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Management intensity alters decomposition via biological pathways

Kyle Wickings · A. Stuart Grandy · Sasha Reed · Cory Cleveland

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Abstract Current conceptual models predict that changes in plant litter chemistry during decomposition are primarily regulated by both initial litter chemistry and the stage—or extent—of mass loss. Far less is known about how variations in decomposer community structure (e.g., resulting from different ecosystem management types) could influence litter chemistry during decomposition. Given the recent agricultural intensification occurring globally and the importance of litter chemistry in regulating soil organic matter storage, our objectives were to determine the potential effects of agricultural management on plant litter chemistry and decomposition rates, and to investigate possible links between ecosystem management, litter chemistry and decomposition, and decomposer community composition and activity. We measured decomposition rates, changes in litter chemistry, extracellular enzyme activity, microarthropod communities, and bacterial versus fungal relative abundance in replicated conventional-till, no-till, and old field agricultural sites for both corn and grass litter. After one growing season, litter decomposition under conventional-till was 20% greater than in old field communities. However, decomposition rates in no-till were not significantly different from those in old field or conventional-till sites. After decomposition, grass residue in both conventional- and no-till systems was enriched in total polysaccharides relative to initial litter, while grass litter decomposed in old fields was enriched in nitrogen-bearing compounds and lipids. These differences corresponded with differences in decomposer communities, which also exhibited strong responses to both litter and management type. Overall, our results indicate that agricultural intensification can increase litter decomposition rates, alter decomposer communities, and influence litter chemistry in ways that could have important and long-term effects on soil organic matter dynamics. We suggest that future efforts to more accurately predict soil carbon dynamics under different management regimes may need to explicitly consider how changes in litter chemistry during decomposition are influenced by the specific metabolic capabilities of the extant decomposer communities.

Keywords Agriculture · Decomposition · Land-use change · Microarthropods · Microorganisms · Plant litter · Soil carbon

K. Wickings (✉) · A. Stuart Grandy
Department of Crop and Soil Sciences, Michigan State University, East Lansing, MI 48824, USA
e-mail: wickings@msu.edu

S. Reed
US Geological Survey, Southwest Biological Science Center, Moab, UT, USA

C. Cleveland
Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT, USA

Introduction

The renewed interest in developing energy alternatives to petroleum is spurring global increases in the rate of land conversion and land-use change, as well as large increases in the rate of agricultural intensification (Secchi et al. 2008; Fargione et al. 2008). For example, in the US alone, corn production is now greater than at any time in the past 60 years (USDA 2009), and the continued demand for productive agricultural land is rapidly driving expansion of crop production into grasslands. The U.S. Department of Agriculture (USDA) Conservation Reserve Program (CRP) currently provides land managers with financial incentives to convert marginal, environmentally sensitive agricultural lands to perennial grasslands that enhance ecosystem services including water, nutrient, and organic matter retention (Lal et al. 2004). However, while there are currently $\sim$13.3 million hectares in the CRP, enrollment is expected to substantially decline over the next several years, as rising prices for corn and soybeans drive increases in the proportion of CRP lands converted to agriculture (Secchi et al. 2008).

While converting grasslands into agriculture could profoundly affect soil organic matter dynamics (and ultimately the flux of CO_2 between the biosphere and the atmosphere; Searchinger et al. 2008), predicting the effects of land-use change and agricultural intensification on the global carbon (C) cycle requires a more complete understanding of the factors that regulate litter decomposition and organic matter chemistry. We know that in general, litter chemistry strongly regulates decomposition and soil organic matter dynamics (Swift et al. 1979; Melillo et al. 1982; Preston et al. 2009) and this is reflected in both conceptual and analytical models of the process (Baum et al. 2009; Rubino et al. 2009). Numerous studies have found that lignin and its phenolic derivatives are chemically protected from microbial attack and may promote the formation of highly stable, large polymers (Stevenson, 1994; Ekschmitt et al. 2005). Consistent with this observation, most soil C models include a pathway in which complex, high-lignin litter can bypass microbial pools and move directly into stable soil organic matter (Parton et al. 1987). Similarly, Kleber et al. (2007) presented evidence that the molecular structure of organic molecules determines their potential interactions with mineral surfaces, and Golchin et al. (1994) demonstrated that decomposition of particulate plant material alters soil structure by stimulating aggregate formation. Still other research highlights the importance of lipids, waxes (Lorenz et al. 2007) nitrogen (N)-bearing compounds (Gleixner et al. 2002) and microbially-derived carbohydrates (Kiem and Kogel-Knabner 2003) in long-term C stabilization. Taken together, these studies provide compelling evidence that plant litter chemistry—either directly or through its effect on the chemistry of microbial decomposition products—can strongly influence soil organic matter dynamics and stabilization.

Current conceptual models predict changes in litter chemistry over the course of decomposition from initial litter chemistry and the extent of mass loss (Couteaux et al. 1995; Wolf and Wagner 1998; Berg 2000; Quideau et al. 2005; Moorhead and Sinsabaugh 2006; Mathers et al. 2007; Berg and McClaugherty 2008). These models suggest consistent changes in the chemical structure of organic matter (e.g., initial increases in N due to immobilization followed by declines in cellulose and relative increases in lignin) as litter passes through the 'decomposer funnel' (Baldock et al. 1992; Gregorich et al. 1996; Moorhead and Sinsabaugh 2006; Grandy and Neff 2008; Herman et al. 2008). While these models appropriately acknowledge the importance of litter chemistry, most do not explicitly consider the potential effects of variations in decomposer community structure and function on litter chemistry and decomposition.

Nonetheless, recent research suggests that decomposer community composition could regulate decomposition (Balser and Firestone 2005; Osler and Sommerkorn 2007; Valaskova et al. 2007; Strickland et al. 2009), and variations in litter chemistry could result in functionally distinct decomposer communities that vary in their ability to metabolize different substrates (Adair et al. 2008; Grandy et al. 2008; Preston et al. 2009). Further, recent evidence suggests that major shifts in ecosystem management could alter soil environmental conditions and drive changes in the composition, abundance and activity of various biota including soil mesofauna and microbes (Bedano et al. 2006; Cole et al. 2008; Jesus et al. 2009; Lauber et al. 2009). Thus, accurately predicting management effects on litter chemistry through time may require explicitly including the effects of variations in decomposer community composition on decomposition.

Given the potentially important but poorly understood interactions between ecosystem management, organic matter chemistry, and soil biota, our goal was to investigate the effects of agricultural management type on litter mass loss, chemistry, and decomposer communities. Here, we addressed three questions: (1) Do mass loss rates of different litter types vary with ecosystem management? (2) Are changes in litter chemistry during decomposition influenced by initial litter chemistry and ecosystem management? and (3) Are patterns of litter mass loss and chemistry related to microbial and mesofaunal community composition and microbial extracellular enzyme activity? We hypothesized that during decomposition, variations in litter mass loss and litter chemistry would vary with management type, and those variations would correlate with management-specific variations in decomposer community structure and function.

Materials and methods

Study site

The study was conducted at the W.K. Kellogg Biological Station (KBS) Long-Term Ecological Research Site (LTER) during the 2008 growing season (June 6–September 22). To assess the effect of ecosystem management on decomposition, we placed litter bags in three ecosystems: conventional-tillage agriculture (CT); no-tillage agriculture (NT), and an early successional old field (OF). Each of the three ecosystem types was replicated four times and each of the 12 experimental plots was 1 ha. Treatment plots were organized following a randomized complete block design. The agricultural systems consist of corn–soybean–wheat rotations and are maintained using Michigan State University recommended best-management practices for fertility and pest management (Crum et al. 2009). Primary cultivation in CT includes chisel-plowing ($\sim$20 cm), which leaves a considerable amount of crop residue exposed at the soil surface, followed by shallow cultivation using a soil finisher ($\sim$10 cm). OF plots were fertilized and cultivated for agricultural production until 1989 at which point most management ended; however, OF sites are burned annually in the spring. OF sites consist of mixed annuals and perennials including numerous grasses (*Bromus inermis*, *Setaria* spp.), asters (*Solidago, Euthamia* spp.), *Chenopodium*, and *Asclepias,* as well as small trees and shrubs such as *Robinia* and *Rhus* spp. (Gross 2008).

Mean annual precipitation at the LTER site is $\sim$890 mm year^{-1} and soils are classified as Kalamazoo (fine-loamy) and Oshtemo (coarse-loamy) mixed, mesic, Typic Hapludalfs (Alfisols) developed on glacial outwash (Crum and Collins 1995). Annual litter inputs in 2007 and 2008 vary between OF and the two agricultural ecosystems. CT and NT receive approximately 650 ± 20.1 g m^{-2} of aboveground corn and 390 ± 16.2 g m^{-2} of aboveground wheat residue, while OF produces an average of $\sim 180 \pm 46.5$ g m^{-2} of aboveground litter (Harwood and Robertson 2009a, b).

Litter bags

Corn and grass leaf and stem material was collected on or near the KBS LTER. Standing dead corn plants were collected in Fall 2007. Live grass shoots (primarily *Bromus inermis*, Leyss) were collected in May 2008 from early successional fields at KBS similar to the ones studied here and dried. Grass shoots were approximately 40–50 cm tall at the time of collection and seed heads were not present. These litter types were selected not only to obtain litter of different starting qualities, but also to utilize litter that was representative of the cultivated and uncultivated experimental systems. Air dried litter was cut into 2–4 cm pieces, homogenized, and placed into 7×7 cm nylon mesh litter bags (1.5 mm mesh size) with a starting mass of $\sim$7 g. Litter bags were placed in direct contact with the soil surface in all plots and secured at their corners to keep them in contact with the soil for the duration of the experiment. Fourty-eight litter bags (24 corn, 24 grass) were placed in each of 12 plots (4 CT, 4 NT and 4 OF) for a total of 576 l bags. Paired bags of the same litter type were placed in contact with one another and were treated as a single unit, but were separated for laboratory analyses. In CT and NT systems, bags with different litter types were placed four corn rows apart. OF bags were placed along two transects (one transect per litter type) and transects were placed $\sim$4 m apart. Within rows and transects, bag pairs were placed $\sim$60 cm apart. All litter bags were placed in the field on June 06, 2008 and corn and grass pairs (12 each) were collected after 6, 17, 26, 39, 72 and 108 days of

decomposition. After collection, bags were stored at 4°C for analysis within 24 h, except litter used for microbial community analysis which was stored at −80°C. After each sampling event, half of the corn and grass litter bags (12 each) were used for the measurement of extracellular enzymes and bacterial and fungal community composition using quantitative polymerase chain reaction analyses (qPCR), and the remaining 24 l bags were used for mesofaunal extraction and for the determination of mass loss and litter chemistry.

Extracellular enzyme activity

Subsamples from each litter bag (0.5 g) were homogenized with 50 mM sodium acetate buffer using a small kitchen blender. Buffer solution was adjusted to pH 6.5 reflecting the pH of surface litter in the field from all three land-use treatments. Homogenates were used to assess the activity of four extracellular enzymes involved in C and nutrient cycling following established methods (Saiya-Cork et al. 2002; Grandy et al. 2007). Briefly, the activity of three hydrolytic enzymes (*β*-glucosidase, *N*-acetyl-*β*-D-glucosidase, and acid phosphatase) was assessed using black, 96-well microplates and compound-specific substrates containing the synthetic fluorescing molecule methylumbelliferone (4-methylumbelliferyl-*β*-D-glucoside EC 3.2.1.21, 4-methylumbelliferyl-*N*-acetyl-*β*-D-glucosaminide EC 3.2.1.14, and 4-methylumbelliferyl-phosphate EC 3.1.3.1). The activity of one oxidative enzyme (phenol oxidase) was also measured using clear 96-well microplates and L-3,4-dihydroxyphenylalanine (L-DOPA EC 1.10.3.2) to assess enzyme activity associated with the breakdown of lignin. All plates were incubated at 15°C for 6–24 h. Hydrolase activity was determined using a flourometer (355 nm excitation and 460 nm emission) and phenol oxidase activity was measured using a spectrophotometer with a 450 nm filter (Thermo Flouroskan and Multiskan, Thermo Scientific, Hudson, NH). Hydrolase activity is reported as μmol of methylumbelliferone h^{-1} g^{-1} litter and that of phenol oxidase is reported as absorbance, also in μmol h^{-1} g^{-1} l.

DNA extraction and quantitative PCR analysis

Microbial DNA was isolated from decomposing litter (Hofmockel et al. 2007; Manerkar et al. 2008; Redford and Fierer 2009) at three different times (June 6, June 23 and September 22) using the MoBio PowerSoil DNA extraction kit (MoBio Laboratories, Carlsbad, CA, USA). Briefly, 0.05–0.15 g of litter was aseptically placed into a bead tube for extraction following the manufacturer's instructions. The relative abundance of bacteria and fungi was quantified using primer sets and PCR conditions from Fierer et al. (2005). The qPCR assays were conducted in 96-well plates with three analytical replicates per sample and per dilution standard. Standard curves to estimate bacterial and fungal small-subunit rRNA gene abundance (16S rRNA genes for bacteria and 18S rRNA for fungi) consisted of a 10-fold serial dilution of a plasmid containing a full-length copy of the gene. Plasmid standards were created from *E. coli* and *Saccharomyces cereviciae* for bacteria and fungi respectively. For all samples, each 25 μl qPCR reaction contained 12.5 μl of PowerSYBR Green PCR Master mix (Applied Biosystems, Foster City, CA, USA), 1.25 μl each of 10 μM forward and reverse primers (Eurofins MWG Operon, Huntsville, AL, USA), and 5 μl of sterile, nuclease free water (Promega, Madison, WI, USA). DNA extracted from all samples was diluted to roughly equal concentrations before analysis, and standard and environmental DNA samples were added at 5 μl per reaction. All reactions were carried out on a StepOne Plus qPCR system (Applied Biosystems) and melt curve analyses and agarose gel electrophoresis were used to confirm that the fluorescence signal resulted from specific PCR products and not from amplification artifacts.

Mesofaunal community composition and mass loss

Within 3–4 h of litter collection, one litter bag from each pair was placed on a modified Berlese funnel (BioQuip, Inc.) for mesofaunal extraction. Over the course of the 5 days extraction, temperature was gradually increased from room temperature (approximately 22°C) to 50°C, mesofauna were extracted into 90% ethyl alcohol and identified to functional groups and morpho-species. After litter was removed from Berlese funnels, mass loss was determined by recording the air-dried litter mass remaining within each bag, and subsamples from each bag were ashed at 500°C in a muffle furnace. All litter mass values were converted to percent ash-free dry mass remaining.

Litter chemistry

The molecular chemistry of litter (collected at 0 and 108 days) was assessed using pyrolysis-gas chromatography/mass spectroscopy (GCMS) following modifications to the procedures outlined in Grandy et al. (2009). Briefly, pulverized litter was pulse-pyrolyzed in quartz tubes on a Pyroprobe 5150 (CDS Analytical Inc., Oxford PA) at 600°C. Pyrolized samples were transferred onto a gas chromatograph at 300°C (Trace GC Ultra, Thermo Scientific) where they were further separated by passage through a heated, fused silica capillary column (60 m × 0.25 mm inside diameter). Gas chromatograph (GC) oven temperature was increased from 40 to 270°C at a rate of 5°C min^{-1} with a final temperature ramp to 310°C (30°C min^{-1}). Finally, compounds were transferred to a mass spectrometer (Polaris Q, Thermo Scientific) via a 270°C heated transfer line where they were ionized at 200°C. Peaks were identified using the Automated Mass Spectral Deconvolution and Identification System (AMDIS V 2.65) and the National Institute of Standards and Technology (NIST) mass spectral library (Grandy et al. 2008; 2009). Compound abundances were determined relative to the size of the largest compound peak within a sample. Samples were also analyzed for total C and N at 0 and 108 days using an elemental analyzer (Costech ECS 4010, Costech Analytical Technologies, Inc, Valencia, CA).

Statistical analysis

Litter mass loss, C and N concentration, and molecular chemistry were analyzed using one- and two-way analyses of variance (ANOVA). Litter molecular chemistry data were also analyzed using non-metric multidimensional scaling (NMS) (Kruskal 1964) using PC-ORD version 4.14 (McCune and Mefford 1999). NMS uses a distance matrix to determine the optimum ordination of samples in multiple dimensions (ordination axes) based upon sample composition (McCune and Grace 2002). As with many ordination techniques, samples that are close to one another in the ordination space are more similar to each other than those that are farther apart. All NMS analyses were run using the Sorensen (Bray-Curtis) distance measure and run parameters included a random starting configuration, an instability criterion of 0.0005, and 20 and 50 runs with real and randomized data, respectively (McCune and Grace 2002). The final number of dimensions was determined using a Monte Carlo simulation, which assessed whether the final solution provided a significant ($P < 0.05$) reduction in stress than would be expected by chance (McCune and Grace 2002). Relationships between chemical groups and ordination axis scores were assessed using Pearson's correlation in SAS (SAS version 8, SAS Institute, 1999). NMS was chosen over other ordination techniques because it is considered most amenable to ecological data that often do not meet assumptions such as normality (McCune and Grace 2002). Correlation was also used to examine relationships among litter chemistry, mass loss, total average enzyme activity, fungal:bacterial ratios and detritivore abundances.

Microbial and mesofaunal abundances (means from individual sampling dates) were analyzed using two-way analysis of variance (ANOVA). Because soil faunal abundance rarely meets the assumptions of normality and linearity, abundance data were square root transformed prior to analysis. Finally, enzyme activity was analyzed using a mixed model analysis for repeated measures using litter and ecosystem type as fixed effects and block as a random effect (SAS version 8, SAS Institute, 1999).

Results

Mass loss and litter chemistry

After 108 days, decomposition rates were significantly higher in grass litter than in corn litter (13.5 vs. 47.5% mass remaining). When litter types were grouped by ecosystem management, litter mass remaining (mean percent of all litter) was lower under CT (21.5%) than under OF (37.2%). In contrast, litter decomposed under NT contained 32.8% of initial mass and did not differ significantly from either CT or OF (Fig. 1).

Prior to decomposition, grass litter had a higher average N concentration, lower average C concentration and a lower C/N ratio than corn litter (Table 1). Grass also had a higher relative abundance of N-bearing compounds and compounds of unknown origin while corn litter had a higher abundance of polysaccharides. At the end of our experiment, corn had significantly higher total C (35.06 vs. 26.23%)

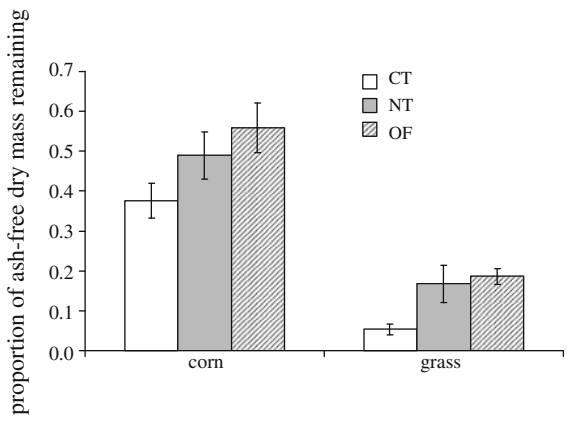

Fig. 1 Management effects on mass loss in corn and grass litter and across ecosystem management types. Data represent the proportion of ash-free dry mass remaining after 108 days. *CT* conventional-till, *NT* no-till, *OF* old-field. Significant one-way ANOVA differences were evident for litter type (grass > corn, $P < 0.05$) and ecosystem management (CT > OF, $P < 0.05$)

and lignin relative abundance than grass while grass had significantly higher total N concentrations (1.64 vs. 0.47%) and lower C/N ratios (Table 1, Figs. 2, 3).

Relative to the initial litter chemistry, decomposition caused an increase in the abundance of lignin derivatives in corn versus a relative decrease in grass (Fig. 3). After decomposition, the abundance of lipids and N-bearing compounds in corn also declined relative to the initial litter (Fig. 3). Following decomposition, corn and grass litter exhibited different chemical responses to ecosystem management, resulting in ecosystem by litter-type interactions for lipids, phenols and N-bearing compounds (Figs. 2, 3) as well as for many individual compounds (Appendix Table 3). Regardless of litter type, C and N concentrations were both significantly higher in litter decomposed in OF than in either the CT or NT plots; however, ecosystem management had no effect on final C/N ratio (Table 1). There was also a significant litter by ecosystem interaction for N in which concentrations were greater in grass decomposed in OF than in CT or NT. Additionally, guaiacol, a lignin derivative, was greater in OF than in CT or NT (Appendix Table 3).

Decomposer community composition and activity

At the end of the experiment, the relative abundance of bacteria was significantly greater in grass than in corn litter and greater in CT than in OF systems (Table 2). Conversely, fungal relative abundance was greater in corn than in grass and greater in OF than in CT treatments. Additionally bacteria were more abundant in corn decomposed in NT systems than in CT or OF. In contrast, fungi were more abundant in corn decomposed in CT and OF than in NT. Fungal:bacterial ratios were lower in grass than in corn and marginally lower in NT and CT vs. OF systems. In addition, the response of bacterial and fungal relative abundance to ecosystem type varied by litter type (Table 2).

Approximately 20–30 mesofaunal taxa were collected at each of the sample dates and although all taxa were cosmopolitan across litter and land-use types, total mesofauna abundance was more than 3-fold greater in grass than in corn ($P < 0.05$) (Fig. 4). Regardless of litter type, the abundance of individual taxa was significantly affected by ecosystem management type (Appendix Table 4). Additionally, total detritivore abundance was strongly affected by an interaction between ecosystem and litter type (Fig. 4). While there was no effect of ecosystem management on total detritivore abundance in corn litter, ecosystem effects were strong in grass; average seasonal detritivore abundance was highest in CT, intermediate in NT and lowest in OF treatments (Fig. 4).

Hydrolytic enzyme activities (β-glucosidase, *N*-acetyl-glucosaminidase and acid phosphatase) were highest in OF systems, intermediate in NT and lowest in CT, and rates were generally higher in grass than in corn (Fig. 5). Phenol oxidase activity was also affected by ecosystem management (CT > NT > OF) but was not significantly affected by litter type (Fig. 5). The activity of all hydrolases typically peaked within the first month of decomposition while phenol oxidase increased steadily over the course of the experiment.

Many of the measured biological and chemical variables were significantly correlated, but the specific relationships varied as a function of litter type (Appendix Table 5). In corn, fungal and bacterial relative abundances were correlated with phenol abundance (fungi negatively and bacteria positively) and detritivore abundance was inversely related to lignin abundance. Hydrolase and oxidase activity in grass were correlated with the abundance of N-bearing compounds. In addition, cellulase correlated positively with lipid abundance and phosphatase

Table 1 Litter C and N and mass loss for litter at time zero after 108 days of decomposition (Sep 22) ($n = 4$)

Litter	Ecosystem	Time zero[a]			Final			Mass loss (%)
		N (mg g^{-1})	C (mg g^{-1})	CN	N (mg g^{-1})	C (mg g^{-1})	CN	
Corn	Conventional				6.2 (1.6)	245.8 (38.8)	46.9 (14.7)	62.3 (4.4)
	No-till	7.29 (0.1)	441.1 (0.4)	60.5 (0.9)	4.5 (0.2)	330.3 (4.35)	72.9 (1.9)	51.0 (6.0)
	Old field				5.4 (0.7)	450.0 (4.0)	86.3 (11.8)	44.1 (6.3)
Grass	Conventional				8.5 (2.2)	208.4 (18.9)	31.9 (14.3)	94.7 (1.4)
	No-till	23.7 (0.8)	433.2 (1.4)	18.3 (0.6)	13.2 (0.5)	225.6 (8.5)	17.1 (0.1)	83.3 (4.7)
	Old field				25.2 (2.1)	379.0 (44.1)	14.9 (0.8)	81.4 (2.0)
ANOVA F-test								
		P-values[b]						
Litter		<0.0001	<0.0001	<0.0001	<0.0001	0.0003	<0.0001	<0.0001
Ecosystem					<0.0001	<0.0001	0.1425	0.0159
Litter × ecosystem					<0.0001	0.7033	0.0845	0.8432

N and C values are in mg g^{-1} of ash free dry litter and mass loss data represent the percentage of total ash free dry mass lost during the entire decomposition period

Numbers in *parentheses* are standard errors

[a] Time zero comparisons are between corn and grass only as these measurements were made prior to litterbags being placed in the field

[b] *P* values are from two-way analysis of variance

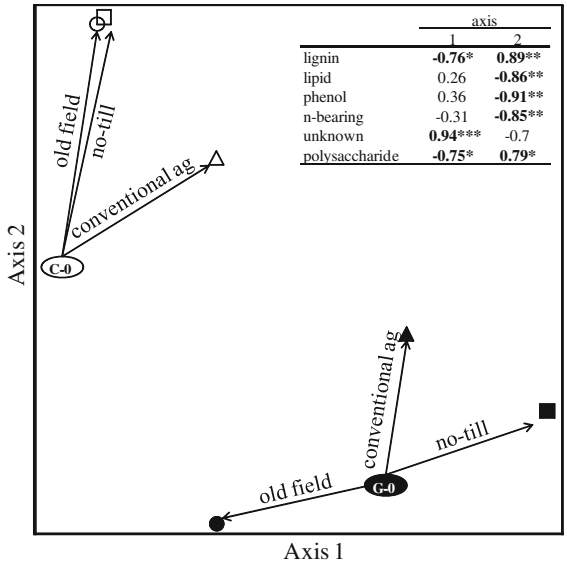

Fig. 2 Non-metric multidimensional scaling (*NMS*) ordination of litter chemistry using relative abundance of chemical classes. C-0 represents corn litter at time zero and G-0 represents grass litter at time zero. *Closed symbols* represent litter after 108 days of decomposition. *Black* denotes grass while white denotes corn (*triangles*-CT, *squares*-NT, *circles*-OF). Table values are Pearson's correlation coefficients (r) for the abundance of various chemical classes against axis scores ($P < 0.05$*, 0.01**, 0.001***)

activity was negatively correlated with the abundance of phenols (Appendix Table 5). Detritivore abundance in grass was positively correlated with total percent mass loss as well as with the abundance of polysaccharides and negatively with that of N-bearing compounds.

Discussion

We found that conventional tillage (CT) significantly accelerated litter decomposition rates relative to the old fields (OF), but decomposition rates in no-till (NT) did not differ significantly from rates observed in either CT or OF. Management type also independently influenced plant litter chemistry during decomposition but the strength of this effect varied with initial litter quality. In the short-term, these management effects on litter decomposition rates and litter chemical transformations will influence the quantity and composition of C that transfers belowground, and this may ultimately have long-term effects on soil organic matter dynamics. Indeed, previous research at this site (Grandy and Robertson 2007) shows that the soil C

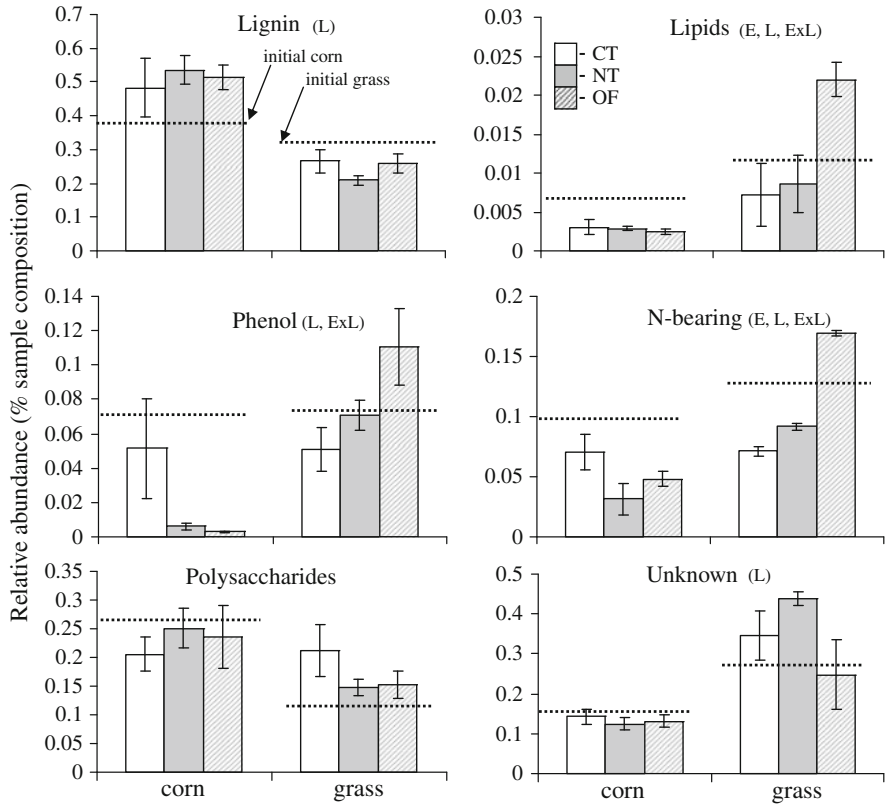

Fig. 3 Relative abundance of chemical classes in corn and grass litter before decomposition (*dashed lines*) and after 108 days of decomposition (Sep 22) (*bars*). Significant differences ($P < 0.05$) are noted by the presence of *uppercase letter* within a panel signifying litter type (*L*) and ecosystem management (*E*) effects, and significant interactions between the two (E × L)

Table 2 Estimated relative abundances of bacteria and fungi (fraction of the sum of total bacterial and fungal abundance) and fungal to bacterial ratio ($n = 2$)

Litter	Ecosystem	Bacteria	Fungi	F:B
Corn	Conventional	0.98 (0.004)	0.02 (0.004)	0.02 (0.004)
	No-till	0.89 (0.02)	0.11 (0.02)	0.13 (0.03)
	Old field	0.77 (0.06)	0.23 (0.06)	0.31 (0.11)
Grass	Conventional	0.98 (0.01)	0.02 (0.01)	0.02 (0.01)
	No-till	0.99 (0.004)	0.01 (0.004)	0.01 (0.004)
	Old field	0.98 (0.002)	0.02 (0.002)	0.03 (0.002)
ANOVA F-test				
	P-values[a]			
	Litter	0.02	0.03	0.02
	Ecosystem	0.03	0.01	0.11
	Litter × ecosystem	0.04	0.04	0.13

Numbers in *parentheses* are standard errors

[a] *P* values are from two-way analysis of variance

concentrations in the upper 5 cm of OF (1000 ± 38.6 g C m^{-2}) are substantially greater than those concentrations in CT (621 ± 51.1 g C m^{-2}) and NT (885 ± 55.1 g C m^{-2}). While no-till soil management offers an opportunity to maintain or restore terrestrial C in areas already used for agricultural production, data from this study and others show that soil decomposer communities, litter chemical transformations, soil aggregation and soil C concentrations differ substantially between NT and OF (Grandy and Robertson 2007). Thus, from a simple soil C mass balance perspective, if one of the goals of agriculture

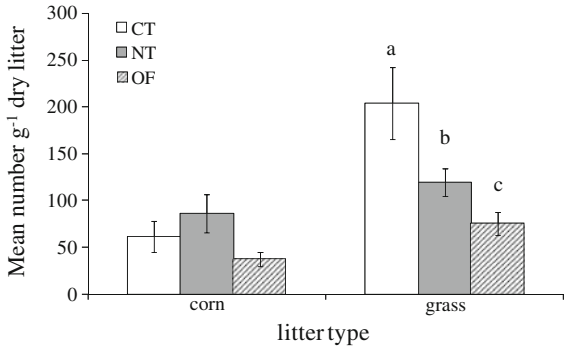

Fig. 4 Mesofaunal abundance (mean number of individuals g^{-1} dry litter ± SE) across all sample dates for corn and grass litter by ecosystem management

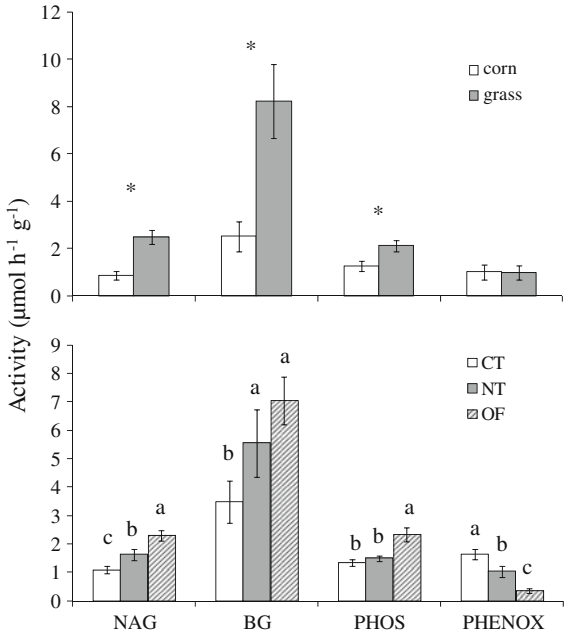

Fig. 5 Seasonal extracellular enzyme activity (mean ± SE) showing litter (*a*) and ecosystem management effects (*b*). Enzymes abbreviations: BG (*β*-glucosidase), NAG (*N*-acetyl-*β*-D-glucosidase), PHOS (*acid phosphatase*), PHENOX (*phenol oxidase*). *Asterisks* and *letters* denote significant differences from one-way ANOVA for *a* and *b*, respectively ($P < 0.05$)

includes minimizing soil C losses, our results suggest that efforts should focus on improving yield intensity in existing agricultural ecosystems rather than expanding agricultural production into grasslands or other unmanaged areas (Davidson and Ackerman 1993; West and Post 2002; Fargione et al. 2008).

A number of biotic and abiotic factors—including differences in decomposer communities or nutrient availability—may be responsible for the observed variation in decomposition rates. Both detritivore abundance and oxidative enzymes are known to contribute positively to decomposition rate (Bradford et al. 2002; Sinsabaugh 2010). We found that CT had higher detritivore abundance than NT, but both agricultural management types had higher detritivore abundance than OF. Further, we found that relative to OF, CT had higher rates of oxidase activity (Benitez et al. 2006). These data suggest that relatively high rates of decomposition in the CT may have been driven, at least in part, by increases in detritivores and oxidative enzyme activity. Although N fertilization in the agricultural systems may also have influenced decomposition rates, NT exhibited similar decomposition rates to OF despite consistently higher concentrations of inorganic soil N in NT (McSwiney 2007). Further, recent research along a N-fertility gradient (with the same soil type and cropping system studied here) showed that N had little effect on litter decomposition rates (Grandy, unpublished data). Thus, while fertilization cannot be ruled out as a contributor to the patterns of mass loss, our data suggest that differences in soil communities (or perhaps variations in other abiotic site conditions) are more likely to explain the differences in decomposition we observed.

Our data indicate that changes in land-use can alter litter decomposition rates. However, predicting the effects of land-use change on overall soil C balance also requires a more complete understanding of how management affects litter chemistry during decomposition, as variations in litter chemistry could affect the long-term dynamics of soil organic matter. We found strong variation in grass litter chemistry among management types. After decomposition, grass residue in CT and NT was enriched in total polysaccharides relative to the initial litter, while grass litter in OF became enriched in N-bearing compounds and lipids. These changes cannot be attributed to differences in mass loss or the extent of decomposition alone, since mass loss in NT was not significantly different from that in OF or CT. Instead, our results suggest that changes in litter chemistry over time were a function of ecosystem management or, more specifically, were a function of variation among sites in abiotic or biogeochemical processes, including decomposer communities.

These effects of ecosystem management on litter chemistry during decomposition stand in contrast to multiple existing models that suggest that changes in litter chemistry over the course of decomposition are predictable from initial litter chemistry and the extent of mass loss (Wolf and Wagner 1998; Quideau et al. 2005; Mathers et al. 2007; Berg and McClaugherty 2008). However, few studies have validated these models, and recent research on the effects of N enrichment on decomposition challenges the notion that litter chemical changes are simply a function of mass loss. For example, N additions to forests and high alpine ecosystems independently altered the chemistry of the light fraction soil organic matter (a pool of highly degraded plant litter) (Neff et al. 2002; Gallo et al. 2005; Grandy et al. 2009), and litter chemistry of a common litter type varied when decomposed in different environments (Moorhead and Sinsabaugh 2006; Adair et al. 2008; Preston et al. 2009). Together, these results indicate that initial litter chemistry and mass loss alone do not explain changes in litter chemistry during decomposition; instead, we suggest that changes in litter chemistry are a function of these factors and their interaction with site-specific conditions that may arise from variations in ecosystem management.

The long-term, ecosystem-level consequences of differences in litter chemical pathways arising from variations in ecosystem management are hard to predict from a short-term decomposition experiment, but we believe they may induce changes in soil organic matter dynamics. We know that changes in the chemistry of plant litter inputs can have important effects on decomposition dynamics (Meier and Bowman 2008; Wieder et al. 2008) and current soil organic matter models predict that recalcitrant litter C can move directly into stable SOM pools. Further, the processes of aggregation and sorption are both strongly influenced by the molecular structure of organic molecules. We anticipate that in situ changes in litter chemistry—such as the disproportionate accumulation of lignin, polysaccharides and lipids that arise from different decomposition pathways—may induce concomitant changes in other important ecosystem processes, including soil organic matter turnover, nutrient cycling, trace gas emissions, and productivity.

Current models do not explicitly consider the potential effects of soil communities on decomposition dynamics but recent studies show that microbial community structure influences a range of ecosystem functions, including rates of litter C mineralization (e.g., Strickland et al. 2009). Functional differences in decomposer communities among our sites also offer a possible explanation for the observed changes in litter chemistry with management. Historical differences in management and environmental conditions can influence decomposer community structure, metabolic functioning, and resource acquisition strategies (Cleveland et al. 2007; Fierer et al. 2007; Rubino et al. 2009), which could translate into different patterns and rates of substrate utilization. For example, distinct microbial communities vary greatly in their capacities to produce enzymes (Lynd et al. 2002; Sinsabaugh 2005), and soil mesofauna exhibit differences in feeding preference, mode of comminution (i.e., scraping and fragmenting), and gut enzyme content (Siepel and de Ruiter-Dijkman 1993; Berg et al. 2004). In the current study, biological communities differed across ecosystems: CT systems had elevated mesofaunal and relative bacterial abundances and enhanced oxidative enzyme activity relative to the OF communities. Old field ecosystems, which occupy the opposite end of the land-use spectrum, had higher fungal relative abundance and higher hydrolytic enzyme activity. These broad-scale differences in decomposer communities could translate into functional differences (e.g., variations in type and amounts of enzymes produced) that contribute to variation in the mineralization of different litter chemical constituents between management systems (Strickland et al. 2009). Soil C models may thus be improved by including decomposer communities and their effects on organic matter chemical transformations and mass loss. The higher lipid abundance in grass litter decomposed in OF relative to the agricultural systems provides additional evidence suggesting that decomposer communities partially drive litter chemistry changes during decomposition. Although lipids in grass litter were composed of both short—(<C20) and long-chain compounds (>C20), the increase in lipid abundance in grass litter under OF may have been driven by an increase in short-chain, microbially-derived compounds (Spaccini et al. 2009). Mass loss was lowest in OF but there was a high input of microbially-derived lipids in this system, which may have been related to increased fungal biomass and hydrolytic enzyme activity. We cannot definitively determine the degree to which differences among

decomposer communities induced changes in litter chemistry or vice versa, and it is even possible that differences in environmental conditions could independently drive changes in both biological communities and organic matter chemistry. However, when interpreted within the context of studies suggesting the importance of decomposer community composition in regulating mass loss rates (Ayers et al. 2009; Strickland et al. 2009), our data suggest that observed differences in community structure could help explain the observed variations in litter chemistry during decomposition.

We suggest that more studies (e.g., using advanced spectroscopic methods) are needed that provide clear insights into the fate of individual compounds or chemical classes during decomposition (*sensu* Preston et al. 2009). Such approaches, coupled with information on soil decomposer communities, could clarify the relative importance of the mechanisms controlling changes in litter chemistry during decomposition and could significantly improve models of litter decomposition. With this knowledge, we will be able to more accurately predict when agricultural intensification is likely to result in changes in decomposer communities that significantly influence decomposition dynamics, including changes in litter chemistry.

Finally, our findings are consistent with other studies showing a correlation between litter N content and decomposer communities (Hobbie 2005; Cole et al. 2008; Herman et al. 2008; Lauber et al. 2008; Allison et al. 2009; Grandy et al. 2009; Harner et al. 2009). Further, our data suggest that N availability may be a primary factor constraining the degree to which communities influence litter chemistry, at least during the initial stages of decomposition. In other words, the effect of community on litter chemistry may be dependent upon the quality of the substrate being decomposed, with higher N and lower lignin litter showing enhanced responses to shifts in communities. Unconstrained by factors such as high lignin or low N availability, unique decomposer communities are potentially more capable of generating decomposition products with ecosystem-specific chemistries. Future studies under controlled environments would help elucidate the specific effects of decomposer communities on both physical and chemical transformations during litter decomposition.

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Appendix

See the Tables 3, 4 and 5.

Table 3 Relative abundance of the top 2–3 compounds in each class from corn and grass litter after 108 days of decomposition ($n = 3$)

Compound		Corn			Grass			ANOVA
	Class	CT	NT	OF	CT	NT	OF	F-test[a]
Vinylguaiacol	Lg	0.21	0.22	0.16	0.002	0.01	0	L
Guaiacol	Lg	0.03	0.02	0.04	0.03	0.03	0.06	
Methoxyeugenol	Lg	0.07	0.14	0.12	0.07	0.03	0.03	L, E × L
1,3-Butadiene	Lp	0.002	0.003	0.003	0.003	0.001	0.002	
Propene	Lp	0	0	0	0	0.003	0.003	
3-Decene	Lp	0	0	0	0.001	0.001	0.002	L
Phenol	Ph	0.01	0.002	0	0.01	0.01	0.02	L, E × L
4-methyl-phenol	Ph	0.02	0.001	0	0.02	0.03	0.03	L, E × L
N-hydroxy-acetamide	N	0.04	0.03	0.04	0.03	0.04	0.06	
Pyrrole	N	0.004	0	0	0.01	0.01	0.02	

Table 3 continued

Compound		Corn			Grass			ANOVA
	Class	CT	NT	OF	CT	NT	OF	F-test[a]
Styrene	N	0.005	0.001	0.001	0.01	0.01	0.01	L, E × L
Pyruvaldehyde	Unk	0.02	0.0003	0.005	0.03	0.03	0.02	
N-Butyl-tert-butylamine	Unk	0.03	0.0001	0.003	0.03	0.02	0.01	E, L, E × L
3-methyl-phenol	Unk	0.01	0.002	0.002	0.01	0.01	0.01	
2,3-dihydro-benzofuran	Ps	0.12	0.14	0.19	0.12	0.05	0.05	L
Furfural	Ps	0.03	0.03	0.02	0.04	0.04	0.03	
2-Furanmethanol	Ps	0.001	0.0003	0.0002	0.003	0.004	0.01	L, E × L

Lg lignin, *Lp* lipids, *Ph* phenols, *N* nitrogen-bearing compounds, *Unk* compounds of unknown origin, *Ps* polysaccharides, *L* litter type, *E* ecosystem management, *CT* conventional till, *NT* no till, *OF* old field

[a] Significant differences were determined by two-way analysis of variance ($P < 0.05$)

Table 4 Average abundance of the most common mesofauna ($n = 8$)

	Litter type		Ecosystem management		
	Corn	Grass	CT	NT	OF
Entomobryidae	5.08 (1.32)b	10.88 (2.53)a	8.29 (2.45)a	5.91 (1.78)a	9.73 (2.03)a
Isotomidae	6.61 (3.75)b	10.49 (5.66)a	23.69 (12.35)a	1.32 (0.7)b	0.63 (0.34)b
Sminthuridae	2.49 (2.24)b	11.84 (11.24)a	14.66 (14.31)a	3.38 (3.2)a	3.46 (2.74)a
Hypogastruridae	0.68 (0.46)b	8.73 (4.99)a	13.79 (7.97)a	0.21 (0.07)b	0.12 (0.1)b
Corylophidae	0.32 (0.14)a	2.13 (0.94)a	0.76 (0.68)ab	1.23 (0.53)a	0.04 (0.01)b
Spiders	0.68 (0.48)a	0.81 (0.36)a	0.14 (0.05)a	0.06 (0.02)a	0.4 (0.18)b
Thysanoptera	0.87 (0.73)b	2.4 (1.77)a	3.39 (2.9)a	1.23 (0.84)b	0.29 (0.05)b

Numbers in *parentheses* are standard errors

Data represent the mean number of mesofauna collected over the entire growing season g^{-1} of dry litter based upon litter type and ecosystem management

Letters denote significant differences within treatment levels (litter type and ecosystem management) based on mixed model analysis ($P < 0.05$)

CT conventional till, *NT* no till, *OF* old field

Table 5 Pearson correlation coefficients (r) between chemical and biological factors

		Lignin	Lipids	Phenols	n-Bearing	Unknown	Polysaccharides	Mass loss[c]
Corn	Chitinase	0.19	−0.3	−0.54	0.15	−0.28	0.08	−0.45
	Cellulase	0.06	−0.22	−0.35	0.16	0.06	0.06	−0.58
	Phosphatase	0.29	−0.14	−0.49	−0.09	−0.19	−0.14	−0.25
	Phenol oxidase	−0.11	0.03	0.5	0.07	0.02	−0.12	0.4
	Fungi	−0.8	−0.56	**−0.85**	0.33	−0.21	0.71	0.05
	Bacteria	0.8	0.55	**0.85**	−0.33	0.21	−0.71	−0.06
	F:B[a]	−0.77	−0.56	−0.79	0.36	−0.28	0.69	0.01
	Detritivores[b]	**−0.8**	−0.13	0.37	0.14	−0.04	0.41	0.18

Table 5 continued

		Lignin	Lipids	Phenols	n-Bearing	Unknown	Polysaccharides	Mass loss[c]
Grass	Chitinase	0.19	0.6	0.61	**0.81**	−0.52	−0.07	−0.34
	Cellulase	0.16	**0.67**	0.64	**0.67**	−0.55	−0.09	−0.2
	Phosphatase	0.45	0.61	0.63	**0.74**	**−0.67**	−0.17	−0.1
	Phenol oxidasegrass	−0.28	−0.6	−0.62	**−0.82**	0.57	0.06	0.29
	Fungi	0.01	0.62	0.35	0.53	−0.38	0.17	−0.12
	Bacteria	−0.03	−0.63	−0.36	−0.54	0.41	−0.19	0.12
	F:B[a]	0.01	0.62	0.35	0.53	−0.38	0.17	−0.12
	Detritivores[b]	0.11	−0.58	−0.55	**−0.83**	0.15	**0.94**	**0.67**

[a] Fungal to bacterial ratio

[b] Detritivores denotes average abundance of detritivorous invertebrates across all sample dates (individuals g^{-1} dry litter)

[c] Average percentage of mass lost over the entire decomposition period

Values in *bold* are significant ($P < 0.05$

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