Land-use legacies regulate decomposition dynamics following bioenergy crop conversion

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Abstract

Land-use conversion into bioenergy crop production can alter litter decomposition processes tightly coupled to soil carbon and nutrient dynamics. Yet, litter decomposition has been poorly described in bioenergy production systems, especially following land-use conversion. Predicting decomposition dynamics in postconversion bioenergy production systems is challenging because of the combined influence of land-use legacies with current management and litter quality. To evaluate how land-use legacies interact with current bioenergy crop management to influence litter decomposition in different litter types, we conducted a landscape-scale litterbag decomposition experiment. We proposed land-use legacies regulate decomposition, but their effects are weakened under higher quality litter and when current land use intensifies ecosystem disturbance relative to prior land use. We compared sites left in historical land uses of either agriculture (AG) or Conservation Reserve Program grassland (CRP) to those that were converted to corn or switchgrass bioenergy crop production. Enzyme activities, mass loss, microbial biomass, and changes in litter chemistry were monitored in corn stover and switchgrass litter over 485 days, accompanied by similar soil measurements. Across all measured variables, legacy had the strongest effect ($P < 0.05$) relative to litter type and current management, where CRP sites maintained higher soil and litter enzyme activities and microbial biomass relative to AG sites. Decomposition responses to conversion depended on legacy but also current management and litter type. Within the CRP sites, conversion into corn increased litter enzymes, microbial biomass, and litter protein and lipid abundances, especially on decomposing corn litter, relative to nonconverted CRP. However, conversion into switchgrass from CRP, a moderate disturbance, often had no effect on switchgrass litter decomposition parameters. Thus, legacies shape the direction and magnitude of decomposition responses to bioenergy crop conversion and therefore should be considered a key influence on litter and soil C cycling under bioenergy crop management.

Keywords: bioenergy, carbon cycling, enzymes, litter–soil decomposition, microbial biomass, switchgrass

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Introduction

Soil carbon (C) sequestration is an essential component of sustainable bioenergy crop management, with plant litter as the main source of soil C inputs. Projected increases in land-use conversion from natural, set-aside, or agricultural lands to bioenergy crop production can lead to substantial gains or losses in system-level C (Zenone *et al.*, 2013); yet, identifying which bioenergy production systems maintain or increase soil C stocks is challenging because land-use history may interact with current management to regulate key soil C processes, including plant litter decomposition trajectories (Foster *et al.*, 2003; Wickings *et al.*, 2011; Liiri *et al.*, 2012). The persistence of previous land-use management has been demonstrated as legacies in an array of ecosystem properties, including microbial community composition

(Liang *et al.*, 2011), nutrient cycling (McLauchlan, 2006), and heterotrophic respiration (Keiser *et al.*, 2011; Goeransson *et al.*, 2013). For example, even decades after land-use change, microbial community structure can be more similar within land-use histories relative to current vegetation or ecosystem management (Jangid *et al.*, 2011). Still, it is not just the presence of a legacy that is important to understanding land-use change, but rather how these legacies shape current ecosystem processes such as decomposition dynamics. Our ability to predict how land-use legacies influence contemporary C dynamics, however, is complicated by the overlying influence of current land use and the quality of current litter inputs that contribute to soil C pools.

Interactions between previous and current land use may be especially important for litter decomposition, which regulates both short-term C fluxes and longer term soil organic matter (SOM) dynamics (Wardle *et al.*, 2004; Gunina & Kuzyakov, 2014). Litter decomposition is a process primarily controlled by the soil decomposer

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community and the soil environment (Allison *et al.*, 2013), both of which are sensitive to current and past land use (Swift *et al.*, 1998; Wickings *et al.*, 2011). Past land use can exert important controls on decomposition due to legacies in soil nutrient status, pH, or the decomposer community (Steenwerth *et al.*, 2002; Fichtner *et al.*, 2014); however, the influence of land-use legacy may be diminished if current land management effects are sufficiently strong. The introduction of multiple disturbances following bioenergy crop conversion, including herbicide and fertilizer applications, and shifts in plant community composition and plant C inputs, can immediately affect the soil environment, including microbial resource availability (Fornara & Tilman, 2008) and soil moisture (Wiesmeier *et al.*, 2013), potentially weakening the influence of legacies (De Vries & Shade, 2013). Thus, the balance of effects from past and current land use on the magnitude as well as direction of decomposition will depend on the relative influence of these various factors on soil environmental conditions and decomposer communities.

The influence of past and current land use on decomposition is also likely mediated by litter quality (Carrillo *et al.*, 2012), where legacy decomposer communities and SOM pools might be more important for low-quality litter. The decomposition of low-quality litter – i.e. high C/N ratio and lignin content – will be strongly influenced by whether or not decomposers are able to subsidize their nutrient and energy requirements from existing SOM pools (Frey *et al.*, 2000; Chigineva *et al.*, 2011; Cleveland *et al.*, 2014), or by the presence or absence of specialized microbes capable of degrading low-quality litter (Moorhead & Sinsabaugh, 2006; Van der Heijden *et al.*, 2008; Wallenstein *et al.*, 2013). Further, if low-quality litter selects for slow-growing, k-selected organisms with long generation times, the community might respond more slowly to current environmental conditions (Wallenstein & Hall, 2012).

To more fully understand decomposition following bioenergy crop conversion, we need to examine decomposer community processes and functions. For instance, shifts in litter and soil microbial biomass may indicate changes in potential biological activity and decomposition rates (Rinkes *et al.*, 2013), while changes in enzyme activities (the catalysts for litter breakdown) can reflect altered microbial nutrient demands (Sinsabaugh *et al.*, 2002). Further, differences in decomposer community composition or changes in nutrient and energy availability may lead to distinct chemistries of decomposed litter (e.g. concentration of lignin- and nitrogen-bearing compounds) and associated microbial by-products entering the soil matrix (Wickings *et al.*, 2011, 2012; Wallenstein *et al.*, 2013). While these parameters are considered here in terms of decomposition dynamics, they

also have important consequences for longer term soil C accumulation rates (Gu *et al.*, 1995; Bradford *et al.*, 2013; Wieder *et al.*, 2014).

Our objective was to evaluate how land-use history interacts with current bioenergy crop management to influence decomposition dynamics of different litter types. We hypothesized that land-use legacies will regulate decomposition dynamics more so than current land use, as prior edaphic properties and microbial community functions regulating litter decay are maintained. However, we further hypothesized that the effect of current land use will be strengthened when the new land use intensifies ecosystem disturbance and the soil environment becomes increasingly altered. Finally, we hypothesized that land-use legacy effects on decomposition dynamics will be stronger in lower quality litter compared to higher quality litter, due to differences in decomposer communities and in the energy requirements needed to carry out decomposition of high and lower quality litter. Using a field litter bag decomposition experiment, we compared sites left in historical land uses (agricultural or a minimally managed grassland) to those that were converted to either corn or switchgrass bioenergy crop production. The agriculture to switchgrass conversion represents a reduction in disturbance when moving from an annual intensive production system to perennial no-till switchgrass management. We consider sites previously in grassland converted to switchgrass to be moderately disturbed, whereas a grassland to corn conversion represents the highest level of disturbance, with a shift in the quality and quantity of plant inputs and an increase in field operations and chemical applications. These sites provide a disturbance gradient with contrasting land-use legacies, in which we evaluate the direction and magnitude of changes in decomposition dynamics of different litter qualities across a range of conversion scenarios.

Material and methods

Experimental sites and design

The field litter decomposition experiment was conducted at the Great Lakes Bioenergy Research Center (GLBRC) (http://glbrc.org/) located at the Kellogg Biological Station Long-Term Ecological Research site (42°24′N, 85°24′W, 288 masl), southwest Michigan, USA from June 2010 to September 2011. The region has a mean annual air temperature of 9.7 °C and an annual precipitation of 920 mm. The dominant soils at the study sites are sandy loam Alfisols, classified as Kalamazoo series (fine-loamy, mixed, mesic Typic Hapludalfs) and Oshtemo series (coarse-loamy, mixed, mesic Typic Hapludalfs), with a pH between 5 and 6.2 (Table 1).

Five large-scale field sites (9–17 ha) within the study area were used to represent a range of land-use legacies and current

Table 1 Mean soil C, N, exoenzyme activities, pH, and microbial biomass C (MBC) by land-use legacy and current crop and 2-way ANOVA P values. Exoenzyme activities and MBC are the average across all eight sampling periods. β-glucosidase, acid phosphatase, tyrosine-amino peptidase, N-acetyl-β-D-glucosidase, and phenol oxidase exoenzymes are abbreviated as BG, PHOS, TAP, NAG, and PHEN, respectively. Soil C and N are reported at Day 0 of litter decomposition and after 485 d of litter decomposition

Legacy	Crop	Soil C (mg g^{-1} soil)		Soil N (mg g^{-1} soil)		Enzyme activity (μmol g^{-1} soil h^{-1})					pH	MBC (mg g^{-1} soil)
		0 days	485 days	0 days	485 days	βG	Phos	TAP	NAG	PHEN		
AGR	C	10.7	10.8	1.03	0.98	0.12	0.24	0.009	0.040	0.426	5.8	196
	SW	8.8	10.7	0.75	1.04	0.14	0.22	0.010	0.043	0.599	6.2	211
CRP	C	20.93	18.83	1.89	1.78	0.21	0.30	0.011	0.066	0.532	5.1	314
	SW	19.2	16.4	1.51	1.55	0.18	0.28	0.010	0.049	0.517	5.0	301
	CRP	16.5	19.7	1.73	1.84	0.22	0.28	0.014	0.069	0.545	5.5	361
Legacy		**	**	*	**	**	*	ns	*	ns	**	**
Crop		*	*	ns	ns	ns	ns	*	*	ns	*	*
Legacy × crop†		ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns

*Denotes significance at $P < 0.05$.
**$P < 0.0001$.
†If interactions were insignificant, main effect ANOVA model results without interaction term are presented.

bioenergy crop production. Two of the field sites were converted to cellulosic bioenergy corn (C) and switchgrass (SW) production in 2010 from previous Conservation Reserve Program (CRP) grasslands dominated by smooth brome grass (*Bromos inermis* Leyss) since 1987, designated hereafter as CRP-SW and CRP-C. A third field site remained in CRP enrollment (CRP-CRP) and served as reference site for prebioenergy conversion. The CRP is a US federal initiative to restore marginal lands that were under agricultural production through the establishment of perennial plant cover (USDA-FSA, 2010). In many cases, enrollment into CRP has increased soil C stocks and fertility (McLauchlan *et al.*, 2006). The remaining two sites were in conventionally managed corn/soybean rotation for 10 years and row crop agriculture for 30 years prior (AG). One of these sites (AG-C) remains in corn production as a reference site for preconversion, while the other site (AG-SW) was converted to switchgrass at the same time as the CRP sites.

The CRP-C and AG-C sites were both planted to no-till corn (*Zea mays*, Dekalb DK-52) in June 2010 (first-year postconversion). No-till planting was followed with herbicide applications and a side-dressing of liquid urea and $NH_4(NO_3)$ at a rate of 112 kg N ha^{-1} in 2010 and 168 kg N ha^{-1} in 2011. The CRP-SW and AG-SW sites were converted in June 2010 to no-till switchgrass (*Panicum virgatum*) combined with oats (*Avena sativa*) as a first-year nurse crop. The switchgrass sites received 55 kg N ha^{-1} in May 2010 with no other agronomic inputs or field operations occurring until aboveground biomass was harvested in October 2011. The CRP-CRP site was left unmanaged except nonharvested grass cutting every 3 years, consistent with prior field management (see Bhardwaj *et al.* (2011) for details).

Litter bags

Corn and switchgrass litter was collected from standing biomass on October 2009 at the GLBRC intensives sites located near the GLBRC scale-up sites used in this study. These plant residues were chosen as they represent the bioenergy crop litter present following conversion, except in the CRP-CRP site, as well as a gradient in litter quality. The initial C/N ratio of collected biomass was 35 for corn and 79 for switchgrass. Corn biomass was dead at the time of collection and included both stalks and leaves. Switchgrass biomass was senesced at the time of collection and included stems, leaves, and some seeds. Air-dried corn and switchgrass biomass were cut into 2–4 cm pieces and homogenized, after which ~7 g of each was placed into 7 × 7 cm 1.5 mm mesh nylon litter bags.

Four replicated transects for each litter type were established in each of the five field sites (CRP-CRP, CRP-SW, CRP-C, AG-C, AG-SW) for litter bag decomposition. Litter bags were placed in direct contact with the soil surface and secured with nails until collection. Replicated transects were located randomly across the field sites to capture the range of field-level variability and were no less than 300 m apart. Spatial independence in this region was previously demonstrated to occur at >40 m for soil mineral N (Robertson, 1987) and given the large distances between our replicates and substantial field-level heterogeneity in these soils, spatial autocorrelation was deemed negligible. Each field site included a total of 32 corn and 32 switchgrass litterbags. Each replicate transect had eight bags of the same litter 0.66 m apart that were sequentially collected over the course of 485 days. Transects were separated by litter types 1.33 m apart and located in-line with planting rows, except in the CRP-CRP sites where transects followed slope contours. All litterbags were placed in the field on June 18th 2010 and were subsequently collected on July 4th August 2nd, August 29th, October 4th of 2010 and May 3rd, June 20th, August 10th, and September 16th of 2011, spanning two growing seasons and 485 days.

Soil samples were collected on the same day as litter bag collection to a depth of 15 cm, using a 5 cm diameter soil corer. This sampling depth captures a soil volume that responds

rapidly to changes in land use, and influences decomposition of recent litter inputs. Fifteen soil cores were randomly taken along transects, composited, and stored at 4 °C along with the litter bags for analyses occurring within 7 days.

Microbial biomass and exocellular enzyme activity

Litter and soil microbial biomass carbon (MBC) were measured within 7 days of collection using the chloroform-fumigation extraction method (Vance *et al.*, 1987) on 10 g dry weight field-moist soil or 1 g dry weight field-moist litter. Following extraction with 45 ml of 0.5 K_2SO_4, samples were stored at −20 °C until analyzed for total dissolved organic C (TOC-L CSH/CSN; Shimadzu; Kyoto, Japan) (see Data S1). MBC was calculated as the difference between fumigated and unfumigated TOC using an K_{EC} (extraction efficiency) of 0.45 (Wu *et al.*, 1990).

Potential exoenzyme activities (EEA) associated with C and nutrient cycling were measured following previously described methods (Saiya-Cork *et al.*, 2002; Grandy *et al.*, 2007). Four hydrolytic enzymes (β-glucosidase; BG, N-acetyl-β-D-glucosidase; NAG, Tyrosine-amino peptidase; TAP, and acid phosphatase; PHOS) and two oxidative enzymes (phenol oxidase; PHENOX, and peroxidase; PEROX) were measured in slurries from field-moist subsamples of 0.5 g dry weight of litter or 1 g dry weight of soil homogenized in a blender with 50 mM sodium acetate buffer. Buffer solution was adjusted to pH 5.47 for litter and 5.58 for soil to reflect average litter and soil environmental pH. Hydrolytic EEA was assessed flourometrically using black, 96-well microplates and compound-specific fluorescing substrates bound to methylumbelliferone (see Data S1) and expressed as nmol h^{-1} g^{-1}. Oxidative activity of phenol oxidase and peroxidase associated with lignin breakdown was measured spectrophotometrically using clear 96-well microplates expressed as nmol h^{-1} g^{-1}.

Litter chemistry

Subsamples from litter bags were air-dried and pulverized with a ball mill for analyses of litter chemical composition and total C and N. Total litter C and N on initial (0 days) and final (485 days) litter samples was quantified on a combustion elemental analyzer (ECS 4010 CHNS-O; Costech Analytical Technologies; Valencia, CA, USA). Litter chemistry was determined using pyrolysis-gas chromatography/mass spectrometry (Py-GC/MS) on pulverized litter samples from Day 0 and Day 485 following previously described protocols (Grandy *et al.*, 2009 and Wickings *et al.*, 2012). Briefly, litter was first pyrolyzed for 20 s at 600 °C and then pyrolysis products were transferred and separated on a GC over a 60 min time period. Compound ionization and detection was performed on an ion trap mass spectrometer (see Data S1). Peaks were then analyzed using the Automated Mass Spectral Deconvolution and Identification System (AMDIS, V 2.65) and the National Institute of Standards and Technology (NIST) compound library. Final compound abundances are reported as percentages, calculated using an individual compound's peak area relative to the total peak area of all identified peaks within a sample.

Data synthesis and statistical analyses

Litter EEA, MBC, C and N, litter mass remaining, litter turnover efficiency (see below), and litter chemistry were analyzed using a linear mixed-model three-way analysis of variance (ANOVA) where replicate was used as a random effect and land-use history, current management, and litter type were treated as fixed effects. Soil EEA, MBC, C and N concentrations, and pH were analyzed using a linear mixed-model two-way ANOVA similar to the litter model except there was no litter type fixed effect. Interactions among fixed effects were initially included in the model but if not significant ($P > 0.05$) were removed and the model was reanalyzed. To satisfy assumptions of normality and homogeneity of variance (Levene's test), ANOVA was performed on log-transformed exoenzyme data. Relationships between litter chemical groups and litter EEA, MBC, and mass remaining were analyzed using Pearson's correlations. Mean differences among fixed effects were assessed using Tukey's test and were considered significant if $P < 0.05$. All ANOVA and correlation analyses were performed in SAS v.9.3 (SAS Institute, 1999).

Litter and soil EEA were also analyzed using nonmetric multidimensional scaling (NMS) in PC-ORD version 4.14 (McCune & Mefford, 1999). The Sorensen (Bray–Curtis) index was used as a distance measure for cumulative hydrolytic enzyme data that was relativized to maximum exoenzyme activity across samples. The output was considered stable if the final solution had a stability <0.0005. Nonmetric multidimensional scaling final solutions were assessed using a Monte Carlo simulation to determine if the final solution provided a significant reduction in stress ($P < 0.05$), where a final solution stress value of <20 is considered acceptable (McCune & Grace, 2002). Correlations were examined between litter EEA in the first matrix and litter mass loss, final litter C and N, litter and soil moisture, litter and soil MBC, soil EEA, soil pH, soil C, and soil N in the second matrix with an r^2 cut off value of 0.1.

In addition to using ANOVA and multivariate methods, we compared the sites left in their historical land use (AG-C and CRP-CRP) to those that were converted to either corn or switchgrass bioenergy production (AG-SW, CRP-SW, or CRP-C) to understand the decomposition response to conversion across different land-use legacies representing a disturbance gradient. The response to conversion was determined as a relative difference between reference sites and converted sites: $(\text{CONVERTED}_{AG/CRP} - \text{REFERENCE}_{AG/CRP})/\text{REFERNCE}_{AG/CRP}$; where converted sites were CRP-SW and CRP-C or AG-SW. Relative differences between sites were considered significant if least square mean differences between compared treatments were $P < 0.05$.

To compare litter exoenzyme activity, hourly activity rates were converted to daily rates and then integrated between sampling points to derive an estimate of cumulative activity. Litter turnover efficiency was determined by dividing cumulative enzyme activity (mmols) by amount of litter lost (g). A turnover efficiency is an estimate for the efficiency at which microbial exoenzymes decompose litter, where a higher turnover efficiency suggests that for the same amount of microbial allocation to exocellular enzyme activity there is a greater mass

of litter lost. The litter decay rate constant (k) was calculated using the single-pool model $X_t = X_0 e^{(-kt)}$; where X_t is the mass remaining at time $= t$ (days), X_0 is the initial mass, and k is a decay rate constant in days^{-1}.

Results

Soil enzyme activities, microbial biomass, and total soil carbon and nitrogen

To understand the factors influencing litter decomposition, we characterized a suite of soil microbial and chemical properties. Land-use legacy, more than current land use, influenced soil EEA and soil MBC (Table 1). Only average TAP and PHENOX enzyme activity in soil were not affected by previous land use ($P > 0.05$). Sites that were converted from CRP or remained in CRP had greater average hydrolytic EEA and average MBC relative to sites that had previously been under agriculture (AG-C, AG-SW), regardless of current management. Significant effects of the current land management on EEA were found only for TAP and NAG. Current land use also had a significant, but smaller effect relative to legacy on MBC. Both EEA and MBC were higher in the

CRP sites that were not converted to bioenergy crops (CRP-CRP).

Initial soil C and N samples were taken during the first transition year to bioenergy crops when litter bags were installed. Soil C and N concentrations differed significantly between land-use legacies and types of conversion. Both soil C and N to 15 cm depth were higher in CRP compared to AG sites immediately after conversion and after 485 days (Table 1); however, it remains unknown if or how soil C at greater depths may affect differences in total C pools between sites. Relative changes in soil C and N between the initial and final sampling dates were not significant within any of the sites, but AG-SW and CRP-CRP tended to have gains in soil C and N, while converted CRP sites trended toward decreases in soil C after 485 days (Figure S1).

Litter mass loss

Both corn and switchgrass litter decomposition rates and total litter mass remaining after 485 days were significantly different between land-use histories and current crop (Table 2). Specifically, decay rates (k) were

Table 2 Litter decomposition parameters by land-use legacy, current crop and litter type, and 3-way ANOVA P values. K is the decomposition rate of litter by day, Mass is the % ash-free mass remaining after 485 days of decomposition; BG, PHOS, TAP, NAG, and PHEN are the cumulative exoenzyme activities after 485 days for β-glucosidase, acid phosphatase, tyrosine-amino peptidase, N-acetyl-β-D-glucosidase, and phenol oxidase, respectively. Turnover activity is the relative cumulative expression of all hydrolytic enzymes to total litter mass lost. C : N is for litter after 485 days of decomposition and MBC is the average of litter microbial biomass C across eight litterbag collection dates

Legacy	Litter	Crop	k (day^{-1})	Mass (%)	Cumulative enzyme activity (mmol g l^{-1}) βG	Phos	TAP	NAG	PHEN	Turnover efficiency (moles)	C : N	MBC (mg kg soil^{-1})
AG	Corn	C	0.0034	19.6	14.5	9.0	0.6	6.7	3.6	17.4	22.1	7.5
		SW	0.0035	19.8	14.3	10.6	0.8	7.3	5.3	12.7	27.0	7.6
CRP		C	0.0025	22.4	22.4	17.6	1.2	11.1	4.5	6.1	18.4	9.6
		SW	0.0026	28.5	16.2	17.5	0.8	9.1	2.3	11.1	24.5	7.7
		CRP	0.0029	25.4	12.7	12.3	1.1	8.0	4.9	13.5	32.5	7.9
AG	Switch grass	C	0.0024	32.9	16.6	10.7	0.7	7.5	3.0	18.5	23.1	6.9
		SW	0.0030	23.5	11.5	7.9	0.6	5.4	4.3	20.1	24.1	6.9
CRP		C	0.0012	56.6	23.5	17.8	0.7	9.8	4.0	6.9	27.1	7.8
		SW	0.0018	41.5	20.9	17.0	0.8	9.8	2.9	10.8	24.3	7.4
		CRP	0.0024	31.0	21.0	16.5	0.7	12.9	2.5	10.5	25.8	7.3
Legacy			**	**	**	**	*	*	ns	**	*	*
Crop			**	**	**	*	ns	ns	ns	*	**	ns
Litter			**	**	*	ns	ns	*	ns	ns	ns	*
Legacy × crop†			*	ns	ns	ns	ns	ns	ns	*	**	*
Legacy × litter			ns	ns	*	ns	*	ns	ns	*	ns	ns
Crop × litter			ns	ns	ns	ns	ns	ns	ns	ns	*	ns

*Significant at $P < 0.05$.
**Significant at $P < 0.0001$.
†If interactions were insignificant, main effect ANOVA model results without interaction term are presented.

highest in corn litter in AG sites. Within AG sites, switchgrass litter decay was affected by current crop, with higher decay rates in AG-SW. Similarly, in the CRP sites, the effect of current crop was only observed in switchgrass litter which had higher decay rates in CRP-CRP. Mass remaining after 485 days was lowest in corn litter decomposed in AG sites (19% mass remaining), while the most litter mass remained in switchgrass litter decomposed under a CRP legacy (31–50%) (Table 2; Figure S2).

Litter enzyme activities and microbial biomass

Litter hydrolytic and oxidative EEAs as well as litter microbial biomass carbon (MBC) were measured over 485 days of decomposition (Table 2). While neither current nor past land use affected oxidative enzyme activity in litter, land-use legacy influenced cumulative BG, PHOS, TAP, and NAG activities. For all hydrolytic enzymes, CRP sites had higher cumulative EEA for both litter types under corn or switchgrass management relative to AG sites. Current land management only influenced BG and PHOS. Though the initial C/N ratio of corn and switchgrass differed considerably (35 vs. 79), a main effect of litter on EEA was only observed for BG and NAG.

Historically CRP sites had higher MBC in litter regardless of current management. In general, corn litter had higher concentrations of MBC relative to switchgrass. Though there was no main effect of current crop on MBC, an interaction between legacy and current crop was observed where the conversion into corn from previously managed CRP sites resulted in higher MBC relative to sites converted to switchgrass or remaining as CRP.

NMS reveals that sites with the same land-use histories had more similar cumulative hydrolytic litter EEA and turnover efficiency than sites with the same current crop management (Fig. 1). Most of the separation (Axis 1; $r^2 = 92\%$) between land-use history was due to higher EEA in CRP sites and higher turnover efficiency in AG sites. Axis 1 was positively correlated with soil enzymes, soil MBC, and the amount of mass remaining. Sites grouped by CRP and that had higher litter enzyme activity were positively associated with soil enzyme activity, MBC, and soil C and N, but were negatively associated with decay rate and turnover efficiency.

Response of soil biological indicators to bioenergy crop conversion

Relative changes in soil decomposition variables between the reference sites and converted sites were
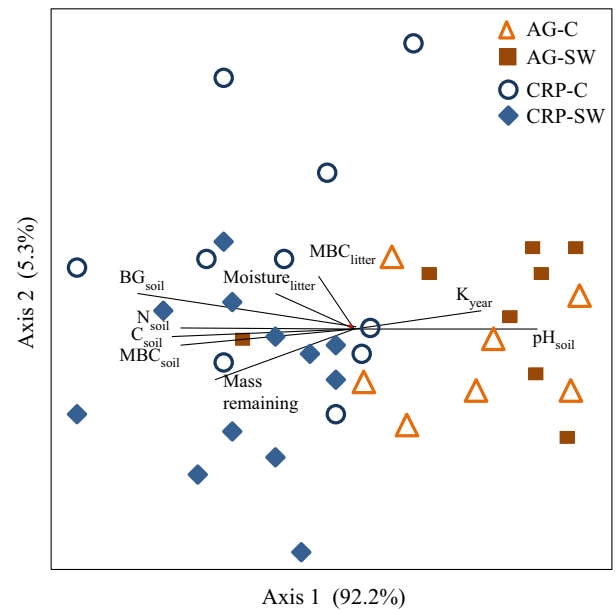

Fig. 1 Nonmetric multidimensional scaling (NMS) ordination of litter enzymes using cumulative hydrolytic enzymes and efficiency. Open symbols represent corn litter and closed symbols represent switchgrass litter. Diamonds and circles denote CRP while squares and triangles denote AG land-use legacies. Secondary matrix correlations included soil BG, MBC, C, N, pH and litter MBC, soil moisture, and mass remaining. Stress = 7.5, $P = 0.0196$ of Type 1 error based on Monte Carlo simulation.

determined to understand the influence of land-use history and current management on the magnitude and direction of decomposition responses to conversion. Soil enzyme and MBC responses to conversion depended most on legacy and, to a lesser extent, the degree of disturbance (Fig. 2). Soil BG, TAP, and PHE-NOX activities increased following conversion from AG-C to AG-SW. The opposite was observed in converted CRP sites, where BG, TAP, and NAG, along with MBC, significantly decreased following conversion relative to the reference CRP treatment. However, the less disturbed CRP-SW sites exhibited greater reduction in BG, NAG, and TAP relative to the more disturbed CRP-C sites. Therefore, the conversion into SW led to increased values of many soil decomposition variables for sites historically in AG, but decreased values of these same variables when sites were historically managed in CRP.

Response of litter decomposition to bioenergy crop conversion

The magnitude of the decomposition response to conversion was significantly greater in the higher quality
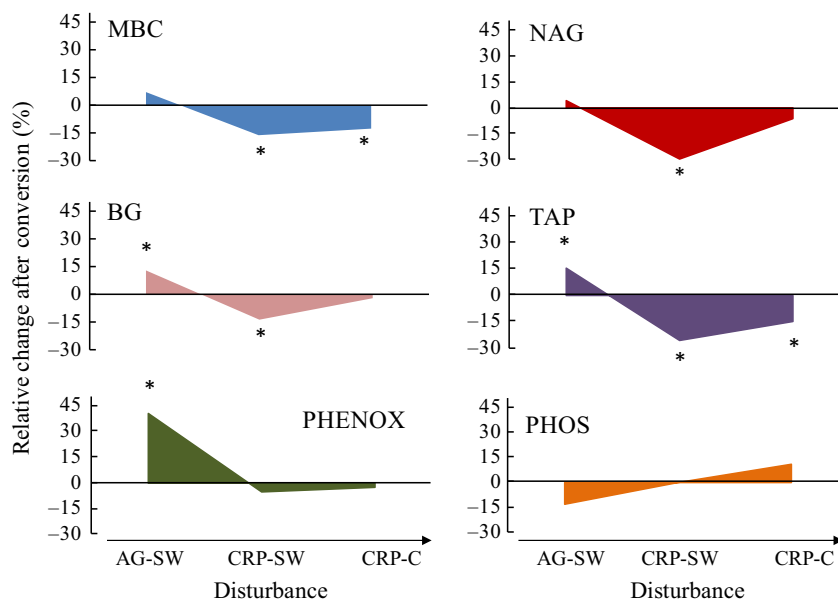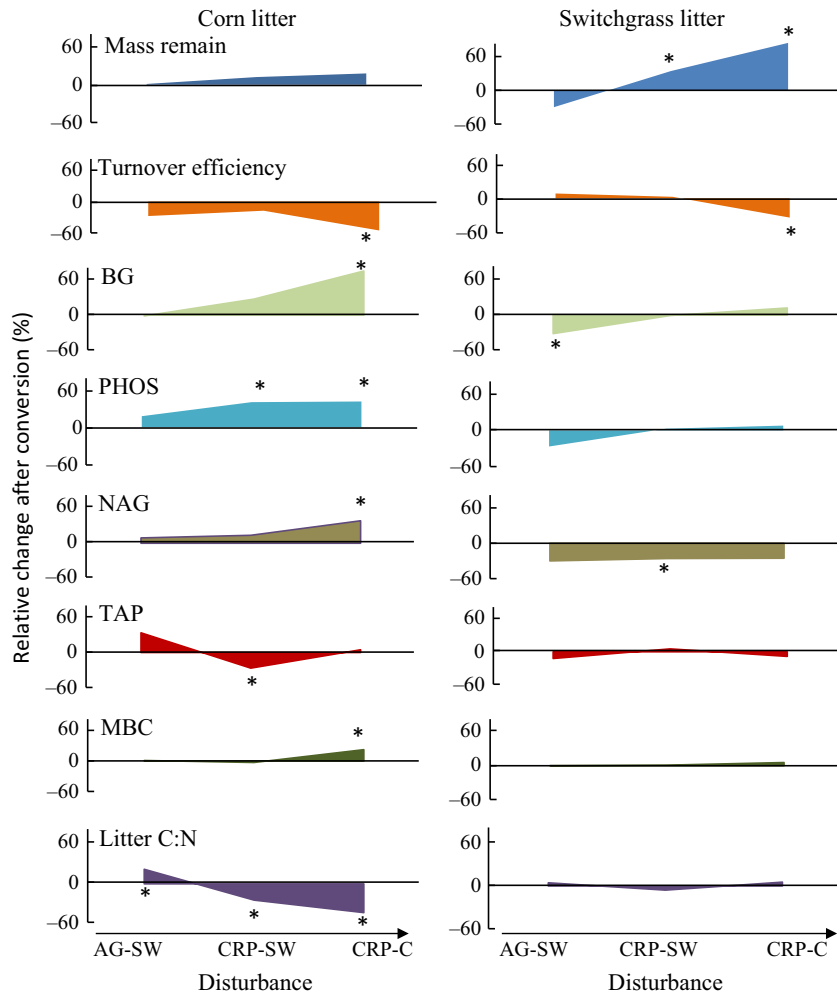
Fig. 2 Relative change in the converted sites soil microbial biomass C (MBC) and enzymes to their reference sites (AG-C and CRP-CRP) where conversion is arranged along a disturbance gradient from reduced (AG-SW) to high disturbance (CRP-C). The position along the y-axis denotes the magnitude and direction of the relative change following conversion where values above 0 are relative increases and values below 0 are decreases. Asterisks denote significant Tukey's *post hoc* mean comparison tests between reference and converted sites ($P < 0.05$).

corn litter relative to switchgrass litter for all variables measured except the mass of litter remaining, where the effect of conversion was often not significant for decomposing switchgrass (Fig. 3). In general, the largest effect of conversion was observed in sites converted from CRP to corn (Fig. 3). CRP conversion into switchgrass, a moderate disturbance, often had no effect on decomposition parameters. The MBC response to bioenergy crop conversion, for example, went from a 1% increase or decrease under switchgrass conversion to a 7% increase under corn conversion. In corn litter, as the conversion disturbance increased, mass remaining, BG, PHOS, NAG, MBC also increased, whereas turnover efficiency, litter C/N and TAP decreased. For instance, AG-SW had a 9% increase in NAG relative to AG-C sites, but a 38% increase was observed in the CRP-C sites. In some cases, the direction of the response to conversion differed depending on land-use history and disturbance, where TAP and litter C/N ratios increased in converted AG sites, but decreased in converted CRP. The direction of the response to conversion also differed depending on litter quality for some of the sites (Fig. 3). Slight decreases were observed for BG, PHOS, and NAG in switchgrass litter, but increased under corn litter. Comparing across all the decomposition parameters, no variable responded consistently to conversion.

Changes in litter chemistry due to bioenergy crop conversion

There was a strong effect of land-use history and current management on final litter chemistry. Lignin-derived compounds, for example, were lower in corn litter in AG-C sites (42% relative abundance) relative to the CRP-CRP sites (54% relative abundance; $P < 0.05$). Corn litter lipid abundance was also lower in AG-C sites compared to the CRP-C sites ($P < 0.05$). An effect of conversion on corn litter chemistry was only observed at CRP sites, and this was most pronounced in CRP sites converted to corn (Fig. 4). For example, in corn litter, lignin derivatives were lower in the CRP-C sites relative to CRP-CRP, but the relative abundances of polysaccharides, proteins, phenolics, and lipids were higher in CRP-C relative to CRP-CRP.

The relative abundances of litter compound classes were regressed against litter decomposition variables, including cumulative enzymes, MBC, and mass remaining (Table 3). Though lignin was strongly influenced by land-use history and current management, none of the decomposition variables were associated with relative amounts of lignin. Litter phenolics, on the other hand were strongly correlated with decomposition variables, and especially BG ($r^2 = +0.68$, $P < 0.0001$). The relative abundances of litter lipids were associated with BG,

Fig. 3 Relative change in the converted sites litter microbial biomass C (MBC), enzymes, litter turnover efficiency, mass remaining, and final litter C:N to their reference sites (AG-C and CRP-CRP) where conversion is arranged along a disturbance gradient from reduced (AG-SW) to high disturbance (CRP-C). Oxidative enzymes were excluded as they were not significant in any of the comparisons. The position along the y-axis denotes the magnitude and direction of the relative change following conversion where values above 0 are relative increases and values below 0 are decreases. Asterisks denote significant Tukey's *post hoc* mean comparison tests between reference and converted sites ($P < 0.05$).

PHOS, and TAP, but most strongly correlated with NAG ($r^2 = +0.75$, $P < 0.0001$).

Discussion

Land-use legacy affects contemporary decomposition dynamics

How soil C cycling will respond to bioenergy crop conversion cannot be predicted without understanding the influence that previous land use has on decomposition dynamics. We found that legacy, which we hypothesized would have a greater effect on decomposition relative to current management, was the strongest driver of differences in all of the measured decomposition parameters and continued to influence decomposition dynamics under bioenergy crop production. In fact, litter decomposition in sites that were converted from unmanaged grasslands to bioenergy corn production was still more similar to unconverted grasslands than to agricultural sites also managed in corn (Table 2, Fig. 1). Sites previously in CRP exhibited higher EEA and MBC in both litter and soil, as well as greater soil C and N, regardless of the current management or litter quality, relative to sites historically in AG. Consequently, even when current management is a significant departure from prior land use, decomposition is still influenced more by previous land use within the first 2 years of conversion.
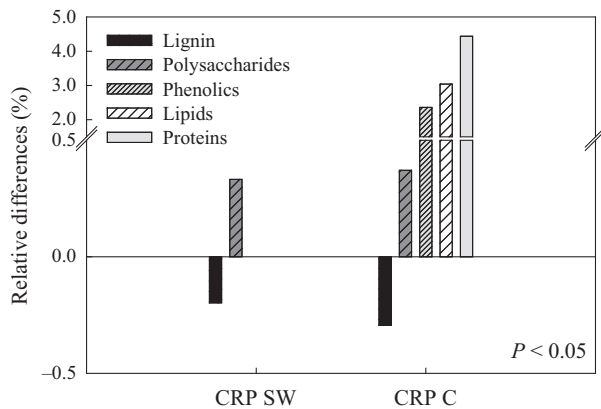
Fig. 4 Significant relative differences ($P < 0.05$) in corn litter chemistry between CRP reference sites and switchgrass sites (CRP-SW) or CRP corn sites (CRP-C). Relative differences are based on the relative abundances of individual compound groups. If treatment or chemical class was not significant ($P > 0.05$), it was not included.

Table 3 Pearson's correlation coefficients (significant values in bold) and P values of relative abundance of litter compound groups, cumulative litter exoenzymes, microbial biomass C, and amount of litter mass remaining

	Lignin	Lipids	Proteins	Phenols
Lignin		−0.26	**−0.49**	−0.32
		ns	<0.05	ns
BG	−0.26	**0.69**	0.30	**0.68**
	ns	<0.0001	ns	<0.0001
PHOS	−0.33	**0.54**	0.23	**0.53**
	ns	<0.005	ns	0.005
TAP	−0.24	**0.42**	0.16	**0.47**
	ns	<0.05	ns	<0.05
NAG	−0.11	**0.75**	0.19	**0.53**
	ns	<0.0001	ns	0.005
MBC	−0.35	0.22	0.23	**0.42**
	ns	ns	ns	<0.05
Mass remaining	−0.30	0.25	0.16	**0.48**
	ns	ns	ns	<0.05

Current land use underlies legacy effects on litter decomposition dynamics

Despite significant land-use legacy effects, we also saw strong decomposition responses to conversion, suggesting that how legacies are manifested in decomposition depends in part on current land use. Conversion into switchgrass bioenergy crop production resulted in a general increase in enzyme activity and MBC on switchgrass litter relative to nonconverted sites. However, this current land-use effect was still mediated by land-use legacy, given that these increases were greater in CRP

relative to AG. We proposed that the effect of current land use will be strengthened under intensified ecosystem disturbance and we were able to detect the influence of current land use in how certain variables respond differently to management. For example, the response to current management in TAP cumulative activity was greater in CRP-SW systems than in CRP-C, possibly reflecting greater N limitation in the less fertilized switchgrass sites (Fig. 3). However, for most other parameters decomposition responses to disturbance in both corn and switchgrass litters were greater in CRP-C relative to CRP-SW. This is consistent with our second hypothesis that the effect of current land use will be stronger when the new system is more intensely managed than the previous land use. The conversion from an unmanaged perennial grassland to a no-till perennial switchgrass system is a less severe disturbance compared to conversion into annual corn bioenergy production. As such, the decomposer community's ability to maintain its prior function is likely less compromised (De Vries & Shade, 2013).

Changes in decomposition dynamics due to differences in current crop management are also apparent in the chemistry of the decomposed litter in converted and reference sites. The significantly higher abundances of phenols, lipids, and polysaccharides in corn litter decomposing under CRP-C relative to CRP-CRP sites may reflect a more active biological community in CRP-C litter. Studies comparing litter chemistry and decomposer communities have observed that differences in litter chemical compound during decomposition are linked to differences in decomposer activity (Filley *et al.*, 2008; Wickings & Grandy, 2011; Wickings *et al.*, 2012). In our study, the greater relative abundances of phenolics and lipids in converted sites were positively correlated with litter EEA and MBC, indicating that changes in decomposer activities are related to changes in litter chemistry following conversion.

Litter quality alters the combined effects of land-use legacy and current land use

Differences in soil nutrient and energy availability can strongly influence litter decomposition dynamics due to their tight coupling (Wardle *et al.*, 2004). However, the strength of this coupling may differ depending on the quality or type of litter, thus complicating the response of decomposition dynamics to land-use conversion. Decomposers of more recalcitrant litter may rely more on surrounding nutrient pools relative to higher quality litter (Freschet *et al.*, 2012; Berglund *et al.*, 2013), are likely to comprise a larger suite of specialized microbes, and may adapt more slowly to disturbance due to their growth strategies (Wallenstein & Hall, 2012; De Vries &

Shade, 2013). From this line of reasoning, we hypothesized that legacies in soil resources and decomposers will be manifested more strongly in the decomposition of lower quality switchgrass litter compared to higher quality litter. Indeed, in many cases, observed decomposition responses to conversion were absent in decomposing switchgrass litter and were strongest in higher quality corn litter, indicating a smaller response to current land use and a greater influence of legacy during switchgrass decomposition. In the CRP sites, the greater decomposition responses in corn litter relative to switchgrass were related to reductions in soil biological activity, MBC, and total C (Figs 2 and 3). Litter quality also influenced the direction of these responses where, for example, the response to switchgrass conversion in AG sites was positive in corn litter, but was negative in switchgrass litter for EEAs and decay rates.

This untidy relationship between litter quality and land use could be the result of multiple complex interactions between litter and soil decomposer communities and their resources. For example, the difference in the magnitude of responses between land-use history and litter types suggests that legacies are buffering against disturbance, but only when a certain type of litter is present. The decomposition response of switchgrass litter is negligible in CRP-SW sites, but strong in AG-SW sites; yet the decomposition response of corn litter is strong in CRP sites relative to the AG sites. It might follow that in corn litter, the AG sites are more adept at maintaining their initial functional capacity, whereas in CRP sites, this would hold true for switchgrass litter, which has a similar chemistry to historical brome grass

plant inputs. This reasoning provides some support for 'litter quality being in the eye of the beholder', (Strickland et al., 2009) or a 'home field advantage' (Gholz et al., 2000; Keiser et al., 2014). In other words, perceived litter quality is in part determined by resource quality history, where communities from CRP sites (with a resource history similar to switchgrass) perceived low quality switchgrass to be of higher quality compared to communities from AG sites. However, this explanation does not necessarily capture the combined effects of current land use and litter quality, nor explain the decomposition response present in switchgrass litter under CRP-C despite being absent in CRP-SW. If we consider the soil responses in combination with litter responses to conversion across our land use and litter types, we see that bioenergy crop conversion, in general, results in significant litter responses, but that the soil responses are sometimes in opposing directions.

A framework for understanding litter–soil interactions following bioenergy crop conversion

We developed a framework to conceptualize the interactions between land-use legacies, litter quality, and current management on soil and litter dynamics and the possible processes driving them (Fig. 5). In AG, conversion into SW resulted in a general increase in soil biological activity and marginally higher soil C and N, whereas the reverse was the case in the CRP. Prior to conversion, the AG sites were under intensive annual crop management with frequent tillage and intensive chemical applications. Compared to an AG legacy,
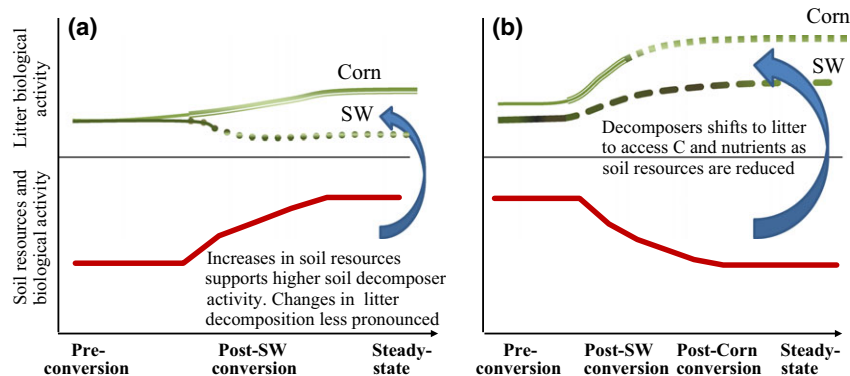
Fig. 5 Conceptual framework of soil and litter responses to bioenergy crop conversion. Patterned lines represent increases or decreases in biological litter activity between corn and switchgrass litters, while narrower lines demonstrate changes in soil resources and soil biological activity. Concurrent changes in litter chemistry are indicated by differences in line patterns. In panel (a) AG sites are converted to switchgrass; soil biological activity and resources increase through time. This increase results in higher corn litter decomposition activity as more microbial biomass is supported and previous energy limitations are alleviated. The conversion of CRP to switchgrass or corn bioenergy crop production is shown in Panel (b) where soil resources and biological activity is reduced, driving the decomposer community to rely more on litter resources to meet energy and nutrient demands. These increases in litter biological activity occur alongside alterations to litter chemistry following bioenergy crop conversion.

switchgrass conversion represents lower disturbance due to a shift from an annual to a perennial crop and reduced inputs of inorganic N, which may suppress microbial biomass (Lu *et al.*, 2011). On the other hand, conversion into bioenergy production in the CRP sites is an increase in disturbance, especially in CRP-C, where we observed substantial declines in soil enzyme activities, MBC, and to a lesser degree total C and N.

The result of these changes to soil resource pools and biological activity (Fig. 5) is reflected in litter decomposition dynamics. Given that conversion from CRP generally reduced soil microbial activity and resource availability, the decomposer community in the CRP sites may be shifting more activity toward litter inputs to meet energy and nutrient demands (Kuzyakov, 2002). Therefore, it is possible that reductions in the CRP soil resource pool are driving decomposers – some of which are known foragers (Frey *et al.*, 2003; Schneider *et al.*, 2012) – toward litter resources. This apparent shift toward litter as a resource is more pronounced in corn litter where biochemical access to litter-derived energy and nutrients is easier (Fig. 5). The AG-SW conversion also enhanced decomposition processes, yet in these sites there is a concurrent increase rather than decrease in soil resources and biological activity. Instead of a shift in the utilization of different resource pools, as may be the case in the CRP sites, the AG sites are better able to support higher decomposition activity as some soil environmental constraints are alleviated. This would be less so in the lower quality switchgrass litter where the return on investment in decomposition would likely be lower (Moorhead *et al.*, 2012).

Though this model is only one of many possible explanations for how bioenergy crop conversion influences litter decomposition dynamics, it links together varied individual responses and feedbacks to create a comprehensive framework of decomposition dynamics across land-use conversion scenarios.

Broader outcome

Land that is idle, unproductive, or highly erodible, such as much of the CRP land, represents likely areas of conversion into bioenergy crop production (Dale *et al.*, 2011). Recent estimates suggest that 7 Mha of current CRP lands could be used for cellulosic bioenergy production and that this could increase to 10 Mha by 2020 (NRC- National Research Council, 2009). Consequently, the conversion of CRP or other degraded or idle lands to cellulosic bioenergy production is considered to be a major component of both current and forecasted land-use change scenarios (Feng & Babcock, 2010). This study addresses how decomposition dynamics will respond in marginal lands such as CRP following conversion relative to sites taken out of intensive food crop production. We show that land-use legacies strongly mediate decomposition responses to biofuel conversion, but interact with current management and litter quality to determine the magnitude and directional effect of biofuel crop production on a critical component of the soil C cycle.

We observed significant shifts in both litter and soil decomposer community activity following CRP conversion, but this response was attenuated when the bioenergy crop was a perennial low-input grass. These alterations to litter decomposition and the communities that carry them out can have long-term consequences on stable soil C pools. For example, the differences in litter chemistry we observed in converted sites relative to the CRP reference sites have the potential to impact soil aggregation rates, inputs to soil resource pools, and physio-chemical interactions between minerals and decomposed litter that are critical to stabilizing soil C (Tiemann & Grandy, 2014).

Though we were able to examine the magnitude and direction of legacy effects and disturbance on litter decomposition responses, uncertainty remains as to how long these observed effects persist. As soil resources and activity decline following CRP conversion, it is possible that at some point current management begins to override any legacy effect. In our short-term study, higher soil and litter enzyme activities were greater in all CRP sites regardless of current management; however, as the length of time since conversion into a more disturbed system such as intensive corn production increases, there is greater likelihood of soil degradation. Nonetheless, our results show that the initial conversion and site selection for bioenergy crop production have important influences on contemporary decomposition and soil C dynamics during bioenergy crop transition, and that switchgrass conversion is more likely to minimize changes to decomposition dynamics following biofuel conversion.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Method details for microbial biomass, enzymes, and litter chemistry.

Figure S1. Percent relative change in soil C and N between 0 and 485 d during litter decomposition. No treatments were significant ($P > 0.05$). Error bars are SE, $N = 4$.
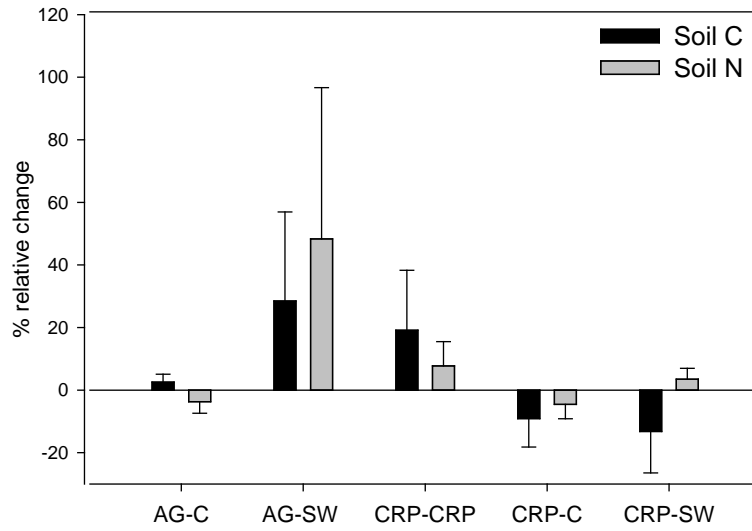
Figure S2. Percent of ash-free litter mass remaining for corn litter (right) and switchgrass litter (left) from 30 to 485 days of field decomposition for historically agricultural sites planted in corn (AG-C) or switchgrass (AG-SW) and historically grassland sites left as grasslands (CRP-CRP) or converted to corn (CRP-C) and switchgrass (CRP-SW).

Figure S1. Percent relative change in soil C and N between 0 and 485 d during litter decomposition. No treatments were significant (p > 0.05). Error bars are SE, N=4.
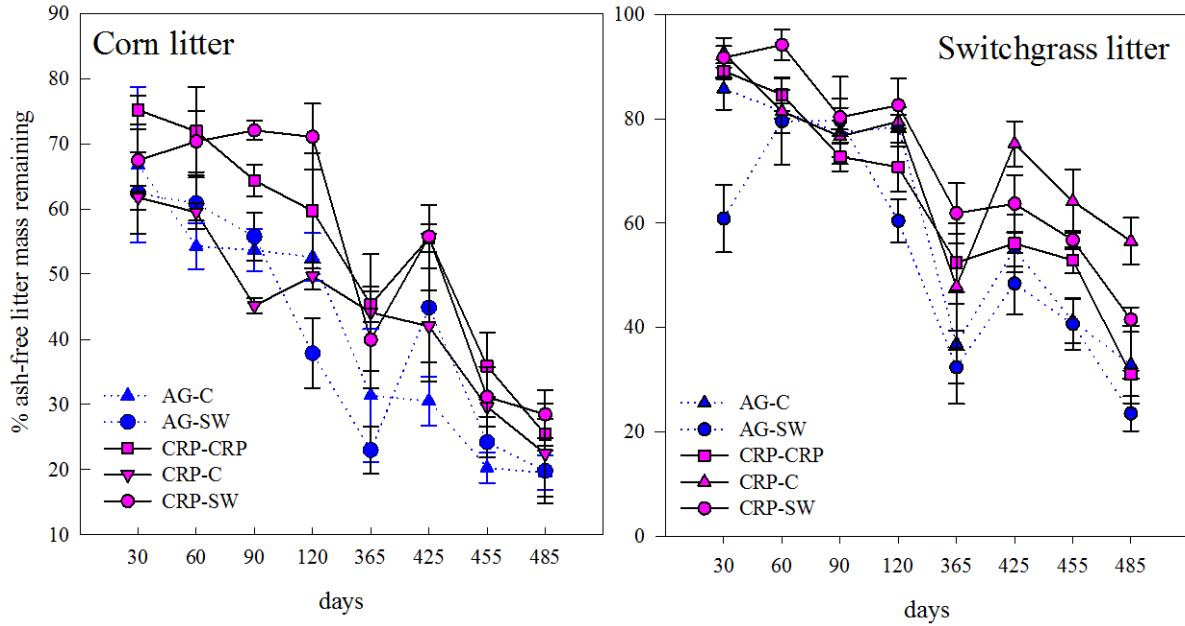
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1 **Method details for microbial biomass, enzymes, and litter chemistry**

2 *Microbial biomass carbon extraction*

3   Soil and litter microbial carbon was determined on soil and litter duplicates of 10g dry

4 weight field-moist soil or 1 g dry weight field-moist litter. One set was immediately extracted by

5 adding 45 mL of 0.5M K_2SO_4 to each sample followed by 1 h of shaking at 350rpm, and then

6 filtered through #5 Whatman filter papers. The remaining set was immediately fumigated under

7 vacuum with chloroform for 24 hrs. Following fumigation, samples were purged of chloroform

8 and extracted in the same manner as the unfumigated samples.

9 *Enzyme substrates and activity*

10   Hydrolytic compound-specific fluorescing substrates were 4-methylumbelliferyl-b-D-

11 glucoside (EC 3.2.1.21), 4-methylumbelliferyl-N-acetyl-b-D-glucosaminide (EC 3.2.1.14), L-

12 Tyrosine 7-amido-4-methylcoumarin (EC 3.4.11) and 4-methylumbelliferylphosphate (EC

13 3.1.3.1) and the oxidative substrate was L-3,4-dihydroxyphenylalanine (L-DOPA, EC 1.10.3.2)

14 plus 10 ul 0.3 M H_2O_2 for peroxidase. Following substrate additions, all plates were incubated at

15 15˚C for 3–24 h when activity was measured. Hydrolase activity was determined using a

16 flourometer (355 nm excitation and 460 nm emission) and phenol oxidase and peroxidase

17 activities were determined spectrophotometrically with a 450 nm filter (Thermo Flouroskan and

18 Multiskan, Thermo Scientific, Hudson, NH).

19 *Litter chemistry*

20 Litter was pyrolyzed at 600 °C for 20 s using a CDS Pyroprobe 5150 pyrolyzer (CDS Analytical,

21 Inc, Oxford, PA). Pyrolysis products were then transferred to a Thermo Trace GC Ultra and

22 separated on a 60 m fused silica capillary column (SGE Incorporated, Austin, TX) (0.25 μm i.d.)

23 over a 60 min period. An ITQ 900 ion trap mass spectrometer (Thermo Fisher Scientific, Austin,

24   TX) with a 200 °C heated electron source and an electron multiplier was used for compound

25   ionization and detection.

26

27

28