers, 1993; Lenz and Eisenbeis, 2000). Across all sampling dates, cp1 bacterial feeders were lowest following termination of the higher C/N sorghum–sudangrass cover crop, and they dramatically increased after harvesting of the lower C/N ratio cowpea summer cover crop. These changes may be related to residue characteristics. Residue with a low C/N ratio is thought to be mainly decomposed by bacteria, resulting in an increase of cp1 bacterial-feeding nematodes (Bongers and Bongers, 1998), whereas residue with higher cellulose and lignin content and a high C/N ratio is more likely to be decomposed by fungi and fungal-feeding nematodes (Wardle and Yeates, 1993).

The soil food web did not become more complex with no-tillage + continuous cropping, contrary to expectations at the onset of the study. The CI value was low in the soil surface layer in all treatments, even with no-tillage + continuous cropping, which had higher fungal biomarkers. The bacterial decomposition pathway seems to have dominated this layer in all treatments. With no-tillage, cp1 bacterial feeders dramatically decreased with depth, compared with standard tillage, which led to the higher CI value with no-tillage for the entire 0- to 30-cm profile.

Omnivorous and predatory nematodes have been shown to decrease due to intensive cultivation (Bouwman and Zwart, 1994: Wardle et al., 1995), although this was not observed here. Conversion to no-tillage has had conflicting outcomes for these nematode groups, with increases only 2 yr after abandoning an arable field (Háněl, 2003) vs. little change between no-tillage and standard tillage during a 5-yr period (Parmelee and Alston, 1986). These differences may be due to variation in response among genera in the cp 4 and 5 categories, requiring more critical analysis of functional taxa (Fiscus and Neher, 2002). An important consideration in such studies is the history of the field site, which, in this case, had been under conventional management and tillage for many years. The SI value, indicating abundance of higher trophic levels of nematodes and of connectance in the food web, was much lower at the start of the experiment than observed in natural systems (Ferris et al., 2001). Increase in the SI value due to changes in management practices may involve a prolonged period of recolonization by sensitive species, requiring many years.

Soil Chemical and Physical Properties

Immobile nutrients such as P and K have been found to accumulate at the soil surface layer under no-tillage systems after >10 yr, due to lack of mixing (Mrabet et al., 2001; Blevins et al., 1983). This trend was found even after only 1 yr in this experiment. With standard tillage, P and K were more evenly distributed in the 30-cm profile, probably due to incorporation of shoots into the subsurface layer. With no-tillage, these nutrients are taken up from the soil by the crop, then deposited and released at the soil surface. In addition to the effects of placement of residue on nutrient concentrations in the soil profiles, upward fluxes of ions due to capillary rise play an important role in their distribution in the soil profile in continuously warm regions with periodic dry periods (Wilcke and Lilienfein, 2005). Such effects may have occurred during summer, especially for NO_3^- in the no-tillage treatments. Greater soil compaction with no-tillage than standard tillage could facilitate capillary rise resulting from irrigation during spring and summer, possibly explaining the higher NO_3^- concentration in the soil surface layer. Denitrification losses during the subsequent rainy period may have been higher with no-tillage, given the higher WFPS that was measured in December (Davidson, 1991; Linn and Doran, 1984; Rice and Smith, 1982).

CONCLUSIONS

In California's Mediterranean-type climate, the accumulation of surface biomass may result in greater fungal activity and contribute to the higher C accumulation in the surface layer of no-tillage + continuous cropping systems compared with the standard tillage + fallow systems typical of vegetable production in this region. The contribution of higher trophic level organisms to soil C storage within the timeframe of this study appears to be minor, since neither omnivorous and predatory nematodes nor the SI value increased with no-tillage. This may be due to lack of colonization potential due to distance from sites with more complex food webs. Decreased yield, more weeds, greater compaction, and a propensity for NO_3^- loss are problems that are currently being addressed in other conservation tillage studies in the region.

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REFERENCES

Alvarez, R., O.J. Santanatoglia, and R. Garcia. 1995. Soil respiration and carbon inputs from in a wheat–soybean rotation under different tillage systems. Soil Use Manage. 11:45–50.

Andrássy, I. 1956. The determination of volume and weight of nematodes. Acta Zool. Acad. Sci. Hung. 2:1–15.

Barker, K.R. 1985. Nematode extraction and bioassays. p. 19–35. *In* K.R. Barker et al. (ed.) An advanced treatise on *Meloidogyne*. Vol. 2: Methodology. North Carolina State Univ. Graphics, Raleigh.

Beare, M.H., R.W. Parmelee, P.F. Hendrix, and W. Cheng. 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecol. Monogr. 62:569–591.

Berkelmans, R., H. Ferris, M. Tenuta, and A.H.C. van Bruggen. 2003. Effects of long-term crop management on trophic levels of nematodes other than plant parasitic nematodes disappear after one year of uniform management. Appl. Soil Ecol. 23:223–235.

Blagodatskaya, E.V., and T.H. Anderson. 1998. Interactive effects of pH and substrate quality on the fungal-to-bacterial ratio and qCO_2 of microbial community in forest soils. Soil Biol. Biochem. 30:1269–1274.

Blevins, R.L., G.W. Thomas, M.S. Smith, W.W. Frye, and P.L. Cornelius. 1983. Changes in soil properties after 10 years of no-tillage and conventionally tilled corn. Soil Tillage Res. 3:135–146.

Bongers, T. 1990. The maturity index: An ecological measure of environmental disturbance based on nematode species composition. Oecologia 83:14–19.

Bongers, T., and M. Bongers. 1998. Functional diversity of nematodes. Appl. Soil Ecol. 10:239–251.

Bongers, T., and H. Ferris. 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Evol. Ecol. 14:224–228.

Bossio, D.A., K.M. Scow, N. Gunapala, and K.J. Graham. 1998. Determinants of soil microbial communities: Effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. Microb. Ecol. 36:1–12.

Bouwman, L.A., and K.B. Zwart. 1994. The ecology of bacterivorous protozoans and nematodes in arable soil. Agric. Ecosyst. Environ. 51:145–160.

Calderón, F.J., L.E. Jackson, K.M. Scow, and D.E. Rolston. 2000. Microbial responses to simulated tillage in cultivated and uncultivated soils. Soil Biol. Biochem. 32:1547–1559.

Carter, M.R. 2005. Long-term tillage effects on cool-season soybean in rotation with barley, soil properties and carbon and nitrogen storage for fine sandy loams in the humid climate of Atlantic Canada. Soil Tillage Res. 81:109–120.

Carter, M.R., and J.B. Sanderson. 2001. Influence of conservation tillage and rotation length on potato productivity, tuber disease and soil quality parameters on a fine sandy loam in eastern Canada. Soil Tillage Res. 63:1–13.

Cavagnaro, T. R., L.E. Jackson, J. Six, H. Ferris, S. Goyal, D. Asami, and K.M. Scow. 2006. Arbuscular mycorrhizas, microbial communities, nutrient availability, and soil aggregates in organic tomato production. Plant Soil 282:209–225.

Cole, C.V., J. Duxbury, J. Frencey, O. Heinemeyer, K. Minami, A. Mosier, K. Paustian, N. Rosenberg, N. Sampson, D. Sauerbeck, and Q. Zhao. 1997. Global estimates of potential mitigation of greenhouse gas emissions by agriculture. Nutr. Cycling Agroecosyst. 49:221–228.

Coleman, D.C., R. Andrews, J.E. Ellis, and J.S. Singh. 1976. Energy flow and partition in selected managed and natural ecosystems. Agro-Ecosystems 3:45–54.

Davidson, E.A. 1991. Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. p. 219–235. *In* J.E. Rogers and W.B. Whiteman (ed.) Microbial production and consumption of greenhouse gases: Methane, nitrogen oxides, and halomethanes. Am. Soc. Microbiol., Washington, DC.

Deen, W., and P.K. Kataki. 2003. Carbon sequestration in a long-term conventional versus conservation tillage experiment. Soil Tillage Res. 74:143–150.

Dick, W.A. 1983. Organic carbon, nitrogen and phosphorus concentrations and pH in soil profiles as affected by tillage intensity. Soil Sci. Soc. Am. J. 47:102–107.

Dick, W.A., and J.T. Durkalski. 1998. No-tillage production agriculture and carbon sequestration in a Typic Fragiudalf soil of northeastern Ohio. p. 59–71. *In* R. Lal et al. (ed.) Management of carbon sequestration in soil. CRC Press, Boca Ration, FL.

Djajakirana, G., R.G. Joergensen, and B. Meyer. 1996. Ergosterol and microbial biomass relationship in soil. Soil Biol. Biochem. 22:299–304.

Doran, J.W. 1980. Soil microbial and biochemical changes associated with reduced tillage. Soil Sci. Soc. Am. J. 44:764–771.

Drijber, R.A., J.W. Doran, A.M. Parkhurst, and D.J. Lyon. 2000. Changes in soil microbial community structure with tillage under long-term wheat–fallow management. Soil Biol. Biochem. 32:1419–1430.

Ettema, C.H., and T. Bongers. 1993. Characterization of nematode colonization and succession in disturbed soil using the Maturity Index. Biol. Fertil. Soils 16:79–85.

Feng, Y., A.C. Motta, D.W. Reeves, C.H. Burmester, E. van Santen, and J.A. Osborne. 2003. Soil microbial communities under conventional-till and no-till continuous cotton systems. Soil Biol. Biochem. 35:1693–1703.

Ferris, H. 2005. Carbon channels and food web structure. J. Nematol. 37:369 (abstr.).

Ferris, H. 2006. Bioindicators. Available at plpnemweb.ucdavis.edu/nemaplex/Ecology/bioindicators.htm (verified 9 Feb. 2007). Univ. of Calif., Davis.

Ferris, H., T. Bongers, and R.G.M. de Goede. 2001. A framework for soil food web diagnostics: Extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18:13–29.

Ferris, H., and M. Matute. 2003. Structural and functional succession in the nematode fauna of a soil food web. Appl. Soil Ecol. 23:93–110.

Ferris, H., R.C. Venette, and K.M. Scow. 2004. Soil management to enhance bacteriovore and fungivore nematode populations and their nitrogen mineralization function. Appl. Soil Ecol. 25:19–35.

Fierer, N., A.S. Allen, J.P. Schimel, and P.A. Holden. 2003. Controls on microbial CO_2 production: A comparison of surface and subsurface soil horizons. Global Change Biol. 9:1322–1332.

Fiscus, D.A., and D.A. Neher. 2002. Distinguishing sensitivity of free-living nematode genera to physical and chemical disturbances. Ecol. Appl. 12:565–575.

Forster, J.C. 1995. Soil nitrogen. p. 79–87. *In* K. Alef and P. Nannipiero (ed.) Methods in applied soil microbiology and biochemistry. Academic Press, San Diego.

Franzluebbers, A.J., G.W. Langdale, and H.H. Schomberg. 1999. Soil carbon, nitrogen, and aggregation in response to type and frequency of tillage. Soil Sci. Soc. Am. J. 63:349–355.

Frey, S.D., E.T. Elliott, and K. Paustian. 1999. Bacterial and fungal abundance and biomass in conventional and no-tillage agroecosystems along two climatic gradients. Soil Biol. Biochem. 31:573–585.

Fu, S., D.C. Coleman, R. Schartz, R. Potter, P.F. Hendrix, and D.A. Crossley. 2000. ^{14}C distribution in soil organisms and respiration after the decomposition of crop residue in conventional tillage and no-till agroecosystems at Georgia Piedmont. Soil Tillage Res. 57:31–41.

Gunapala, N., R.C. Venette, H. Ferris, and K.M. Scow. 1998. Effects of soil management history on the rate of organic matter decomposition. Soil Biol. Biochem. 30:1917–1927.

Háněl, L. 2003. Recovery of soil nematode populations from cropping stress by natural secondary succession to meadow land. Appl. Soil Ecol. 22:255–270.

Hendrix, P.F., R.W. Parmelee, D.A. Crossley, D.C. Coleman, E.P. Odum, and P.M. Groffman. 1986. Detritus food webs in conventional and no-tillage agroecosystems. Bioscience 36:374–380.

Holland, E.A., and D.C. Coleman. 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68:425–433.

Ingham, R.E., J.A. Trofymov, E.R. Ingham, and D.C. Coleman. 1985. Interaction of bacteria, fungi, and their nematode grazers: Effects on nutrient cycling and plant growth. Ecol. Modell. 55:119–140.

Jackson, L.E. 2000. Fates and losses of nitrogen from a ^{15}N-labelled cover crop in an intensively managed vegetable system. Soil Sci. Soc. Am. J. 64:1404–1412.

Jackson, L.E., F.J. Calderón, K.L. Steenwerth, K.M. Scow, and D.E. Rolston. 2003. Responses of soil microbial processes and community structure to tillage events and implications for soil quality. Geoderma 114:305–317.

Jarecki, M.K., and R. Lal. 2005. Soil organic carbon sequestration rates in two long-term no-till experiments in Ohio. Soil Sci. 170:280–291.

Kapusta, G., R.F. Kransz, and J.L. Matthews. 1996. Corn yield is equal in conventional, reduced, and no tillage after 20 years. Agron. J. 88:812–817.

Kay, B.D., and A.J. VandenBygaart. 2002. Conservation tillage and depth stratification of porosity and soil organic matter. Soil Tillage Res. 66:107–118.

Kiger, C.E., and J.H. Grove. 1999. Corn residue placement influence on no-tillage winter wheat development. p. 290. *In* Agronomy abstracts. ASA, CSSA, and SSSA, Madison, WI.

Kisselle, K.W., C.J. Garrett, S. Fu, P.F. Hendrix, D.A. Crossley, D.C. Coleman,

and R.L. Potter. 2001. Budgets for root-derived C and litter-derived C: Comparison between conventional tillage and no tillage soils. Soil Biol. Biochem. 33:1067–1075.

Kogel-Knabner, I. 2002. The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biol. Biochem. 34:139–162.

Lenz, R., and G. Eisenbeis. 2000. Short-term effects of different tillage in a sustainable farming system on nematode community structure. Biol. Fertil. Soils 31:237–244.

Liebig, M.A., D.L. Tanaka, and B.J. Wienhold. 2004. Tillage and cropping effects on soil quality indicators in the northern Great Plains. Soil Tillage Res. 78:131–141.

Linn, D.M., and J.W. Doran. 1984. Effects of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and non-tilled soil. Soil Sci. Soc. Am. J. 48:1267–1272.

Lundquist, L.J., L.E. Jackson, K.M. Scow, and C. Hsu. 1999. Changes in microbial biomass and community composition, and soil carbon and nitrogen pools after incorporation of rye into three California agricultural soils. Soil Biol. Biochem. 31:221–236.

Lupwayi, N.Z., and K. Paustian. 1999. Soil microbial biomass and carbon dioxide flux under wheat as influenced by tillage and crop rotation. Can. J. Soil Sci. 79:273–280.

Martin, J.P., and K. Haider. 1979. Biodegradation of ^{14}C-labeled model and cornstalk lignin, phenols, model penolase humic polymers, and fungal melanins as influenced by a readily available carbon source and soil. Appl. Environ. Microbiol. 38:283–289.

McCarty, G.W., N.N. Lyssenko, and J.L. Starr. 1998. Short-term changes in soil carbon and nitrogen pools during tillage management transition. Soil Sci. Soc. Am. J. 62:1564–1571.

Mikola, J., and H. Setala. 1998. No evidence of trophic cascades in an experimental microbial-based soil food web. Ecology 79:153–164.

Miranda, K.M., M.G. Espey, and D.A. Wink. 2001. A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. Nitric Oxide 5:62–71.

Mitchell, J.P., W. Horwath, and R. Southard. 2003. Transitioning tomato and cotton production to conservation tillage in California's San Joaquin Valley. Am. Soc. for Hortic. Sci. Centennial Conf., Providence, RI. 3–6 Oct. 2003. HortScience 38:822 (abstr.).

Mitchell, J.P., C. Summers, T.S. Prather, J. Stapleton, and L.M. Roche. 2000. Potential allelopathy of sorghum–sudan mulch. Abstr. of the Annu. Int. Conf. of the Am. Soc. for Hortic. Sci., 97th, Lake Buena Vista, FL. 23–26 July 2000. HortScience 35:442.

Mrabet, R., K. Ibno-namr, F. Bessam, and N. Saber. 2001. Soil chemical quality changes and implications for fertilizer management after 11 years of no-tillage wheat production systems in semiarid Morocco. Land Degrad. Develop. 12:505–517.

Needleman, B.A., M.M. Wander, G.A. Bollero, C.W. Boast, G.K. Sims, and D.G. Bullock. 1999. Interaction of tillage and soil texture: Biologically active soil organic matter in Illinois. Soil Sci. Soc. Am. J. 63:1326–1334.

Neher, D.A. 2001. Role of nematodes in soil health and their use as indicators. J. Nematol. 33:161–168.

Nelson, D.W., and L.E. Sommers. 1982. Total carbon, organic carbon, and organic matter. p. 539–594. *In* A.L. Page et al (ed.) Methods of soil analysis. Part 2. Chemical and microbiological properties. 2nd ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI.

Ogle, S.M., J.F. Breidt, M.D. Eve, and K. Paustian. 2003. Uncertainty in estimating land use and management impacts on soil organic carbon storage for US agricultural lands between 1982 and 1997. Global Change Biol. 9:1521–1542.

Olsen, S.R., and L.E. Sommers. 1982. Phosphorus. p. 403–430. *In* A.L. Page et al (ed.) Methods of soil analysis. Part 2. Chemical and microbiological properties. 2nd ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI.

Parmelee, R.W., and D.G. Alston. 1986. Nematode trophic structure in conventional and no-till agroecosytems. J. Nematol. 18:403–407.

Paustian, K., O. Amdren, H.H. Janzen, R. Lal, P. Smith, G. Tian, H. Tiessen, M. Noordwijk, and P.L. Woomer. 1997. Agricultural soils as a sink to mitigate CO_2 emissions. Soil Use Manage. 13:230–244.

Persson, T. 1983. Influence of soil animals on nitrogen mineralization in a Scots pine forest. p. 117–126. *In* P. Lebrun et al. (ed.) Proc. Int. Colloq. of Soil Zool., 8th, Dieu-Brichart, Ottignies-Louvaine-La Neuve. Univ. Catholique de Louvain, Belgium.

Persson, T., E. Baath, M. Clarholm, H. Lundkvist, E. Soderstrom, and B. Sohlenius. 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a Scots pine forest. p. 419–459. *In* T. Persson (ed.) Structure and function of northern coniferous forests. An ecosystem study. Ecol. Bull., Stockholm.

Phillips, D.A., H. Ferris, D.R. Cook, and D.R. Strong. 2003. Molecular control points in rhizosphere food webs. Ecology 84:816–826.

Powlson, D.S., P.C. Brookes, and B.T. Christensen. 1987. Measurement of soil microbial biomass provides an early indication of changes in total soil organic matter due to straw incorporation. Soil Biol. Biochem. 19:159–164.

Puget, P., and R. Lal. 2005. Soil organic carbon and nitrogen in a Mollisol in central Ohio as affected by tillage and land use. Soil Tillage Res. 80:201–213.

Rice, C.W., and M.S. Smith. 1982. Denitrification in no-till and plowed soils. Soil Sci. Soc. Am. J. 46:1168–1173.

Sakamoto, K., and Y. Oba. 1994. Effect of fungal to bacterial biomass ratio on the relationship between CO_2 evolution and total soil microbial biomass. Biol. Fertil. Soils 17:39–44.

Schlesinger, W.H. 1984. Soil organic matter: A source of atmospheric CO_2. p. 111–127. *In* G.M. Woodwell (ed.) The role of terrestrial vegetation in the global carbon cycle. John Wiley & Sons, New York.

Sherrod, L.A., G.A. Peterson, D.G. Westfall, and L.R. Ahuja. 2005. Soil organic carbon pools after 12 years in no-till dryland agroecosystems. Soil Sci. Soc. Am. J. 69:1600–1608.

Six, J., E.T. Elliott, and K. Paustian. 1999. Aggregate and soil organic matter dynamics under conventional and no-tillage systems. Soil Sci. Soc. Am. J. 63:1350–1358.

Six, J., D. Frey, R.K. Thies, and K.M. Batten. 2006. Bacterial and fungal contribution to carbon sequestration in agroecosystems. Soil Sci. Soc. Am. J. 70:555–569.

Soltanpour, P.N., J.B. Jones, Jr., and S.M. Workman. 1982. Optical emission spectrometry. p. 29–65. *In* A.L. Page et al. (ed.) Methods of soil analysis. Part 2. Chemical and microbiological properties. 2nd ed. Agron. Monogr. 9. ASA and SSSA, Madison, WI.

Sparling, G.P. 1997. Soil microbial biomass, activity and nutrient cycling as indicators of soil health. p. 97–119. *In* C. Pankhurst et al. (ed.) Biological indicators of soil health. CAB Int., Wallingford, UK.

Thiet, R.K., S.D. Frey, and J. Six. 2005. Do growth yield efficiencies differ between soil microbial communities differing in fungal:bacterial ratios? Reality check and methodological issues. Soil Biol. Biochem. 38:837–844.

Thomas, G.W. 1996. Soil pH and soil acidity. p. 475–490. *In* D.L. Sparks et al. (ed.) Methods of soil analysis. Part 3. Chemical methods. SSSA Book Ser. 5. SSSA, Madison, WI.

Thornton, C.W., and G.R. Matlack. 2002. Long-term disturbance effects in the nematode communities of South Mississippi woodlands. J. Nematol. 34:88–97.

Vance, E.D., P.C. Brookes, and D.S. Jenkinson. 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19:703–707.

Viketoft, M., C. Palmborg, B. Sohlenius, K. Huss-Danell, and J. Bengtsson. 2005. Plant species effects on soil nematode communities in experimental grasslands. Appl. Soil Ecol. 30:90–103.

Wardle, D.A., R.D. Bardgett, J.N. Klironomos, H. Setälä, W.H. Van der Putten, and D.H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–1633.

Wardle, D.A., and G.W. Yeates. 1993. The dual importance of competition and predation as regulatory forces in terrestrial ecosystems, evidence from decomposer food-webs. Oecologia 93:303–306.

Wardle, D.A., G.W. Yeates, R.N. Watson, and K.S. Nicholson. 1995. The detritus food-web and the diversity of soil fauna as indicators of disturbance regimes in agro-ecosystems. Plant Soil 170:35–43.

Wilcke, W., and J. Lilienfein. 2005. Nutrient leaching in Oxisols under native and managed vegetation in Brazil. Soil Sci. Soc. Am. J. 69:1152–1161.

Yang, X.M., and B.D. Kay. 2001. Impacts of tillage practices on total, loose- and occluded-particulate, and humified organic carbon fractions in soils within a field in southern Ontario. Can. J. Soil Sci. 81:149–156.

Yeates, G.W. 1994. Modification and qualification of the nematode maturity index. Pedobiologia 38:97–101.

Yeates, G.W., T. Bongers, R.G.M. de Goede, D.W. Freckman, and S.S. Georgieva. 1993. Feeding habits in soil nematode families and genera: An outline for soil ecologists. J. Nematol. 25:315–331.