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The soil microbial carbon pump: From conceptual insights to empirical assessments

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Abstract

The global soil carbon (C) pool is massive, so relatively small changes in soil organic carbon (SOC) stocks can significantly alter atmospheric C and global climate. The recently proposed concept of the soil microbial carbon pump (MCP) emphasizes the active role of soil microbes in SOC storage by integrating the continual microbial transformation of organic C from labile to persistent anabolic forms. However, the concept has not been evaluated with data. Here, we combine datasets, including microbial necromass biomarker amino sugars and SOC, from two long-term agricultural field studies conducted by large United States bioenergy research programs. We interrogate the soil MCP concept by investigating the asynchronous responses of microbial necromass and SOC to land-use change. Microbial necromass appeared to preferentially accumulate in soil and be the dominant contributor to SOC accrual in diversified perennial bioenergy crops. Specifically, ~92% of the additional SOC enhanced by plant diversity was estimated to be microbial necromass C, and >76% of the additional SOC enhanced by land-use transition from annual to perennial crops was estimated to be microbial necromass. This suggests that the soil MCP was stimulated in diversified perennial agroecosystems. We further delineate and suggest two parameters—soil MCP *capacity* and *efficacy*—reflecting the conversion of plant C into microbial necromass and the contribution of microbial necromass to SOC, respectively, that should serve as valuable metrics for future studies evaluating SOC storage under alternative management in changing climates.

KEYWORDS

amino sugars, bioenergy cropping systems, MCP capacity, MCP efficacy, microbial necromass, soil organic carbon

1 | INTRODUCTION

As a result of fossil fuel combustion, increasing greenhouse gas concentrations in the atmosphere are leading to global warming (Camill, 2010), which will continue to alter ecosystem services and degrade human welfare and well-being (Rossati, 2017). Global soil carbon (C) stocks are about three times greater than atmospheric C stocks (Jackson et al., 2017), so slight changes in soil organic C (SOC)

stocks will impact global climate (Fargione et al., 2018; Lal, 2010; Rustad, Huntington, & Boone, 2000; Stockmann et al., 2013). Agricultural soils are a significant part of the overall reduction strategy, so investigations into the accumulation and stabilization of SOC in agricultural systems have increased considerably in recent years (Poffenbarger et al., 2020; Smith et al., 2020; Zomer, Bossio, Sommer, & Verchot, 2017). In the policy realm, the *4 per 1,000 Initiative* calls for an annual increase in SOC stocks of 0.4% on agricultural lands

globally to reduce the CO₂ concentration in the atmosphere (COP21, 2015; Rumpel, Lehmann, & Chabbi, 2018).

Soil microbes influence SOC stocks in more ways than simply liberating C to the atmosphere via decomposition, where much of the C accessed by microbes is respired as CO₂ (i.e., catabolism). They also take up C, build their bodies, and eventually die (i.e., anabolism). These processes of constant C turnover via assimilation and biomass construction, and subsequent cell death and metabolic products, can be conceptualized as “pumping” microbial residues into spaces and configurations of organic matter that can persist in soils for decades to millennia (Cotrufo, Wallenstein, Boot, Deneff, & Paul, 2013; Liang, Amelung, Lehmann, & Kästner, 2019; Liang, Schimel, & Jastrow, 2017; Schimel & Schaeffer, 2012). The concept of the soil *microbial carbon pump* (MCP) emphasizes the activity of soil microbes continuously “processing” C and introducing new compounds in soils, some becoming stabilized via “entombing” effects (Liang et al., 2017). While the soil MCP concept is conceptually compelling, it remains elusive because of a lack of mechanistic understanding and insufficient assessment of existing empirical studies that somewhat ineffectively link microbial necromass with SOC dynamics.

2 | EMERGENCE OF THE SOIL MCP CONCEPT

Our understanding of soil organic matter (SOM) genesis is rapidly changing. Historically, structural compounds of plant residues (mostly lignin) were thought to be the main source of stable SOC (Martens, 2000; Rasse, Rumpel, & Dignac, 2005). But most stabilized SOC has a signature indicative of microbial metabolites rather than plant constituents (Kallenbach, Frey, & Grandy, 2016; Lehmann, Kinyangi, & Solomon, 2007; Miltner, Bombach, Schmidt-Brücken,

& Kästner, 2012); therefore, there is growing acceptance that SOC abundance in an ecosystem is primarily driven by microbial anabolic activity, that is, continuous microbial growth and death (Bradford, Keiser, Davies, Mersmann, & Strickland, 2013; Cotrufo et al., 2013; Haddix, Paul, & Cotrufo, 2016; Kallenbach et al., 2016; Poelau et al., 2019; Sokol & Bradford, 2019; Figure 1).

By synthesizing available knowledge and reconciling different mechanistic views on microbe-mediated C cycling in soil, Liang et al. (2017) formulated a conceptual framework for demonstrating plant C transformation and deposition into the soil C pool via microbial metabolic processing. One key element of the framework is that the soil MCP integrates the positive effect of long-term microbial assimilation processes on SOC storage through the “in vivo microbial turnover pathway.” Of course, plants provide the initial input of C to soil via litter and root exudation, but most stabilized SOC is derived from microbial anabolic processing of plant tissues (Kallenbach et al., 2016; Kästner & Miltner, 2018; Liang, Cheng, Wixon, & Balsler, 2011). The soil MCP concept highlights the role of necromass inputs in soil C storage as products of microbial anabolism. A recent meta-analysis showed that microbial necromass can make up more than half of topsoil SOC pool in temperate ecosystems (Liang et al., 2019). Therefore, assessing and characterizing microbial necromass dynamics in the soil are important to improving field management that enhances soil MCP contribution to SOC storage and to modifying terrestrial C cycling models so that we can improve SOC projections under alternative climates.

Decades-long bioenergy experiments offer an opportunity to assess the soil MCP concept in agricultural ecosystems by providing an appropriate land-use model with critical data relevant to projected widespread land-use changes. Sustainable bioenergy cropping

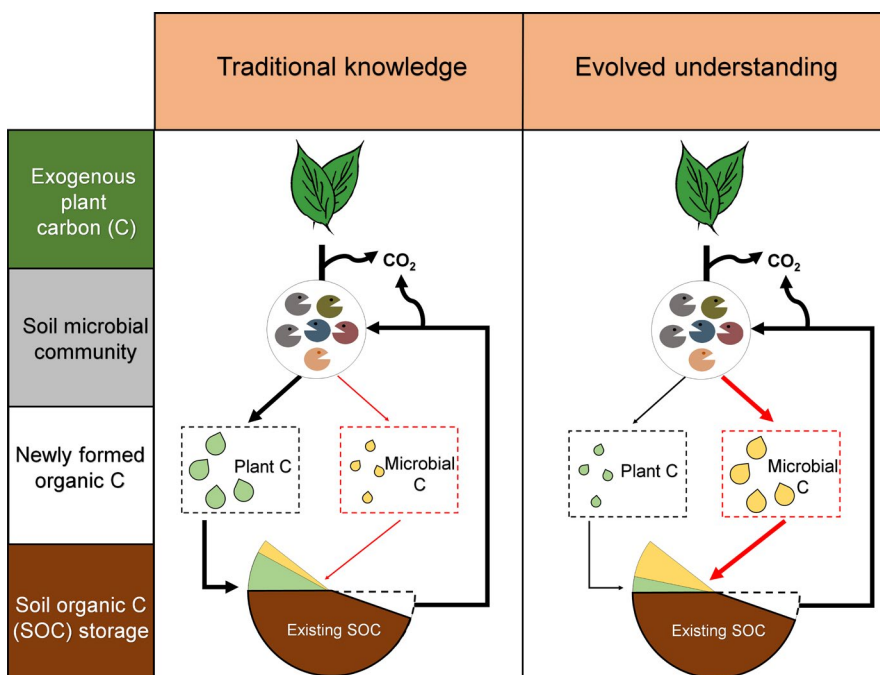


FIGURE 1 Brief illustration of soil organic carbon (C) formation paradigms that demonstrate microbial activity to “process” C, in which the evolved understanding highlights microbial ability to produce long-lasting compounds that accumulate in soil. Arrows represent fluxes among pools. Traditional knowledge of soil C formation focused on partial degradation of plant detritus by microbial catabolism (black lines), as shown in the left-hand panel. However, there is mounting evidence that microbial anabolism (red lines) also plays an important role—microorganisms can directly transform C into persistent forms via necromass depositions, as shown in the right-hand panel. The thickness of the arrow representing pathways may vary depending on the ecosystems

systems are beneficial to humans because they have the potential to provide energy while addressing climate change by offsetting anthropogenic greenhouse gas emissions with enhanced SOC storage (Gelfand et al., 2020; Robertson et al., 2017). Therefore, understanding C sequestration mechanisms in these ecosystems should help us increase SOC accumulation via social and economic incentives for bioenergy cropping system performance.

Differentiating the C in microbial residues from non-microbial organic C makes direct measurement of microbial necromass in soil difficult. However, soil microbial necromass biomarkers exist that can overcome this challenge as well as circumvent the logistical challenges of using isotopes to track the flow of C into necromass. Particularly, useful biomarkers are amino sugars because they are absent in plants, relatively stable to fluctuations in microbial activity, and can persist in soils for a long time after cell death (Amelung, Miltner, Zhang, & Zech, 2001; Ding et al., 2019; Joergensen, 2018; Liu et al., 2019; Ma et al., 2018). Since microbial living biomass contributes negligibly to soil amino sugars, they are good indicators of microbial necromass (Glaser, Turrión, & Alef, 2004; Joergensen, 2018). By assessing amino sugars in soils, we can investigate microbial necromass dynamics at the community level (fungi and bacteria; Amelung et al., 2001; Ding, Liang, Zhang, Yuan, & Han, 2015; Glaser et al., 2004; Guggenberger, Frey, Six, Paustian, & Elliott, 1999) and assess the contributions of necromass to SOC storage under different environmental conditions (Bai et al., 2017; Engelking, Flessa, & Joergensen, 2007; Khan, Mack, Castillo, Kaiser, & Joergensen, 2016; Liang et al., 2019; Murugan & Kumar, 2013; Ye et al., 2019).

3 | MICROBIAL NECROMASS IN BIOENERGY CROPPING SYSTEMS

We used SOC and amino sugars data from two long-term cropping system experiments in the United States—the Wisconsin Integrated Cropping Systems Trial (WICST; Sanford, 2014; Sanford et al., 2012), partially supported by the US Department of Energy–Great Lakes Bioenergy Research Center, and the University of Illinois Energy Farm (UIEF) (Anderson-Teixeira et al., 2013), partially supported by the Energy Biosciences Institute and now the Center for Advanced Bioenergy and Bioproduct Innovation. At WICST, we investigated Mollisols to ~100 cm depth with high diversity (HD) and low diversity (LD) tallgrass prairie restoration treatments (25 and 6 species sown, respectively) 9 years after planting (Liang et al., 2016). At UIEF, we examined the surface 10 cm on Mollisols with three well-established biomass cropping systems—annual crops (maize–maize–soybean rotation, MMS), switchgrass, and mixed prairie—that were harvested annually after each of six growing seasons (Zhu, Liang, Masters, Kantola, & DeLucia, 2018). Detailed site information can be found in Supplementary File S1.

Past work at these sites investigated the impacts of cropping systems on amino sugars to understand plant composition and

diversity effects on soil microbial composition (Liang et al., 2016; Zhu et al., 2018). Here, we estimated fungal and bacterial necromass C based on the knowledge that soil glucosamine (GluN) is mainly from fungal cell walls, while soil muramic acid (MurA) is exclusively from bacterial cell walls as described by Appuhn and Joergensen (2006). Briefly, to calculate fungal necromass C, we subtracted bacterial GluN from total GluN first assuming that MurA and GluN occur at a 1:2 molar ratio on average in bacterial cells. Then, we multiplied fungal GluN by the averaged conversion factor of 9 to obtain fungal necromass C. Bacterial necromass C was estimated by multiplying MurA by the averaged conversion factor of 45 assuming that gram-positive bacteria and gram-negative bacteria occur at a ratio of 65% to 35% (Appuhn & Joergensen, 2006), for detailed calculations, see Supplementary File S2. We then compared changes in the stocks of microbial necromass (the sum of fungal and bacterial necromass C) and SOC across gradients and over time to infer the effects of treatments on soil MCP contribution to SOC dynamics.

After 9 years at WICST, HD plantings had higher total amino sugars (+0.21 Mg increase) and SOC accrual (+2.57 Mg increase, 25.96 Mg in HD vs. 23.40 Mg in LD) within a 0.2-ha plot to a depth of 100 cm compared to LD plantings (Table S1). By scaling-up amino sugars to microbial necromass C (Supplementary File S2), we found HD plots had higher microbial necromass C accumulation (+2.36 Mg increase, 10.86 Mg in HD vs. 8.50 Mg in LD) indicating that ~92% of the additional SOC was estimated to be microbial necromass C (Figure 2a). The average proportions of microbial necromass C in the whole SOC pool were ~42% in the HD plots and ~36% in the LD plots.

After a 6-year land-use transition from annuals to perennials (from 2008 to 2014) at UIEF, switchgrass increased amino sugars (+0.22 Mg) and SOC (+2.67 Mg, 18.40 Mg in 2014 vs. 15.73 Mg in 2008) within a 0.7-ha plot to a depth of 10 cm, the mixed prairie increased amino sugars (+0.21 Mg) and SOC (+2.34 Mg, 17.36 Mg in 2014 vs. 15.02 Mg in 2008), while the maize–maize–soybean rotation slightly increased amino sugars (+0.03 Mg) but decreased SOC (–0.48 Mg, 14.72 Mg in 2014 vs. 15.21 Mg in 2008; Table S2). By scaling up amino sugars to microbial necromass C, we found the increase in microbial necromass C (+2.03 Mg, 12.71 Mg in 2014 vs. 10.68 Mg in 2008) was ~76% of the additional SOC in switchgrass and ~93% (+2.17 Mg of necromass C, 12.70 Mg in 2014 vs. 10.53 Mg in 2008) of the additional SOC in mixed prairie (Figure 2b). The average proportion of microbial necromass C in the whole SOC pool of all the samples at UIEF was ~70%.

Our results suggest that higher levels of microbial anabolism were responsible for additional SOC formation under more diverse perennial communities. The increasing SOC pools appeared to be renewed by microbial necromass, which became a higher proportion of the additional SOC pools while the proportional increase in non-microbial necromass was smaller. This phenomenon is similar to the divergent accumulation patterns of microbial necromass and plant lignin in grassland soils reported in Ma et al. (2018). These results may stem from plant functional complementarity in higher diversity treatments (Fornara & Tilman, 2008) where root biomass and turnover can be higher (Lange et al., 2015; Sprunger, Oates,

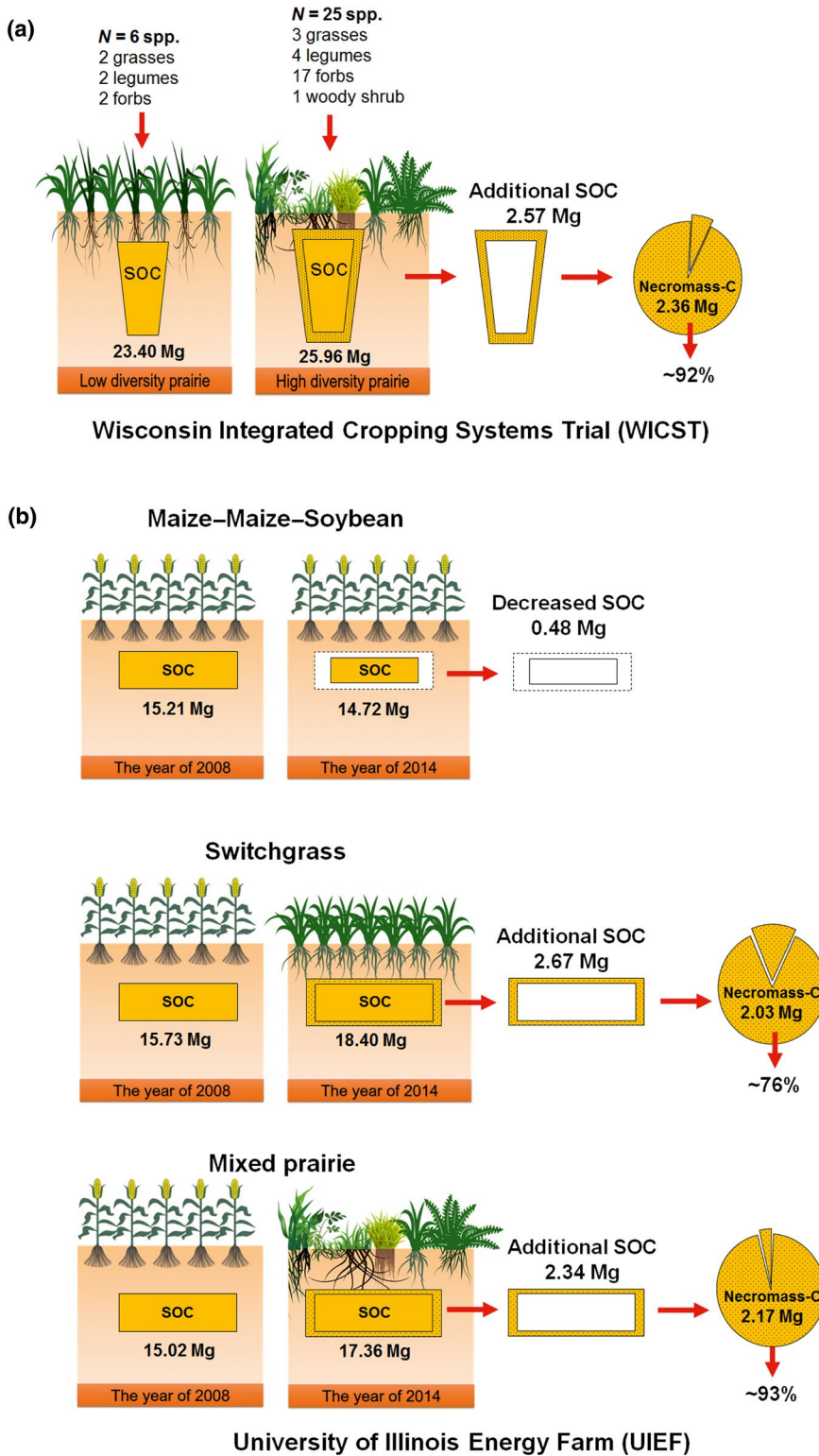


FIGURE 2 Illustration of the changes in microbial necromass carbon (C) and soil organic carbon (SOC). Changes to 100 cm depth under restored perennial grassland communities sown with two levels of plant species richness at the Wisconsin Integrated Cropping Systems Trial (WICST), where the “additional SOC” pool under high diversity prairie was comprised of ~92% microbial necromass C (a); after 6 years of alternative bioenergy cropping systems in the University of Illinois Energy Farm (UIEF), where the “additional SOC” pool under switchgrass was comprised of ~76% microbial necromass C and under mixed prairie was ~93% (b)

Jackson, & Robertson, 2017), stimulating microbial processing of root inputs of C (Lange et al., 2015; Liang et al., 2016; Prommer et al., 2020). As well, perennial crops are known for higher root inputs relative to annual crops (Anderson-Teixeira et al., 2013; Tiemann & Grandy, 2015). Although microbial necromass did not contribute to SOC increase in the annual crops, they showed relative stability compared to the non-microbial necromass fractions

that significantly decreased after the 6-year UIEF experiment. Meanwhile, the estimated microbial necromass proportions in the whole SOC pool were ~40% at WICST and ~70% at UIEF, indicating significant C contributions by plants. Litter quality and the extent of soil C saturation can jointly influence the relative proportions of microbial- and plant-derived SOC (Castellano, Mueller, Olk, Sawyer, & Six, 2015; Sokol, Sanderman, & Bradford, 2019).

We recognize that the relationship of biomarker amino sugars to actual microbial necromass can be highly variable across soil types (Liang et al., 2019). However, our necromass comparisons were all on the same type of soil, which should minimize concern about conversion factor-variability to some extent. The conversion factors were based on living biomass from cultured microbes under sufficient substrates (Appuhn & Joergensen, 2006), while recognizing that there is limited knowledge about conversion factors for soil microbes under starvation (Joergensen, 2018; Liang et al., 2019). Moreover, except for the microbial cell wall, living microbial biomass and necromass are different in other components, which may result in differing turnover over longer periods (Joergensen, 2018). These differences would introduce uncertainties when the conversion factors were used to assess microbial necromass. However, the stability of conversion factors has been clarified by Appuhn and Joergensen (2006), and their applications and values have been recognized and acknowledged in recent years (Joergensen, 2018; Liang et al., 2019). More precise quantification of soil microbial necromass depends on development and validation of alternative methods that characterize soil protein or relic DNA (Carini et al., 2016; Miltner et al., 2012). However, soil protein extraction, separation techniques, and interfering substances obstruct the application of soil protein (Benndorf et al., 2009) and no clear conversion factors for DNA to microbial necromass have been proposed (Liang et al., 2019).

4 | SOC ACCUMULATION DRIVEN BY SOIL MCP IN MORE DIVERSE PERENNIAL PLANTINGS

We compared relative changes of amino sugars and SOC from these two studies (for detailed calculations, see Supplementary File S3), reasoning that positive effects of the soil MCP on SOC storage would lead to a faster accumulation of amino sugars relative to the whole SOC pool in diversified perennial cropping systems. Past results from WICST indicated more diverse perennial grass communities had higher abundances of lipids and amino sugars across the 100-cm soil profile (Liang et al., 2016), leading us to expect that these plots would stimulate microbial biomass production and necromass accumulation. Relative to the LD treatment, the HD treatment increased amino sugars by 18.52% and SOC by 10.97% (Figure 3a; Table S1), indicating a higher rate of accumulation of microbial necromass in soil than that of SOC with greater plant diversity.

Our past work at UIEF led us to expect that conversion from annual to perennial crops would affect the soil MCP with implications for SOC storage (Zhu et al., 2018). When using the relative change in SOC as the baseline, amino sugar accumulation rates were higher in the perennials (switchgrass = 0.86, mixed prairie = 0.94) than the annual cropping systems (maize–maize–soybean = −0.56), suggesting greater microbial necromass contribution to SOC formation in the soils with perennial vegetation (Figure 3b; Table S2).

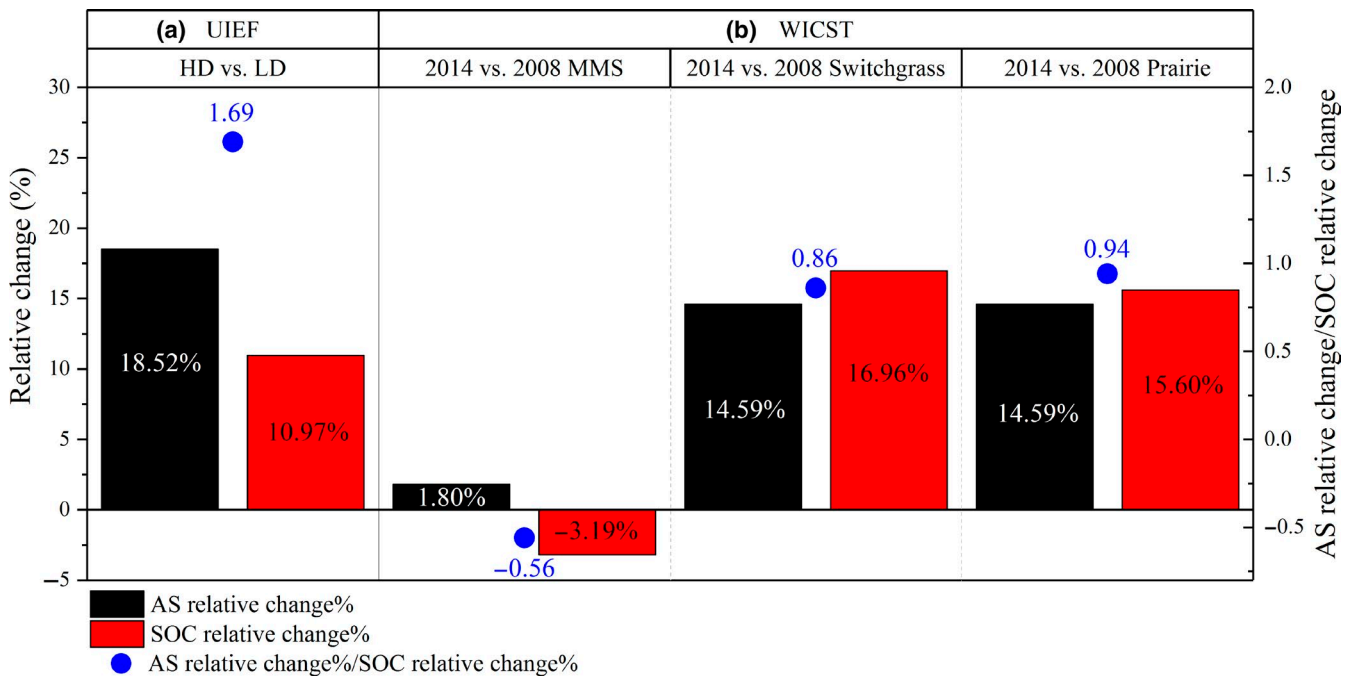


FIGURE 3 Relative changes in amino sugars (AS) and soil organic carbon (SOC). Relative changes in AS and SOC to 100 cm depth under restored perennial grassland communities sown with two levels of plant species richness at the Wisconsin Integrated Cropping Systems Trial (WICST; a), and alternative bioenergy cropping systems in the University of Illinois Energy Farm (UIEF) after 6 years (b), where the WICST calculates the relative changes between diversity treatments and the UIEF calculates the relative changes between years within each cropping system (see Supplementary File S3 for specific calculations). In (a), HD and LD mean high and low diversity plantings, respectively. In (b), MMS means maize–maize–soybean rotation

5 | SOIL MCP CAPACITY AND EFFICACY AS INDICATORS OF SOC STORAGE

To assess the effects of the soil MCP on SOC storage, we characterized two key parameters of the soil MCP model—*capacity* and *efficacy*. Soil MCP “capacity” describes the absolute accumulation of microbial necromass in the soil (represented by microbial necromass biomarker-amino sugars content of soil), reflecting the conversion of plant-derived C into microbial products via microbial anabolism. Soil MCP “efficacy” represents the contribution of microbial necromass to SOC (represented by the ratio of amino sugars to SOC).

Higher amino sugar content in a soil should correspond to greater MCP capacity, as we observed in the HD compared to the LD plots at WICST (Table S1), and in the perennial plots in 2014 relative to 2008 at UIEF (Table S2). Higher ratios of amino sugar to SOC correspond to greater soil MCP efficacy, meaning greater microbial necromass contributions to SOC. While this approach does not advance our mechanistic understanding of SOC transformations, it provides a practical strategy for soil C characterization indicative of the potential for management changes to affect SOC stabilization.

While assessing whether and how the soil MCP contributes to the SOC pool during complex and dynamic soil processes, we noted that soil MCP efficacy tightly corresponded to soil MCP capacity and SOC dynamics. If the relative increase in soil MCP capacity exceeds that of SOC, MCP efficacy would be increased, and vice versa; if the relative increase in MCP capacity is equivalent to that of SOC, MCP efficacy would be constant. As one part of the SOC, it is important to note that, microbial necromass does not fully determine the quantity of SOC, but it does affect SOC composition and quality. Typically, a larger proportion of microbial necromass in the SOC pool (i.e., higher MCP efficacy) will indicate more C likely is being stored in long-lasting forms (such as mineral-associated microbial-derived organic matter) and not being liberated readily from the soil (Córdova et al., 2018; Sokol et al., 2019). Thus, MCP efficacy can be a useful assessment of SOM stability. Irrespective of whether the quantity of SOC is increased or decreased, a satisfactory operation of the soil MCP in accumulating SOM will lead to a higher proportion of microbial necromass, which may correspond to more persistent SOC associated with a higher potential of microbial-derived C stabilized in the soil C pool. Soil MCP capacity and efficacy should be characterized across gradients and over time to improve our quantification and prediction of SOC accumulation in soils.

6 | CONCLUSIONS

We assessed the soil MCP in accumulating SOC pools and interpreted how it was affected by land-use changes by investigating changes in microbial necromass and SOC under long-term experimental bioenergy cropping systems. Compared to annual bioenergy crops, perennial grasslands grown and harvested for bioenergy supported higher soil MCP “capacity” (i.e., greater accumulation of microbial necromass) leading to greater contribution of microbial necromass to recently accumulated SOC. Perennial

grassland of higher diversity further improved both the soil MCP “capacity” and “efficacy” (i.e., greater contribution of microbial necromass to the whole SOC pool) to increase and stabilize the SOC pool. The MCP metrics delineated here should serve as valuable parameters in climate and ecological models and stimulate interest in new studies related to the role of the soil MCP in soil C stabilization.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

C.L. conceived the ideas. X.Z. and C.L. performed laboratory work and analyzed data. R.D.J., E.H.D. and J.M.T. supervised field experiments. All authors were involved in the preparation of the manuscript and approved the final version.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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