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No-tillage conversion of harvested perennial grassland to annual cropland reduces root biomass, decreases active carbon stocks, and impacts soil biota

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ABSTRACT

Landscape conversion to agricultural use historically began with tillage, a practice now known to dramatically and often negatively affect soil properties and ecosystem processes in grassland dominated ecosystems. However, converted landscapes are generally dominated by annual crops and intensive management compared to the diverse, perennial plant communities they replace. As a result, the effects of tillage and changes in plant community composition are often confounded. To control for tillage, we imposed a randomized complete block design on a never-tilled grassland with two treatments: (1) perennial grassland and (2) never-tilled annual cropland converted from grassland using herbicides. Our objective was to determine what changes in soil properties and soil biota occur with the conversion of perennial grassland to annual never-tilled cropland. Soil physical and chemical properties, microbial biomass, bacterial and nematode assemblage structure, and root biomass were measured to a depth of one meter. Without tillage, conversion from perennial grassland species to annual crops reduced belowground root biomass to 43% of prior biomass. Three years after conversion, readily oxidizable carbon and microbial biomass were significantly lower in annual never-tilled cropland versus perennial grassland in the surface 40 cm. No consistent changes in bacterial or nitrogen fixing community composition were detected. Nematode community structure was significantly different between grassland and cropland, and nematode assemblages were dominated by taxa typical for disturbed, nutrient poor conditions. Our results show that even in the absence of tillage and under best management practices, annual cropping can reduce soil carbon and impact soil biota and food webs important in nutrient cycling after just three years.

1. Introduction

The conversion of perennial-dominated, native plant communities into agricultural cropland typically results in degradation of soil and water quality and dramatic shifts in soil flora and fauna and the ecosystem services they provide (MEA, 2006; Bai et al., 2008). These conversions alter the soil ecosystem in no less than two fundamental ways, cultivation of the soil and the replacement of perennial plant communities with annual crops.

Tillage has dramatic effects on the soil ecosystem, reducing soil C and N (Lamb et al., 1985; Mann, 1986; Huggins et al., 1998; Davidson and Ackerman, 1993), degrading soil structure (Reicosky et al., 1997), and altering soil food webs by reducing microbial biomass (Wardle, 1992), food web complexity (Berkelmans et al., 2003; Sanchez-Moreno et al., 2006; Okada and Harada, 2007), or otherwise altering community structure (Parmelee and Alston, 1986; Lenz and Eisenbeis, 2000; Jackson et al., 2003). Likewise, the replacement of perennial plant communities with annual crops has important impacts for soil properties and biota due to shifts in rooting architecture and activity. Annual crops, in general, are photosynthetically active for shorter periods of time, and have shallower rooting depths and lower root densities than perennial grasslands (Jackson et al., 1996; Baker and Griffis, 2005; Glover et al., 2007). Through root turnover and rhizodeposition, perennial roots maintain SOC (Anderson and Coleman, 1985; McConnell and Quinn, 1988) and more complex soil food webs that regulate important nutrient transformations (Freckman and Ettema, 1993; Neher, 1999).

Because tillage and shifts to annual cropping generally occur together in landscape conversions, separating the effects of each factor on soil carbon and soil biota is often difficult. The numerous studies that have examined the effects of annual crop production on soil carbon and nitrogen stocks in the grassland region of the USA (Swanson, 1915; Lamb et al., 1985; Buyanovsky et al., 1987;

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Dodds et al., 1996; Ajwa et al., 1998; Huggins et al., 1998; Mikhailova et al., 2000; Mikhailova and Post, 2006; Omonode and Vyn, 2006) have all involved agricultural conversion by tillage. Moreover, many studies examine sites where agricultural conversions took place in times of poor soil management (e.g., excessive tillage and poor nutrient management regimes).

Our objective was to determine what changes in soil quality and soil biota occur with the conversion of a perennial grassland into never-tilled, annual-cropland, using current best management practices. To our knowledge this is the first study to convert native, perennial grassland to annual cropland with no current or prior tillage. We hypothesized that the conversion would reduce soil carbon and diminish soil food web structure.

2. Materials and methods

2.1. Site descriptions

The study site was located in a never-tilled bottomland grassland in Niles, Ottawa County, Kansas (N′ 38.58.145, W′ 97.28.616) used for hay production for more than 75 years. The study site soil, formed on an alluvial terrace, is a fine-silty, mixed, mesic, Cumulic Haplustoll (USDA Soil Taxonomy; FAO Cumulic Phaeozem). The plant community consists of over 26 species, all of which are native tallgrass prairie species except for a few non-native, cool-season, annual grass species. Several warm season grasses, including big bluestem (*Andropogon gerardii* Vitam), little bluestem (*Schizachyrium scoparium* Nash), and indian grass (*Sorghastrum nutans* L.) constitute 73% of the total groundcover. Native perennial legumes comprise 9%, native non-leguminous perennial forbs comprise 2%, and non-native annual grasses comprise 11% of plant cover. The land owners mow the vegetation to a height of 8–10 cm once each year in June or July and then remove the hay. They have never applied fertilizer to the site but have burned it periodically. The site has been owned by members of the same family since the hay harvesting began, and management practices are consistent with those recommended for the region (Towne and Ohlenbusch, 1992).

In Summer 2003 we established three replicate blocks in a randomized complete block design. Each block contained two 10 m by 20 m plots, one of which was randomly assigned an annual crop, never-tilled treatment (NT) and the other, a perennial grass (PR) treatment. The existing plant communities in NT plots were sprayed multiple times with herbicide before NT plots were initially planted to soybeans (*Glycine max*) in Summer 2004 (Table 1). Soybeans were again planted in 2005 and followed by sorghum (*Sorghum bicolor*) in 2006, and wheat *(Triticum aestivum*) in 2006 and 2007 (Table 1). NT field management followed typical regional practices for the respective crops (KSU, 1996, 1997) with periodic herbicide and ammonium fertilizer applications (Table 1). Management practices in PR plots remained identical to historical practices for the study site overall.

2.2. Root biomass

Roots were extracted from samples collected on May 27, 2008, at which time we estimated wheat root biomass to be at its peak. Three, 6-cm diameter soil cores from each of the PR and NT plots were collected to a depth of 1 m and separated into sections of 0–10, 10–20, 20–40, 40–60, 60–80, and 80–100 cm. Roots were separated from soil by hydropneumatic root washing (Smucker et al., 1982). Soil and roots were deposited in a six manifold washer where gentle air and water bubbling removed soil particles, and roots were floated onto a submerged sieve. Roots were dried at 50 °C for 48 h and weighed to determine root mass per soil volume and mass per soil area was calculated.

2.3. Soil properties

Soils were sampled three times, 2, 2 1/2 and 3 years after plot establishment: (i) June 20, 2006, (ii) October 6, 2006, and (iii) June 20, 2007. Soil cores (four-centimeter diameter) were taken to a depth of 1 m in a transect across NT and PR sites. Three cores were taken from each plot and separated into 0–10, 10–20, 20–40, 40–60, 60–80 and 80–100 cm soil depth increments. The three samples from each depth were bulked and mixed until complete homogenization. Subsamples of soils were air-dried for analysis of soil chemical and physical properties, refrigerated at 4 °C for microbial biomass and nematode analyses, or stored at −20 °C for molecular analyses.

Soil chemical and physical properties of samples collected in June 2006 and 2007 were analyzed at The Land Institute (TLI) and at the Soil Testing Laboratory at Kansas State University (STL-KSU). Analyses at TLI included pH (Robertson et al., 1999), bulk density by weighing soil samples of known volume after drying at 105 °C to constant weight (Jareell et al., 1999), percent clay by the hydrometer method (Elliott et al., 1999), water stable aggregates (WSA) by wet-sieving (Seybold and Herrick, 2001), and readily oxidizable carbon (ROC; Weil et al., 2003). Briefly ROC was determined on air dried soil, ground and sieved to 0.5 mm. 2.5 g of soil was placed in a 50 ml centrifuge tube filled with 20 ml of 33 M potassium permanganate ($KMnO_4$) solution. The soil and KMnO4 are shaken for exactly 2 min to oxidize the "active" carbon in the sample. The sample is settled using $CaCl_2$ for a minimum of 5 min and the supernatant is diluted with distilled water and measured for absorbance with a 550 nm Hach colorimeter.

Table 1
Management of never tilled crops 2003–2007.

Year	Season	Operation	Product	Rate or yield (kg ha^{-1})
2003	Summer	Herbicide (3X)	Glyphosate	0.25 a.i.[a]
2004	Spring	Herbicide (3X)	Glyphosate	0.25 a.i.[a]
	Summer	Plant	Soybeans	Crop failed due to weed problems
2005	Spring	Herbicide (3X)	Glyphosate	0.25 a.i.[a]
	Summer	Plant	Soybeans	65
	Fall	Harvest	Soybeans	584
2006	Spring	Herbicide	Glyphosate	0.25 a.i.[a]
	Summer	Plant	Sorghum cover crop	8
	Fall	Plant	Wheat	135
	Fall	Fertilize	Monoammonium phosphate	65
2007	Spring	Fertilize	Urea	112
	Summer	Harvest	Wheat	1747

[a] a.i. = active ingredient of respective herbicide.

Analyses at KSU included SOM by the Walkley–Black procedure, SOC and total N by dry combustion on a LECO CN 2000 combustion analyzer, total phosphorus (P) by a modified Kjeldahl digestion after an ammonium acetate extraction, and total potassium (K) by flame atomic absorption. The University of Missouri Agricultural Experimental Station (1998) provides additional details on analyses performed at KSU.

Soil microbial biomass (MBC) was determined from June 2007 samples using the simultaneous chloroform fumigation extraction (sCFE) method (Fierer et al., 2003). Briefly, 10 g of soil from each sample were weighed into two 70 ml glass vials. Forty ml of 0.05 M K_2SO_4 were added to both vials, and 0.5 ml of EtOH-free CH_3Cl were added to one of the vials. Soil-free blanks were also prepared. Vials were sealed and shaken at 150 rpm for 4 h. Extracts were centrifuged for 15 min at 1500 rpm and the supernatant was vacuum filtered through 0.45 μm Whatman filter paper. Microbial biomass extracts were bubbled for 30 min with air to remove any residual CH_3Cl and stored at −20 °C until analysis. Dissolved organic carbon was determined using an O.I. Analytical Model 1010 TOC Analyzer (OI Analytical, College Station, TX, USA) at the University of California Davis Stable Isotope Facility. MBC was calculated as the difference between chloroform and non-chloroform (control) samples divided by a K_{EC}-factor of 0.35 (Sparling et al., 1990).

2.4. Soil bacterial communities

Bacterial community composition was assessed by terminal restriction fragment length polymorphism (T-RFLP) (Liu et al., 1997) for the June 2006, October 2006, and June 2007 samples. Using previously described methods (Culman et al., 2006), 16S RNA bacterial genes were amplified by polymerase chain reaction (PCR) using the fluorescently labeled forward primer 27f (5′-[6FAM] AGA GTT TGA TCM TGG CTC AG-3′) and the unlabeled reverse primer 1492r (5′-TAC GGY TAC CTT GTT ACG ACT T-3′). Three, 50 μl reactions of each sample were pooled and amplified DNA was subject to separate restriction enzyme digests with both HhaI and Sau96 I restriction enzymes. Digested DNA was purified and submitted for terminal fragment-size analysis to Cornell University's Biotechnology Resource Center, Ithaca, NY. Multiple enzymes confirmed trends found in bacterial data and so only data generated from HhaI are reported. T-RFLP analyses were also performed to characterize free-living diazotrophic populations in soils on June 2007 samples. The analyses targeted *nifH*, the structural gene for nitrogenase reductase, with the methods described by Culman et al. (2010).

2.5. Soil nematode communities

Nematode communities were enumerated and identified in the June 2006, October 2006, and June 2007 samples. Nematodes were extracted from 200 to 300 g soil using a combination of decanting–sieving and Baermann funnel methods (Barker, 1985). Samples were sieved through a 0.246 mm sieve to remove larger particles and onto a 36 μm sieve to separate nematodes from excess water. Samples were washed into beakers and placed on Baermann funnels for 48 h. Nematodes were counted using a dissecting microscope and the first 200 nematodes encountered in the sample identified at 200× to 400× to genus or family within one week of extraction, or fixed in 4% formalin until identification.

Nematodes were assigned to trophic groups according to Yeates et al. (1993) and colonizer-persister (cp) groups based on Bongers (1990), and Bongers and Bongers (1998). The cp scale classifies nematodes into five groups from microbial feeders with short life cycles and high fecundity (cp 1 and 2) to omnivores and predators with long life cycles and greater sensitivity to perturbation (cp 4 and 5). Standardized indices of food web structure and function based on characteristics of nematode assemblages allow the effects of environmental stress, dominant decomposition channels, and soil suppressiveness to plant parasites and pathogens to be determined (Bongers, 1990; Wardle et al., 1995; Lenz and Eisenbeis, 2000; Ferris et al., 2001; Ferris and Matute, 2003). Soil food web indices were calculated after Ferris et al. (2001). The Structure Index (SI) is based on the relative abundance of nematodes in higher trophic groups and cp levels and indicates soil food web length and connectance. The Basal Index (BI) enumerates the predominance of nematode groups that are tolerant to disturbance.

2.6. Statistical analysis

2.6.1. Root biomass and soil properties

The PROC MIXED procedure, SAS v.9 (Cary, NC, USA) was used to perform analysis of variance (ANOVA) on the soil, microbial biomass, and root biomass data. Depth and treatment were treated as fixed effects and block as a random effect. Repeated measures were used for depth for soil and root biomass data. For microbial biomass depth was a covariate due to limited degrees of freedom. All soil variables were measured at the June 2007 sampling with significance differences determined at $\alpha = 0.05$ level of probability. When appropriate, we converted soil data to volumetric units (e.g., mass per volume) in order to account for differences in soil bulk density. All means reported for soil physical, biological and chemical data are lsmeans. Volumetric ROC values determined from June 2007 samples for the three upper depths (0–0.4 m) were summed and the ANOVA performed on the resulting sums.

2.6.2. Bacterial and nematode community composition

To discern similarity of bacterial and nematode communities we used a non-metric multidimensional scaling (NMS) ordination with the Sørensen (Bray-Curtis) distance measure (PC-ORD version 4.0 software; McCune and Grace, 2002) using the following parameters: 10 runs with real data, 0.005 stability criterion, and 10 iterations to evaluate stability. NMS analyses were performed on presence/absence data for 279 bacterial terminal restriction fragments for 16S, and 64 nematode taxa. We selected a 2 or 3-dimensional solution based on final stress values and Monte Carlo randomization tests. The final stress and instability values for reported 2-dimensional T-RFLP, and 3-dimensional nematode data were 11.96, <0.005 and 14.33, <0.005, respectively. Correlations between each NMS ordination axis and all soil variables/nematode indices were measured for the nematode community with the *envfit* function in the vegan package in Oksanen et al. (2008). This function tests the significance of the correlations with Monte Carlo tests (1000 permutations) and overlays significant vectors on the NMS ordination. Soil variables and nematode indices that were of primary interest are reported. Final stress values for the conversion study and five county study were 22.3 and 23.9, respectively. We also employed a multiple-response permutations procedures (MRPP) to test the significance of relationships between the experimental factors (treatment, depth, date) within the nematode and bacterial community datasets (Mielke, 1984; McCune and Grace, 2002). The Sørensen distance measure was used to assess the affect of each experimental factor on community structure.

We performed an analysis of variance on the nematode indices data using the PROC MIXED procedure in SAS v.9, where the sampling date was treated as a repeated measure and soil depth as a covariable. We used repeated measures to account for multiple sampling dates with this univariate data.

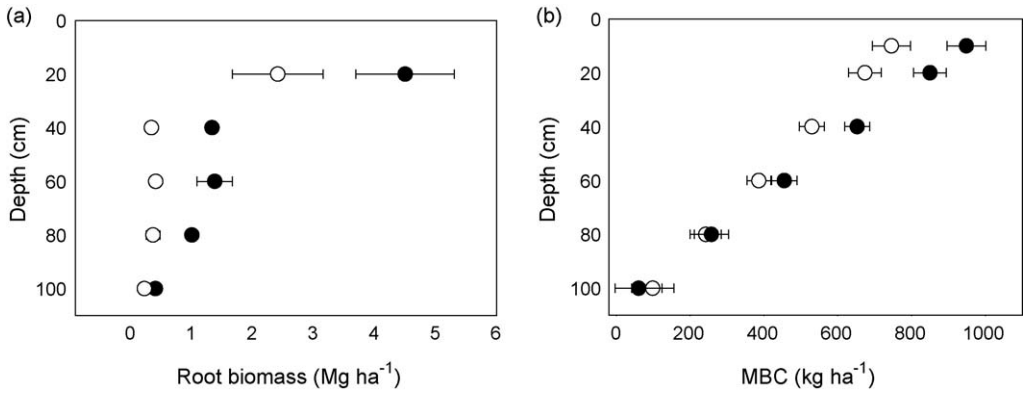

Fig. 1. (a) Root biomass (Mg ha^{-1}) in perennial grasslands sites (closed circles) and never-tilled cropland (open circles) at estimated peak wheat biomass (May 2008). Significant differences were detected at all depths. (b) Relationship of microbial biomass carbon (MBC) to depth in perennial grasslands (closed circles) and never-tilled cropland (open circles). Significant differences were detected to 40 cm. Bars indicate the standard error of the mean.

3. Results and discussion

3.1. Root biomass

We measured significant differences in root biomass between no-till (NT) and perennial grass (PR) plots at all depths (Fig. 1a). The ANOVA for root biomass was significant for treatment ($p = 0.039$) and for depth ($p < 0.0001$) with no treatment by depth interaction. Overall, NT plots contained only 43% of the root biomass measured in PR plots in the surface 1 m of soil (3.77 Mg ha^{-1} vs. 8.63 Mg ha^{-1}; Fig. 1a). Differences were apparent even in the surface 0–40 cm soil depth (the primary rooting zone for wheat), where root biomass in NT plots was less than half that measured in PR plots (2.8 Mg ha^{-1} vs. 5.8 Mg ha^{-1}). Perennial roots were more evenly distributed vertically through the soil profile compared to wheat roots. Root biomass between 60 and 100 cm in PR plots was more than twice that measured in NT plots (1.41 Mg ha^{-1} vs. 0.60 Mg ha^{-1}). Previous root data collected from the site also indicated roots in perennial grasslands extended 1 m deeper than wheat roots (Glover et al., 2010).

Large differences in root biomass between wheat roots and perennial grasslands have been previously reported (Buyanovsky et al., 1987). Our root biomass values of 8.63 Mg ha^{-1} from grasslands fall within the range typically reported for tallgrass prairies (7–21 Mg ha^{-1}; Rice et al., 1998) and wheat root biomass were lower than values to 50 cm reported by Buyanovsky and Wagner (1987) (3.7 Mg ha^{-1} vs. 4.7–5.6 Mg ha^{-1}). The greater biomass and deeper distribution of roots in PR plots suggest that the perennial plant communities provide a relatively greater contribution of organic carbon to the soil, thus providing more belowground energy inputs for biological activity throughout the soil profile (Anderson and Coleman, 1985; McConnell and Quinn, 1988; Leake et al., 2006; Ruf et al., 2006; Fornara and Tilman, 2008).

3.2. Soil properties

Three years after conversion, we did not detect significant differences between NT and PR plots on a range of soil physical and chemical properties (Table 2). Because tillage was not used, we did not expect to find changes in texture or structure. Given the short period of time since conversion, we also did not expect to measure significant differences in relatively static soil properties, such as SOC, total N and P.

Although we did not detect significant treatment effects on ROC levels at any single depth, when values for the surface three soil depths (0–40 cm) were summed and analyzed, ROC was significantly lower (4%) in NT plots than PR plots ($p = 0.024$). ROC, one gauge of active carbon, measures the simple carbohydrates, amino acids, and sugars in SOC that are easily hydrolyzed and oxidized (Loginow et al., 1987) making them easily accessible by microbial communities. Small changes in ROC and other labile fractions of SOC may provide an early indication of soil degradation or improvement in response to management practices (Weil et al., 2003). Changes in active carbon pools can be two to four times greater than changes in total C after the initiation of new management practices (Elliott et al., 1994; Marriott and Wander, 2006) and they are more highly correlated with other soil quality indicators including microbial respiration, aggregate stability and plant productivity (Weil et al., 2003). Although these differences are small compared to the total SOC losses of 29% after 75 years of annual tilled agriculture measured in the region at similar sites (Glover et al., 2010), they show soil fertility losses after conversion to annual crops in the absence of tillage.

3.3. Soil microbial biomass

Given the central role that microbial communities play in nutrient and energy cycling, changes in microbial biomass carbon (MBC) serve as useful indicators of how management practices affect the soil ecosystem, with reductions in biomass generally indicating negative impacts on ecosystem processes (Singh et al., 1989; Garcia and Rice, 1994; Wardle, 1998). MBC was significantly reduced to 40 cm in NT plots compared to PR plots, but no differences were detected below 40 cm (0–10 cm $p = 0.0097$, 10–20 cm $p = 0.0087$, 20–40 cm $p = .0148$; Fig. 1b). In the top 10 cm MBC levels were 202 kg ha^{-1} (20%) lower in NT plots. The reductions in MBC observed in the annual croplands could have resulted from several factors, including reduced inputs from plants via roots exudation and rhizodeposition (Wardle, 1992; Paterson, 2003; Waldrop et al., 2006), fertilization with inorganic N (Garcia and Rice, 1994; Lovell et al., 1995; Bardgett et al., 1999; Treseder, 2008), herbicide application (Sanyal and Shrestha, 2008), and/or decreases in plant diversity with concurrent decreases in the diversity of C substrate (Zak et al., 2003; Waldrop et al., 2006). Although other studies have reported large reductions in MBC in cultivated soils compared to perennial grasslands (Jenkinson and Powlson, 1976; Lynch and Panting, 1980a,b; Schimel et al., 1985; Acosta-Martinez et al., 2007), to our knowledge, this is the first study recording changes in MBC following conversion of native (albeit harvested) tallgrass prairie to an annual agricultural crop, without ever applying tillage.

Table 2
Soil properties from 6 depths[a,b,c].

Depth	Trt	Clay (%)	WSA (%)	Total P (Mg ha^{-1})	Total N (Mg ha^{-1})	SOC (Mg ha^{-1})	SOM (Mg ha^{-1})	ROC (Mg ha^{-1})
0–10 cm	NT	23	89	0.53	2.91	33.15	55.31	1.05
	PR	23	90	0.49	2.75	32.47	54.39	1.01
10–20 cm	NT	30	89	0.55	2.39	27.03	48.58	0.73
	PR	30	87	0.56	2.4	28.31	48.78	0.8
20–40 cm	NT	35	85	0.96	3.52	39.52	67.77	0.99
	PR	36	85	1.01	3.43	39.11	67.18	1.02
40–60 cm	NT	38	79	0.98	2.32	25.17	43.27	0.6
	PR	34	74	1.03	2.16	24.82	38.39	0.58
60–80 cm	NT	35	74	1.03	1.6	17.3	29.39	0.42
	PR	33	75	1.12	1.48	17.53	27.19	0.37
80–100 cm	NT	35	74	1.15	1.32	16.39	24.49	0.32
	PR	34	74	1.2	1.23	18.59	25.59	0.3

[a] Significant differences were detected in 0–40 cm for bulked ROC ($p = 0.029$).
[b] All data reported on analyses from June 2007 sampling, except WSA which were analyzed from the Sept 2006 sampling.
[c] WSA: Water stable aggregates, P: phosphorus, N: nitrogen, SOC: soil organic carbon, SOM: soil organic matter, ROC: readily oxidizable carbon.

3.4. Soil bacterial communities

Sampling date and depth were the largest drivers of bacterial community structure according to NMS analysis (Fig. 2). Communities separated by date along axis 1 (explaining 31% of the variation) and by depth along axis 2 (explaining 58% of the variation). Despite the treatment effects on MBC levels measured in the surface depths, consistent treatment differences between NT and PR were not found in bacterial community structure (data not shown). Likewise, consistent treatment differences between NT and PR were not exhibited in the N-fixing community (data not shown). Reductions in MBC with no detectable differences in community structure could have resulted from reductions in only specific bacterial groups or from reductions in fungal communities that were not measured here (Bardgett et al., 1999; Wakelin et al., 2007). Continued monitoring will be necessary to detect possible shifts in microbial communities over time.

3.5. Soil nematode communities

Nematodes, a diverse and abundant group of soil fauna, participate at multiple trophic levels making them key indicators of soil food webs and processes (Bongers and Bongers, 1998). Differences in nematode community structure generally reflect concurrent changes in diverse soil biotic groups and ecosystem processes including N mineralization, pest suppression and C sequestration (Berkelmans et al., 2003; Ferris and Matute, 2003; Hohberg and Traunspurger, 2005). We measured significant treatment, depth and sampling date effects on nematode community structure based on NMS ordination of nematode taxa to a depth of 40 cm (all factors, $p < 0.0001$). Despite the large variance in nematode communities, management history had a strong effect on them (Fig. 3).

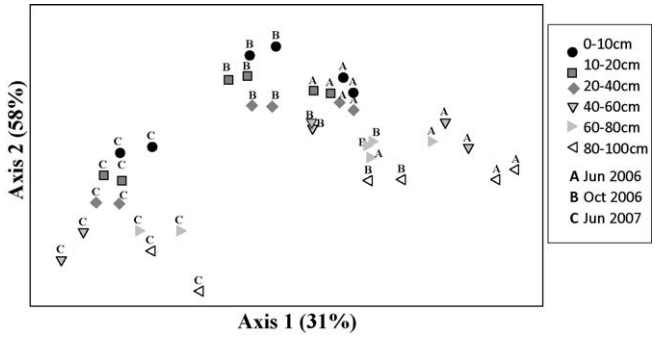

Fig. 2. Non-metric multidimensional scaling analysis of bacterial community structure at 6 depths (0–100 cm). Each data point represents the average of 3 replicates. Groups of bacterial communities are significantly different for depth and year ($p < 0.001$). Axis 1 (date) explains 31% of the variation in bacterial community structure between samples, axis 2 (depth) explains 58% of the variation.

Additional information on soil food web characteristics may be inferred by grouping nematode taxa according to their functions and rating overall populations by standardized indices such as the structure index (SI) and basal index (BI) (Ferris et al., 2001). Nematode communities in NT plots were characterized by a 60% higher BI over all depths (0–100 cm) relative to PR plots (39 and 23, respectively) indicating impoverished nutrient status and stressed conditions in NT plots (BI; $p = 0.053$, Table 3) (Ferris et al., 2001). A higher BI in NT may be a function of reduced inputs of readily accessible carbon from plant roots, where root biomass was less than half that of PR (Dong et al., 2008). Basal indicator organisms have relatively short generation times and high reproductive rates that allow them to survive in nutrient poor as well as nutrient rich conditions and tolerate environmental stress (Bongers and Bongers, 1998). Annual systems with long fallow periods, during which few biological inputs from plant roots and shoots are available to feed the soil food web, often have higher BI levels than

Table 3
Means and standard errors (SE) of nematode soil food web indices.

Depth	Trt	Structure index	Basal index
		Mean ± SE	Mean ± SE
0–100 cm[a]	NT	61.69 ± 2.54	26.75 ± 1.36
	PR	70.33 ± 2.39	21.96 ± 1.45
0–10 cm	NT	70.7 ± 3.3	23.8 ± 2.7
	PR	82.3 ± 2.5	14.5 ± 1.8
10–20 cm	NT	75 ± 3.8	20.6 ± 3.2
	PR	82.8 ± 3.4	14 ± 2.5
20–40 cm	NT	69.9 ± 3.2	22.9 ± 2.7
	PR	74.8 ± 3.2	19.9 ± 2.4
40–60 cm	NT	59.3 ± 4.1	29.2 ± 2.5
	PR	69.7 ± 5	22.7 ± 3
60–80 cm	NT	51.3 ± 6.1	34.8 ± 3.6
	PR	64.3 ± 6	27.3 ± 4.2
80–100 cm	NT	60.4 ± 5.5	30 ± 4
	PR	59.2 ± 7.5	30.9 ± 4.5

NT: Never-tilled annual cropland and PR: perennial grassland.
[a] Treatment differences for SI and BI were significant ($p = 0.060$ and 0.053, respectively) with no treatment by depth interaction.

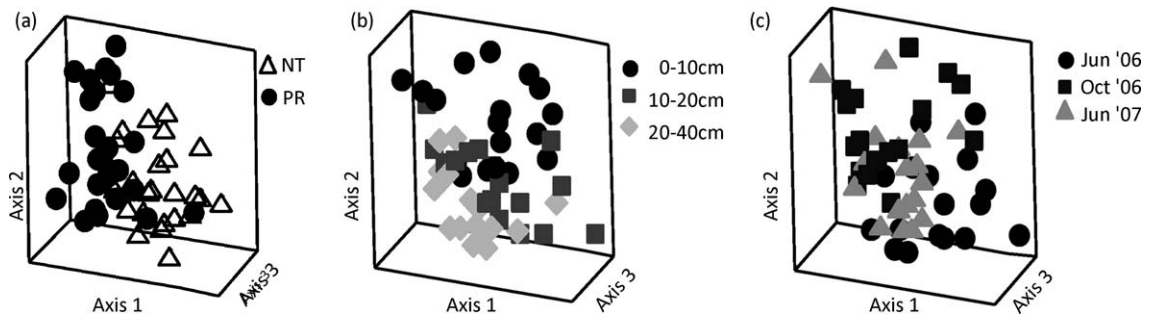

Fig. 3. Non-metric multidimensional scaling analysis of the surface 3 depths (0–40 cm) of the nematode community. The three panels display the same data with individual samples coded for the three experimental factors: management history (a), depth (b), and sampling date (c). Significant differences were detected between groups of nematode communities for treatment, depth and date ($p < 0.0001$). Never-tilled annual cropland (NT) and perennial grassland (PR).

systems with continuous crop growth (Wang et al., 2006; DuPont et al., 2009).

Relative to nematode communities in NT plots, communities in PR plots had higher assemblage structure over all depths (SI; $p = 0.060$, Table 3). A high SI indicates nematode communities rich in predators and omnivores, trophic groups associated with low stress and low disturbance environments (Ferris et al., 2001, 2004). Large numbers of predator/omnivores in highly structured systems may perform top-down regulation which can significantly reduce plant parasite pressure (Khan and Kim, 2007; Sanchez-Moreno and Ferris, 2007) and improve plant primary productivity. Nematode communities under perennials often have significantly greater structure than annual crops (Sohlenius and Sandor, 1987; Freckman and Ettema, 1993; Neher and Campbell, 1994). In adjacent fields, Culman et al. (2010) report that SI values are not only greater in perennial grasslands than croplands, but also that the treatment effects on SI increase with depth. Reductions in soil food web structure under annual crops may have resulted from several factors typical in annual cropping systems including reduced root biomass and diversity (Wardle et al., 2005; Ilieva-Makulec et al., 2006), fertilization with inorganic N (Tenuta and Ferris, 2004), application of herbicides (Mahn and Kästner, 1985), or increased machinery traffic (Bouwman and Arts, 2000).

3.6. Correlations between nematode communities and soil properties

Comparisons of intact and converted landscapes have often been made long after conversion, making it difficult to identify which properties and processes would serve as sensitive, early indicators of degradation. We analyzed relationships between management practices, soil properties and nematode communities in PR and NT plots in our study (hereafter referred to as the 'conversion study'; CS; Fig. 4a) and, for purposes of comparison, we also analyzed similar relationships amongst data collected from five other paired harvested perennial grassland (PR) and annual crop (AG) sites (hereafter referred to as the 'long term study; LTS') as described by Culman et al. (2010) (Fig. 4b). The data points represent nematode communities from individual samples made up of 64 genera analyzed with NMS. Vectors represent the correlations of soil properties and nematode indices with nematode communities. The length and angle of each vector represent the strength and direction of the relationship to the nematode community. Nematode communities were significantly different between perennial and annual systems in CS (Fig. 4a) as well as FCS (Fig. 4b). Treatment differences are represented in Axis 1, while differences in depth are represented in Axis 2.

Nematode communities in perennial systems (LTS and CS) were associated with a high SI and nematode communities in annual systems were associated with a high BI (Fig. 4a and b). In CS three years after conversion, the vectors illustrate a strong, positive relationship between nematode communities in PR plots with high SI values, and nematode communities in NT plots with high BI values ($R^2 = 0.66$, 0.65, respectively; Fig. 4a). These relationships are similar to those measured in LTS fields after 75–100 years of production ($R^2 = 0.42$ for SI; $R^2 = 0.36$ for BI; Fig. 4b). The similar characterizations of nematodes in long-term annual cropping

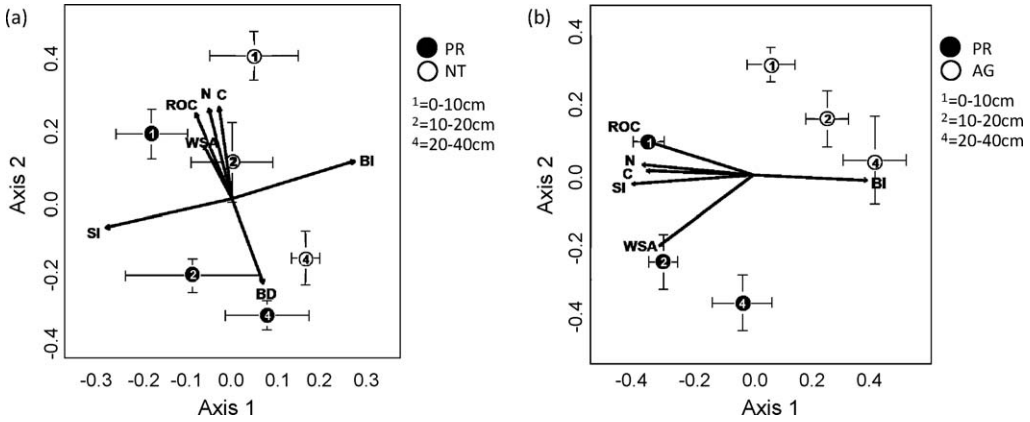

Fig. 4. Nematode community structure 0–40 cm showing differences in management history and environmental variables. (a) Conversion study plots with never-tilled annual cropland (NT) and perennial grassland (PR), (b) long term study managed for 75–100 years as annual-cropland (AG) and perennial grassland (PR). The data points represent nematode communities from individual samples (composed of 64 identified taxa) analyzed with NMS and vectors represent the correlations of soil properties and nematode indices with nematode communities. The length and angle of the vector represent the strength and direction of the relationship to the nematode community. All vectors depict statistically significant correlations ($\alpha = 0.05$). WSA: Water stable aggregates, ROC: readily oxidizable carbon, BD: bulk density, N: nitrogen, C: carbon, SI: structure index, BI: basal index.

systems and never-tilled annual crops after only three years suggest that nematodes may be useful early indicators of soil ecosystem change.

In contrast to the nematode indices, the relationship between nematode communities and soil properties is different in plots recently converted to annual crop production compared to those converted nearly a century ago. In LTS, vectors for soil C, N and water stable aggregates (WSA) were correlated with nematode communities in grasslands (Fig. 4b). In our CS study (Fig. 4a), soil properties were not highly correlated with nematode communities in the grassland sites. Instead, ROC, N and WSA were positively correlated with nematode communities in upper depths according to NMS analysis. Since reductions in soil C, N and WSA can take decades, more time is needed to determine if conversion will affect these properties similarly to the trends observed in the long-term study.

4. Conclusions

In this study we examined the changes in soil properties and biota following the conversion of a perennial grassland to a never-tilled, annually cropped field. Although tillage was specifically controlled for, other factors known to affect soil properties and biota (e.g., application of inorganic N fertilizer and herbicides, and reduced plant root biomass and diversity) were not. These factors are typical in modern no-till cropping systems and may have contributed to differences between the two production systems. Nevertheless, observed shifts in labile carbon pools and soil biota occurring with no-tillage conversion of perennial grassland to annual cropland suggest that reductions in soil quality and biological function associated with landscape conversion are not driven by tillage alone.

We found that the no-tillage conversion of perennial grassland to annual cropland reduced the active soil carbon fraction (ROC) and changed the composition of soil biotic communities after 3 years. Root biomass under annual crops was less than half that of perennial grasslands suggesting that large root-derived energy sources may contribute to composition of soil biota and accumulation of soil C. Although reductions in soil carbon and related soil biota in never-tilled plots were small, some patterns are similar to those seen by Culman et al. (2010) after 75 years of tilled, annual agriculture and may signal successive changes in other soil biota and associated soil physical properties. Further study is needed to determine whether our ability to support ecosystem services and high yield in our global agricultural fields is limited by tillage alone, or ultimately by our high reliance on annual crops.

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