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Do corn-soybean rotations enhance decomposition of soil organic matter?



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Abstract

Aims Corn and soybean crops are often grown in rotation, requiring lower nitrogen (N) inputs than continuous corn. However, soil organic carbon (C) may be declining in corn-soybean systems despite sustained residue inputs. We asked whether corn-soybean rotations increase decomposition of litter and soil C as compared with continuous corn.

Methods We incubated soils from a long-term field experiment including continuous corn and both phases of the corn-soybean rotation. Soils were amended with corn litter, soybean litter, or no litter. We measured natural abundance C stable isotopes (δ^{13} C values) in respiration and microbial biomass to partition C sources. *Results* Addition of soybean litter increased microbial biomass while corn did not. However, corn litter addition consistently increased (i.e., primed) soil C decomposition while soybean litter did not. Soils most recently

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planted to corn following soybeans had the greatest soil C decomposition and N mineralization irrespective of litter addition, and they decomposed corn litter faster and had a faster priming response than the other treatments.

Conclusions Our data support the hypothesis that alternating inputs of N-rich soybean litter and relatively Npoor corn litter could enhance litter and SOC decomposition by driving microbial growth following the soybean phase and stimulating priming following the corn phase. Increased decomposition and N mineralization from litter and SOC in corn-soybean rotations may contribute to the soybean N credit but could also contribute to longer-term soil C and N declines, consistent with field data.

Keywords Carbon-use efficiency · Carbon stable isotopes · Microbial biomass · Nitrogen mineralization · Priming · Soybean nitrogen credit

Introduction

Corn (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr.) crops grown in rotation are the dominant land cover and source of primary productivity in the Corn Belt of the midwestern United States, where a smaller area is under continuous corn cultivation (Prince et al. 2001; Yu et al. 2018). Impacts of these cropping systems on soil carbon (C) and nitrogen (N) cycling have received intensive study. Major soil organic C losses followed the conversion of historical grasslands to

croplands, spurring interest in management to promote C accrual (Huggins et al. 1998; Russell et al. 2005; Chambers et al. 2016). Corn Belt cropping systems produce ongoing losses of reactive N to water and the atmosphere which are derived from both fertilizer/ manure inputs and extant soil organic matter, prompting a focus on ecosystem-scale N balances (Jaynes and Karlen 2008; David et al. 2010; Martinez-Feria et al. 2018). Nevertheless, ongoing trends in soil C and N under corn-soybean cultivation remain uncertain. Changes in soil C stocks are primarily determined by the balance of crop residue inputs and decomposition of residues and extant C. Greater residue inputs contribute to greater soil C under continuous corn than cornsoybean rotations (Russell et al. 2009; Poffenbarger et al. 2017). However, potential differences in decomposition of litter and soil C between these cropping systems have received less attention and are the focus of our present study.

In several sites throughout the Corn Belt, soil C and N appeared to have stabilized after decades of cornsoybean cultivation, or may be increasing under continuous corn (Russell et al. 2005; David et al. 2009; Poffenbarger et al. 2017). Other studies suggested ongoing declines in soil C under corn-soybean rotations (Liebig et al. 2002; Huggins et al. 2007), as well as a decreased efficiency by which crop residues are retained as soil C in corn-soybean rotations as compared to continuous corn (Poffenbarger et al. 2017). Given that changes over annual to decadal periods are notoriously difficult to detect in large and heterogeneous pools, it is not surprising that the effects of corn-soybean cropping systems on soil C and N stocks remain unclear. However, a long-term synthesis of measurements from across the Corn Belt also demonstrated apparent ongoing losses of soil N (Tomer et al. 2017), along with stable or increasing crop productivity (Yu et al. 2018). Observations of decreasing soil N are also consistent with net negative balances of N inputs vs. outputs measured at the scale of agricultural catchments (Jaynes and Karlen 2008; Gentry et al. 2009; David et al. 2010). In this context, we sought to assess mechanisms that could potentially contribute to ongoing soil C and N losses in these systems. We pose the question: could cornsoybean rotations increase the decomposition of existing soil C and mineralization of associated N due to microbial dynamics associated with fluctuating litter quality?

Corn and soybean rotations involve a temporal fluctuation in the quantity and chemical composition of crop residue production, whereby corn and soybean decompose at different rates and alter the availability of mineral N (Green and Blackmer 1995). Their impacts on decomposition of extant soil C remain unclear, however. Corn typically produces a more than two-fold greater mass of total residue inputs (above- plus belowground) with a higher C:N ratio than soybean (Russell et al. 2009; Jarchow et al. 2015). Decomposition of corn residue in soil thus leads to a significantly longer period of net N immobilization than observed during soybean residue decomposition, which decreases the availability of mineral N for plants (Green and Blackmer 1995). This difference in N mineralization dynamics between corn and soybean litter is a major contributor to the "soybean N credit," whereby corn grown following soybean typically requires lower inputs of mineral N to achieve optimum yields than corn following corn (Green and Blackmer 1995; Gentry et al. 2001).

Beyond their well-known differences in residue decomposition rates, corn and soybean grown in rotation may also impact the decomposition of extant soil C and subsequent litter inputs. Positive priming of soil C decomposition, defined as an increase in the decomposition of extant soil C in response to new residue inputs, has been demonstrated in many soils and is frequently linked to microbial nutrient demand (Kuzyakov 2010). That is, when a microbial community is confronted with substrates with high C:N relative to their biomass, microbes produce enzymes to degrade soil C to acquire associated N. Conversely, a recent study demonstrated that addition of synthetic N fertilizer to soils under continuous corn cultivation directly suppressed decomposition, presumably by satiating microbial N demand (Mahal et al. 2019). Priming of soil C decomposition induced by corn or soybean root growth has been demonstrated during short-term lab experiments (Helal and Sauerbeck 1984; Fu and Cheng 2002), as well as in field experiments where corn was grown on soils previously planted to pasture or other crops (Mazzilli et al. 2014; Kumar et al. 2016). However, we are unaware of studies that have explicitly examined impacts of priming and its temporal dynamics in the context of corn-soybean rotations. Previous syntheses indicated that crop rotations often increase microbial biomass and decomposition rates relative to monocultures (McDaniel et al. 2014; Tiemann et al. 2015), that microbial growth is a key driver of priming (Kuzyakov 2010), and that microbes grow more efficiently on litter with low C:N ratios (Manzoni et al. 2012). Thus, we propose that cornsoybean rotations could provide ideal conditions for priming: alternating substrates with low and high C:N would fuel microbial growth on the low C:N substrate (soybean) and enhance subsequent decomposition of litter and soil C following addition of the high C:N substrate (corn).

Here, we asked how litter quality (corn vs. soybean) and cropping history (corn after soybean, soybean after corn, and continuous corn with partial residue removal) affected the decomposition of litter and soil C, N mineralization, and microbial biomass production. To isolate these drivers and partition multiple sources of C loss, we used laboratory incubations of soils from a long-term (10 y) no-till field experiment in central Iowa, USA (Jarchow et al. 2015). We used naturalabundance C stable isotope (δ^{13} C) measurements to partition soil respiration and microbial biomass between corn (C_4) and soybean (C_3) sources. We hypothesized that 1) soybean litter decomposes more rapidly and produces more microbial biomass than does corn litter; 2) priming of soil C decomposition is greater following addition of corn litter than soybean litter; 3) soils planted to corn following soybean have greater rates of litter and soil C decomposition and N mineralization than soils planted to soybean following corn or continuous corn.

Methods

Field experiment

We collected soil samples from the Comparison of Biofuels Systems (COBS) experiment, which is located near Iowa State University in north-central Iowa, USA (41.9212 °N, -93.7499 °W). The predominant soil series at this site are Webster silty clay loam (fine-loamy, mixed, superactive, mesic Typic Endoaquoll) and Nicollet loam (fine-loamy, mixed, superactive, mesic Aquic Hapludoll). For this study, we compared soils that had been managed under continuous corn cultivation or corn-soybean rotations for 10 years (2008-2017). Both phases of the corn-soybean rotation were grown in separate plots during every year, such that three field treatments were examined: continuous corn, corn grown after soybean (corn after soy), and soybean grown after corn (soy after corn). Each treatment had four replicates (0.15 ha plots) arranged in a randomized complete block design. All treatments were managed without tillage and residue was partially removed (52%

removal on average; 3.2 Mg ha^{-1} from the continuous corn treatment. Because residue production from soybean was less than half that of corn in the corn-soybean rotations (Jarchow et al. 2015), partial residue removal from the continuous corn treatment served to decrease differences in above-ground residue inputs between the corn-soybean rotations and the continuous corn treatments. Rates of N fertilization varied based on soil nitrate measurements and averaged 158 kg N ha⁻¹ y⁻¹ for corn grown in rotation with soybean (no N was applied during the soybean phase). Further management details are provided by Jarchow et al. (2015).

Soil sampling and incubation

Soils were sampled in October 2017 (prior to harvest) from six locations in each field plot from 0 to 15 cm depth using a stainless-steel corer (2.5 cm diameter) and were combined to form a composite sample from each plot (any surface residue was pushed aside prior to sampling the mineral soil). Samples were stored in sealed plastic bags at 4 °C for one week prior to the incubation, and representative subsamples were oven dried to determine moisture content. Soils from each field plot were incubated under each of three litter amendment treatments: added corn litter, added soybean litter, and no added litter. Thus, our experiment had a split-plot design: three cropping system treatments with four field replicates each, and three litter amendment treatments applied to soil from each field plot, for a total of 36 experimental units. Litter (corn and soybean leaf and petiole tissues) was collected from senesced standing biomass at the time of soil sampling, dried at 65 °C, and ground to pass a 1 mm mesh. We used this approach to focus on the most rapidly decomposing components of corn and soybean litter and their contrasting C:N ratios (Russell et al. 2009), given that corn and soybean stalks have greater lignin content and more similar C:N (Córdova et al. 2018). For each experimental unit, we combined 5 g soil (dry mass equivalent) and 0.05 g of litter (where applicable) in an open 50 mL centrifuge tube, mixed the contents by shaking side to side (bulk density was similar to 1 g cm^{-3}), and placed each tube in a glass jar (0.95 L). These ratios of soil:litter are similar in magnitude to what surface soils receive at the field site, given above-ground residue inputs of 2–9 Mg ha⁻¹ y^{-1} (Jarchow et al. 2015). To maintain microaggregate structure, soils were not sieved, but coarse roots and

macrofauna (earthworms) were removed where present. Moisture was adjusted to 65% water-filled pore space by adding deionized water as necessary.

Soil-litter mixtures were then frozen for one week to simulate natural winter conditions at the field site and thawed at 4 °C for 24 h. Jars with samples were fitted with gas-tight lids and two butyl septa for gas sampling and flushing and were purged with humidified CO₂-free air to remove ambient CO₂ from the jar headspace by venting to the atmosphere. Mole fractions and δ^{13} C values of soil-respired CO₂ were measured periodically throughout the 193-day incubation by sampling the headspace of each jar using a syringe with stopcock and injecting a 5 mL gas sample into a tunable diode laser spectrometer (TGA200A, Campbell Scientific, Logan, UT) as described previously (Hall et al. 2017). All δ^{13} C values were calibrated against reference gases traceable to World Meteorological Association primary standards and are reported in %o notation relative to Vienna Pee Dee Belemnite. Following each headspace sampling, jars were purged with humidified CO₂-free air and remained sealed until the subsequent sampling date, such that we measured the complete cumulative CO₂ production over the duration of the incubation. Headspace CO2 was measured at two- to four-day intervals during the first three weeks of the experiment, and progressively at one-, two-, or three-week intervals thereafter as fluxes stabilized (Fig. 1). Deionized water was added following headspace sampling to replenish minor soil moisture losses (due to water vapor loss during flushing) at approximately monthly intervals.

At the beginning and end of the experiment, soil subsamples (2 g dry mass equivalent) were extracted in a 1:5 mass ratio with 2 M potassium chloride (KCl) solution for colorimetric measurement of ammonium and nitrate + nitrite using phenol-hypochlorite and sulfanilamide-NED colorimetric methods, respectively. Net N mineralization was calculated as the difference between total KCl-extractable mineral N measured at the end and beginning of the incubation. Soil organic C and N concentrations in the pre-incubation soils and litter were measured by combustion on an elemental analyzer coupled to an isotope ratio mass spectrometer (Thermo Finnigan Delta Plus XL, Waltham, MA). These soil subsamples were fumigated with hydrochloric acid vapor prior to analysis to remove any trace carbonates that may have been present.

Microbial biomass C and δ^{13} C values of pretreatment and post-treatment soil samples were measured using chloroform fumigation-incubation, whereby soil respiration is measured following treatment with chloroform vapor, which lyses cells and increases C availability to re-establishing microbes (Jenkinson and Powlson 1976). Briefly, samples were fumigated with chloroform under vacuum for 24 h, brought to 65% water-filled pore space, and incubated in jars following purging of the headspace with CO₂-free air as described above. Accumulated CO₂ was measured after 7, 14, and 21 days, by which time CO₂ production from fumigated samples was comparable with controls. Microbial biomass C was calculated as the difference in CO₂-C production between fumigated and non-fumigated samples over 14 days. The δ^{13} C values of microbial biomass were calculated using the chloroform fumigated and non-fumigated controls as follows, where the subscripts fum, control, and mic denote the fumigated samples, controls, or calculated microbial contributions, respectively:

$$\delta^{13}C_{mic} = \frac{\delta^{13}C_{fum}CO_{2_fum} - \delta^{13}C_{control}CO_{2_control}}{CO_{2_mic}} \quad (1)$$

Data analysis

In the samples that received added corn or soybean litter, we quantified contributions to soil respiration from litter C vs. extant soil C in a given sample using δ^{13} C measurements of respired CO₂ and two-end-member mixing models:

$$f \text{litter_t} = \frac{\delta^{13} C_{\text{obs_t}} - \delta^{13} C_{\text{litter}}}{\delta^{13} C_{\text{control_t}} - \delta^{13} C_{\text{litter}}}$$
(2)

Here, *f*litter_t denotes the calculated fraction of CO₂ derived from litter at each measurement period (time *t*), $\delta^{13}C_{obs}$ denotes the observed $\delta^{13}C$ value of respired CO₂ at time *t*, $\delta^{13}C_{litter}$ is the end-member value for litter-derived C (constant over time), and $\delta^{13}C_{control}$ is the observed $\delta^{13}C$ value of soil respiration at each time *t* from control soils that did not receive added litter. Corn and soybean litters had bulk $\delta^{13}C$ values of -13.2% and -29.1%, respectively. We assigned $\delta^{13}C_{litter}$ values in the mixing model that were 2% greater (-11.2% and -27.1% for corn and soybean, respectively) than measured bulk litter $\delta^{13}C$ (Hall et al. 2017), assuming

Fig. 1 Trends in CO₂ production **a** and δ^{13} C of CO₂ **b** over time plotted by cropping and litter addition treatments. Symbols denote cropping treatments (continuous corn, corn after soybean, and soybean after corn, respectively). Yellow, green, and brown colors denote litter addition treatments (corn, soybean, and no litter, respectively)



 $\delta^{13} C$ of CO_2 (‰)

-30

0

50

experiment, and that carbohydrates are 2%o enriched in δ^{13} C relative to bulk litter C, on average (Bowling et al.

100

Day of experiment

150

Springer

200

2008). This assumption was necessary to account for high δ^{13} C values observed early in the experiment for samples receiving corn litter (Fig. 1b), which were often greater than corn bulk litter δ^{13} C values. In several limited cases early in the experiment where observed δ^{13} C values were even greater than the defined C₄ endmember, these values were corrected by subtracting observed analytical uncertainty of the δ^{13} C measurements ($2\sigma = 0.6\%$). After calculating *f*litter _t, the fraction of respiration derived from soil (*f*soil _t) was calculated by difference:

$$f \text{soil}_t = 1 - f \text{litter}_t$$
 (3)

From the control soils (no litter added), we further partitioned soil respiration between C_4 (dominantly corn) and C_3 (dominantly soybean) sources using a two-end-member mixing model:

$$fC3 = \frac{\delta^{13}C_{obs_t} - \delta^{13}C_{C4}}{\delta^{13}C_{C3} - \delta^{13}C_{C4}}$$
(4)

Here, fC3 is the fraction of soil respiration derived from C₃-C, and $\delta^{13}C_{C4}$ and $\delta^{13}C_{C3}$ are the end-member values for corn and soybean described above. The fraction of respiration derived from C₄-C was calculated by difference:

$$fC4 = 1 - fC3 \tag{5}$$

We note that legacy C_4 and C_3 inputs from other plant species growing at the site prior to the present corn and soybean treatments may have also contributed to soil respiration. However, the long-term (decades) management of the study site under corn and soybean cultivation prior to the 10-year experiment implied the dominance of corn- and soybeanderived C as respiration sources. Therefore, we refer to C₄- and C₃-derived C as corn- and soybeanderived C, respectively. Given that C pools with sub-annual to decadal turnover times dominate soil respiration, impacts of changing atmospheric $\delta^{13}C$ values and other long-term fractionating processes in soil, such as microbial carboxylation of soil CO₂ (Ehleringer et al. 2000), should have relatively minor impacts on the mixing model results.

Fluxes of CO_2 derived from litter and soil C were calculated by multiplying total CO_2 fluxes by their fractional contributions. Similarly, C_3 - and C_4 -C contributions to respiration were calculated from the control soils. We calculated priming at each time point *t* as the difference in soil C losses between samples from the same cropping system that received litter and those that did not:

 $Cprimed_t = Csoil_amended_t-Csoil_control_t$ (6)

Patterns in C loss from litter and soil over time were quantified by fitting multiple-pool first-order decay models to observed trends in proportion C mass remaining (Fig. 2) for the combined replicates from each treatment using the nls function for non-linear regression in R version 3.5.1. The optimum number of pools for each respiration component (litter and soil) in each cropping system was selected by comparing model AIC values and trends in model residuals among nested models with one, two, or three C pools. The AIC model selection approach does not involve direct comparison of the fitted parameters among models, but rather balances model goodness of fit with parsimony when comparing models of increasing complexity. For example, a threepool model took the form:

$$Pr(t) = P_{\text{very}_fast} \left(e^{-k_{very}_fast} \right) + P_{\text{fast}} \left(e^{-k_{fast}t} \right)$$
$$+ \left(1 - P_{\text{fast}} - P_{\text{very}_fast} \right) \left(e^{-k_{slow}t} \right)$$
(7)

Where Pr(t) is the proportion of C mass remaining at time t, P_{verv} fast is the initial proportion of C in a "veryfast" pool, P_{fast} is the initial proportion of C in a "fast" pool, $(1 - P_{\text{fast}} - P_{\text{very fast}})$ is the initial proportion of C in a "slow" pool, and k_{fast} and k_{slow} are decomposition rate constants (y^{-1}) . Mean turnover times were expressed as the inverse of the k values (y). Rate constants and pool sizes calculated from multiple-pool firstorder models of CO₂ and δ^{13} C time series are widely used to provide inference into decomposition processes among treatments (Collins et al. 2000). Indeed, Reichstein et al. (2000) suggested that this method helps differentiate treatment effects that are consistent over time from transient differences in C mineralization. Differences in a given decomposition model term compared among either the cropping system or litter addition treatments were considered significant with nonoverlapping 95% confidence intervals with the Tukey correction for multiple comparisons. Based on the cumulative final C flux data, we assessed effects of cropping treatments, litter addition treatments, and their interactions on decomposition of litter C, soil C, priming, and N mineralization using ANOVA and Tukey post-hoc comparisons.



Fig. 2 Production of CO_2 from added litter C **a** and soil C **b**, and corresponding trends in cumulative mass loss of litter **c** and soil C **d** over time. Note that panels **c** and **d** have different y-axis scales for clarity. Symbols denote cropping treatments (continuous corn,

Results

Soil carbon, respiration, and decomposition modeling

Soil organic C and total N averaged $23 \pm 1 \text{ mg C g}^{-1}$ and $1.8 \pm 0.1 \text{ mg N g}^{-1}$, respectively, and neither parameter (nor the C:N ratios) differed significantly among

corn after soybean, and soybean after corn, respectively). Yellow, green, and brown colors denote litter addition reatments (corn, soybean, and no litter, respectively)

cropping treatments (Table 1). Total CO₂ production from soils that received added litter was initially 6- to 18-fold greater than unamended soils, declining to a 1.2to 1.4-fold difference after 190 days (Fig. 1a, Supplementary Table 1). In litter-amended soils, δ^{13} C values of soil-respired CO₂ were initially similar to endmember values of corn and soybean litter and gradually converged towards the soils with no added litter, which had intermediate δ^{13} C values (Fig. 1b). In soils without added litter, the continuous corn treatment consistently had the greatest δ^{13} C values, followed by soy after corn and soy after corn. The latter two treatments converged after approximately 96 days (Fig. 1b).

Trends in respired C were best fit by exponential decay functions that included either two or three pools each for litter and soil (Fig. 2, Table 2). The mean R^2 values for litter and soil C decomposition models were 0.994 and 0.999, respectively, and all models had $R^2 > 0.98$. Several decomposition rate constants were estimated as zero, indicating a constant decomposition flux independent of mass remaining. The inverse of the rate constant is the mean turnover time: decomposing litter was best described as the combination of a fast pool with turnover times between 1 and 5 weeks, and a slow pool with turnover times between 11 months and 11 years (varying between litter types and among cropping treatments). The fast pools comprised 45-61% of total litter C among treatments, with the balance allocated to the slow pools (Table 2). Soybean litter consistently decomposed faster than corn litter (significantly greater k-values for the fast pool; Fig. 2, Table 2). However, cropping treatments altered decomposition of corn litter: the proportion of corn litter C in the fast pool tended to be greatest, and the slow pool the was significantly smaller in corn after soy soil than the other cropping treatments.

Decomposition of soil C was best approximated with three-pool models in most treatments, with the exception of continuous corn and soy after corn soils amended with soybean litter, which were best fit with two-pool models. For three-pool models, the very fast pool had turnover times of one to three days and comprised 0.3– 1.2% of soil C; the fast pool had turnover times of one to eight months and comprised 2–7% of soil C; and, the slow pool had turnover times of 17–24 years and comprised 93–99% of soil C (Table 2). Addition of corn litter, but not soybean litter, increased the proportion of soil C in the very-fast soil pool relative to the no-litter controls (P < 0.05; Table 2). Soils from the corn after soy cropping treatment had a larger proportion of soil C in the fast pool than the others (P < 0.05; Table 2).

Cumulative decomposition

Differences in modeled decomposition rates and pool distributions among treatments translated to differences

in cumulative decomposition of litter and soil C and net N mineralization. Cumulative decomposition of added litter C (Fig. 3a) differed between corn and soybean litters (P=0.0002) and among cropping treatments (P=0.023), with a marginally significant interaction (P=0.05). Pairwise contrasts revealed that cumulative soybean litter decomposition was significantly greater than corn litter decomposition only in the continuous corn soils. Soybean litter decomposition was highest in continuous corn soil (29% higher than soy after corn; P=0.03) and intermediate in corn after soy soil. In contrast, corn litter decomposition was highest in corn after soy soil, where C loss was 29% and 25% higher than continuous corn and soy after corn, respectively (P < 0.05).

Cumulative decomposition of soil C (Fig. 3b) also differed among litter treatments (P < 0.0001) and cropping treatments (P = 0.0006), with no significant interaction (P = 0.47). Cumulative soil C decomposition in soils receiving corn litter was 32% greater than soybean litter and 42% greater than the no-litter samples (P < 0.0001), averaged across cropping treatments. Cumulative soil C decomposition from corn after soy soil was 20% greater than soy after corn (P = 0.008) and 28% greater than continuous corn (P < 0.001).

In the control soils (no litter added), the contributions of corn- vs. soybean-derived C to CO₂ differed significantly among cropping treatments (Fig. 4; P < 0.01). Decomposition of corn-derived C was significantly greater (P = 0.005) in corn after soy soils ($840 \pm 45 \ \mu g$ C g⁻¹) than soy after corn ($564 \pm 63 \ \mu g$ C g⁻¹), with intermediate values in continuous corn ($729 \pm 15 \ \mu g$ C g⁻¹). However, decomposition of soybean-derived C was equivalent between corn after soy ($413 \pm 17 \ \mu g$ C g⁻¹) and soy after corn ($368 \pm 47 \ \mu g$ C g⁻¹) soils, with significantly lower values (P = 0.01) in continuous corn ($210 \pm 11 \ \mu g$ C g⁻¹; Fig. 4).

Prior to the incubation, mineral N was significantly greater (P = 0.03) in the soy after corn soils ($11 \pm 2 \ \mu g \ N \ g^{-1}$) than corn after soy ($7 \pm 2 \ \mu g \ N \ g^{-1}$) or continuous corn ($6 \pm 1 \ \mu g \ N \ g^{-1}$). Net N mineralization differed significantly between litter treatments (P < 0.0001) and cropping treatments (P = 0.0004) with no significant interaction (Fig. 3c, Supplementary Table 2). Net N mineralization was more than two-fold greater in soils amended with soybean litter. However, net N mineralization was 25–28% greater in the corn after soy soils than the other two cropping treatments, irrespective of the litter addition treatment applied.

a) Cropping system	Soil C (mg g^{-1})	Soil N (mg g^{-1})	Soil C:N	Soil δ^{13} C (‰)
continuous corn	23.3 (0.4)	1.8 (0.2)	12.9 (0.2)	-16.7 (0.1)
corn after soy	24.0 (0.4)	1.9 (0.2)	12.5 (0.2)	-17.2 (0.3)
soy after corn	22.5 (0.6)	1.8 (0.4)	12.7 (0.4)	-16.9 (0.3)
b) Litter type	Litter C (mg g^{-1})	Litter N (mg g^{-1})	Litter C:N	Litter δ^{13} C (‰)
corn	405 (8)	14 (1)	29.9 (0.5)	-13.2 (0.1)
soybean	429 (1)	22 (1)	19.8 (0.2)	-29.1 (0.1)

Table 1 Characteristics of a) incubated soils and b) litter amendments (values in parentheses are standard errors, n = 4)

Microbial biomass

At the beginning of the experiment, microbial biomass C averaged 88 μ g C g⁻¹ and tended to be greater in the corn after soy soils (102±15 μ g C g⁻¹) than continuous corn (90±9 μ g C g⁻¹) and soy after corn (70±28 μ g C g⁻¹), although differences were not significant. Corn was the dominant C source for initial microbial biomass, comprising approximately 69%, 65%, and 86% in the corn after soy, soybean-corn, and continuous corn soils.

At the end of the experiment, total microbial biomass C significantly differed among litter addition treatments (P = 0.0001) and was significantly greater in soils amended with soybean than corn litter or no litter (P < 0.05; Fig. 5, Supplementary Table 3). Microbial biomass C in soils amended with soybean litter was approximately equally derived from corn ($53 \pm 3\%$) and soybean ($47 \pm 3\%$) C, and it was primarily derived from corn in soils amended with corn litter ($91 \pm 3\%$) and the control ($88 \pm 4\%$).

Table 2 Decomposition parameters modeled using first-order decay models with two or three pools, where P is the proportion of C, and k is the decomposition rate constant

Component	Litter type	Cropping treatment ^a	Pvery fast	P _{fast}	P _{slow}	$\begin{array}{c} k_{very\text{-}fast} \\ (y^{-1}) \end{array}$	$\begin{matrix} k_{fast} \\ (y^{-1}) \end{matrix}$	$\begin{array}{c} k_{slow} \\ (y^{-1}) \end{array}$
litter	corn	continuous corn	_	0.49 (0.02)	0.51 (0.02) ^{b,c}	_	9.7 (0.5) ^A	0.00 (0.09)
		corn after soy	_	0.61 (0.02)	0.39 (0.02) ^a	_	8.9 (0.3) ^A	0.09 (0.10)
		soy after corn	-	0.45 (0.01)	0.55 (0.01) ^c	-	12.3 (0.5) ^A	0.19 (0.05)
	soybean	continuous corn	_	0.55 (0.01)	0.45 (0.01)	_	37.7 (2.1) ^B	1.09 (0.11)
		corn after soy	-	0.53 (0.01)	0.47 (0.01)	-	$34.8(1.7)^{B}$	0.85 (0.09)
		soy after corn	_	0.45 (0.01)	0.55 (0.01)	_	$42.3 (3.4)^{\mathrm{B}}$	0.55 (0.09)
soil	corn	continuous corn	$0.0115\;(0.0005)^{\rm A}$	0.073 (0.19)	0.92 (0.19)	162 (22)	1.5 (2.5)	0.000 (0.133)
		corn after soy	$0.0103 \ (0.0010)^{\rm A}$	0.028 (0.001)	0.96 (0.00)	162 (30)	11.6 (1.2)	0.057 (0.004)
		soy after corn	$0.0081 (0.0004)^{\rm A}$	0.060 (0.025)	0.93 (0.03)	148 (19)	2.8 (0.9)	0.000 (0.028)
	soybean	continuous corn	$0.0029 (0.0003)^{\rm B}$	0.021 (0.003)	0.98 (0.00)	370 (198)	6.0 (0.9)	0.029 (0.005)
		corn after soy	_	0.021 (0.001)	0.98 (0.00)	-	8.9 (0.5)	0.051 (0.003)
		soy after corn	_	0.015 (0.001)	0.98 (0.00)	-	16.2 (2.2)	0.058 (0.003)
	none	continuous corn	$0.0016 (0.0002)^{\rm B}$	$0.013 \ (0.001)^a$	0.99 (0.00)	144 (50)	6.1 (0.9)	0.043 (0.003)
		corn after soy	$0.0014 (0.0003)^{\rm B}$	$0.019 \ (0.001)^{b}$	0.98 (0.00)	179 (102)	7.9 (0.8)	0.057 (0.003)
		soy after corn	$0.0015 \ (0.0002)^{\mathrm{B}}$	0.013 (0.001) ^a	0.99 (0.00)	222 (97)	6.6 (0.9)	0.044 (0.003)

^a Each model represents the best fit solution for the four replicates within a given cropping treatment by litter type by C component combination

^b Values in parentheses are standard errors, n = 4; values with different lower-case letters indicate significant Tukey-corrected differences among cropping systems for a given C component and litter treatment, and upper-case letters indicate significant Tukey-corrected differences among litter treatments and cropping systems for a given C component



Fig. 3 Cumulative decomposition of added litter C a and soil C b and net soil N mineralization c plotted by cropping treatments (indicated by labeled rectangles on the upper x axis) and type of added litter (indicated by labels on the lower x axis and colored bars). Error bars indicate standard errors (n=4). Cropping

treatments, litter treatments, and their interaction significantly affected litter C decomposition **a**, and both main treatments (but no interaction) significantly affected soil C decomposition **b** and net N mineralization **c**

Priming of soil C loss

Priming of soil C loss in the corn and soybean litter amendment treatments peaked on the first sampling date and declined rapidly thereafter, punctuated by a brief period of negative priming for both soybean and corn litters at days 4 and 12, respectively (Fig. 6a). After that, positive priming continued to occur in all soils that received corn litter until at least day 96. However, cropping treatments differed in temporal dynamics of priming, and positive priming tended to be more rapid in corn after soy soils than the other treatments between days 20 and 73 (P < 0.10for pairwise comparisons with the others on all of these days; Fig. 6b). The rapid priming response observed in the corn after soy soils persisted even after accounting for differences in litter mass remaining among cropping treatments (Fig. 6c). However, by the end of the experiment, cumulative priming of soil C loss (Fig. 7) differed between litter treatments (P = 0.001) but not among cropping treatments (P = 0.44), with no significant interaction (P = 0.49). Corn litter addition caused significant soil C loss across all soils (P < 0.0001) while priming from soybean litter did not differ from zero (P = 0.37). Cumulative priming from corn litter addition measured $434 \pm 56 \ \mu g \ C \ g^{-1}$ (Fig. 7). In comparison, decomposition of soil C from samples that received soybean litter or no litter measured $1076 \pm 40 \ \mu g$ C g^{-1} (Fig. 3b). Thus, on average, priming from corn litter addition increased SOC loss to 140% of the soils that received no litter or soybean litter.

Discussion

Our data indicated that the identity of the previous crop and any added litter had key impacts on the decomposition dynamics of soil organic matter in corn-soybean rotations, which differed from continuous corn. Supporting our first hypothesis, soybean litter decomposed faster than corn litter within a given soil (Table 2) and drove a net increase in microbial biomass derived from soybean C (Fig. 4). In contrast, corn litter addition did not significantly increase microbial biomass despite the fact that its cumulative decomposition was statistically equivalent to that of soybean in soils from both phases of the corn-soybean rotation (Fig. 3a, Fig. 4). Supporting our second hypothesis, corn (but not soybean) litter addition consistently primed the decomposition of soil C, with the most rapid priming effects and greatest corn litter decomposition in soils from the corn following soybean treatment (Table 2, Fig. 3a, Fig. 6). In contrast, addition of soybean litter had no significant impact on decomposition of extant C and did not cause net priming of soil C decomposition (Fig. 7). Supporting our third hypothesis, microbial biomass,



Fig. 4 Cumulative decomposition of soil C from control soils (no litter added) plotted by cropping treatment; shading in the bars indicate contributions of corn- and soybean-derived C to decomposition as partitioned with δ^{13} C values. Error bars indicate standard errors (n = 4). Treatments with different lower-case and upper-case letters differed significantly in corn- and soybean-derived C decomposition, respectively

decomposition of corn litter and soil C, and N mineralization were consistently greatest in soils planted to corn after soybean, even as these soils maintained high decomposition rates of soybean-derived C (equivalent to the soybean after corn treatment). We interpret this finding as a logical consequence of hypotheses 1 and 2: microbial biomass increased during the decomposition of soybean litter, and when confronted with N-poor corn litter, microbes depolymerized organic matter to release N, thus increasing rates of litter and soil C decomposition and N mineralization.

Together, our results suggest a mechanism whereby corn-soybean rotations could enhance mineral N availability by increasing the decomposition rates of both new corn litter inputs and extant soil organic matter. This mechanism may represent an unacknowledged contributor to the well-known phenomenon of decreased N fertilizer requirements for corn grown after soybean known as the soybean N credit (Green and Blackmer 1995; Gentry et al. 2001). It could also potentially contribute to long-term soil C and N losses if the observed increases in decomposition were not offset by other mechanisms. These include increased production of microbial necromass from low C:N litter and its subsequent accrual in soil C (Cotrufo et al. 2013), sorption of soluble litter decomposition products (Córdova et al. 2018) or changes in physico-chemical protection of soil C mediated by increased production of microbial detritus (Tiemann et al. 2015). Although these mechanisms have been demonstrated in longer and more diverse crop rotations, where soil C tends to increase relative to monocultures, corn-soybean rotations remain a notable exception where soil C gains are not typically observed (Russell et al. 2009; McDaniel et al. 2014; Tiemann et al. 2015).

The fact that we did not observe significant differences in soil C concentrations among the field plots sampled in this study (Table 1) is not surprising, given high spatial heterogeneity and large pool sizes that challenge the detection of even large changes in soil C over decadal scales (Goidts et al. 2009). We also note that soil C concentrations in these cultivated soils are much lower than under reference prairie conditions (David et al. 2009; Russell et al. 2005), and thus far from saturation. Finally, we emphasize that our findings from this study are empirical and not normative; there are substantial environmental costs associated with



Fig. 5 Microbial biomass C measured at the end of the experiment, plotted by litter addition treatment (cropping treatments did not differ significantly); shading in the bars indicate contributions of corn and soybean C to microbial biomass C partitioned using δ^{13} C values. The dashed line indicates initial microbial biomass C, which did not differ significantly among cropping treatments. Error bars indicate standard errors (*n* = 12). Treatments with different lower-case and upper-case letters differed significantly in corn- and soybean-derived microbial biomass C, respectively

increased N fertilization requirements and potential changes in pest or disease pressure in continuous corn vs. corn-soybean rotations (Gentry et al. 2013), irrespective of any differences in soil C or N concentrations. These collective tradeoffs should also be considered in the context of other potential cropping systems, such as longer and more diverse crop rotations involving small grains and forage legumes, many of which appear effective in maintaining or accruing soil C and N in our region (Russell et al. 2009; Liebman et al. 2013).

Contrasting biogeochemical impacts of corn vs. soybean litters

As expected, added soybean litter decomposed faster than corn litter in accordance with its lower C:N ratio, leading to greater net N mineralization as microbial N demand was satisfied by the litter rather than exogenous sources (Green and Blackmer 1995; Parton et al. 2007). In our study, the absence of priming induced by soybean litter suggests that litter N was largely sufficient to sustain microbial N demand during its decomposition (Kuzyakov 2002). In contrast, the significant priming and lack of net microbial biomass growth observed following corn litter addition was consistent with microbial N limitation (Kuzyakov 2002), a lower microbial C-use efficiency imposed by N limitation (Manzoni et al. 2012), and/or increased turnover of extant microbial biomass driven by priming (Kuzyakov 2010). The burst of soil-derived CO₂ observed immediately after corn litter addition (Fig. 6) likely reflected this latter mechanism. Conversely, the greater initial mineral N availability observed in the soybean after corn soils could have explained the slower decomposition of added soybean litter in that treatment, e.g. by downregulating microbial production of non-specific decomposition enzymes as often observed in response to mineral N enrichment (Janssens et al. 2010). We used leaf residue amendments in this study given their importance for N supply in corn and soybean cropping systems (Green and Blackmer 1995) and their high abundance relative to roots (mean root:shoot ratios measured 0.05 at this site; Jarchow et al. 2015) but the potential impacts of adding leaves vs. roots deserve further exploration.

Faster priming and greater litter and SOC decomposition in soils where corn followed soybean

All soils exhibited significant priming when amended with corn litter, but the timescale of the response differed among cropping treatments and was fastest in soils from the corn after soybean treatment (Fig. 6). One plausible explanation for faster priming and the consistent and significant increase in corn litter decomposition, soil C decomposition, and N mineralization in soils



Fig. 6 Priming of soil C decomposition plotted over time for each measurement date **a** or as a cumulative flux over time **b** or vs. litter mass remaining **c**. Priming is defined as the additional loss of soil C resulting from litter addition relative to an unamended control. Symbols denote cropping treatments (continuous corn, corn after soybean, and soybean after corn, respectively). Yellow, green, and brown colors denote litter addition treatments (corn, soybean, and no litter, respectively)



Fig. 7 Cumulative priming of soil C decomposition plotted by the type of added litter, averaged across cropping treatments because of no significant differences in total priming; error bars indicate standard errors (n = 12)

from corn after soybean involves the legacy of increased microbial growth on the previous year's soybean litter. This litter was likely to have decomposed during the most recent growing season (corn phase) just prior to soil sample collection. At the beginning of our laboratory incubation, this soybean-fed microbial community was confronted with detritus from the most recently grown corn roots, which had senesced just before soils were collected. Decomposing these residues likely required additional N, thus stimulating enzymatic attack on soil organic matter, as well as leading to greater decomposition of added corn litter, as we observed (Fig. 3a). This would also explain the fact that soils from this treatment (corn after soy) sustained high rates of decomposition of older soybean-derived C (Fig. 4) despite being most recently planted to corn.

Other explanations for these results are possible but less likely. Differences in residue inputs, especially roots, are key drivers of soil C dynamics in continuous corn and corn-soybean rotations under conventional management (Russell et al. 2009; Brown et al. 2014). However, in our study, these differences cannot explain faster decomposition of added corn litter (Fig. 3a) nor the sustained decomposition of soybean-derived C in the corn after soy treatment (Fig. 4). Furthermore, in the control soils (no litter added), the mean mass ratio of C decomposed to CO_2 relative to net N mineralization was similar among all three cropping treatments (32–33) despite their differences in total soil C decomposition (Fig. 3b). This consistent coupling between mineralization of C and N would not be expected if differences in recent residue inputs were responsible for differences in soil C decomposition among cropping treatments, as corn and soybean vary substantially in their C:N ratios (Green and Blackmer 1995). In addition, the partial (~52%) above-ground residue removal from the continuous corn treatment in this 10-year experiment served to minimize long-term differences in above-ground residue inputs between continuous corn and the cornsoybean rotation soils by compensating for decreased residue inputs during the soybean phase (Jarchow et al. 2015). To minimize differences in the most recent above-ground corn residue inputs between the continuous corn and corn after soy treatments, soils were sampled prior to harvest, when partial residue removal occurred. Finally, shallow fine roots are arguably the most important sources of C inputs to these systems (Russell et al. 2009), and their biomass (0-30 cm) was statistically similar among soy after corn, soy after corn, and continuous corn treatments for most years of this study (Jarchow et al. 2015).

Implications for the fertility of corn-soybean rotations

Our findings have intriguing implications for soil C and N cycling in corn-soybean cropping systems. Previous work suggested that the soybean N credit results from a combination of increased net N mineralization relative to that in continuous corn production and an increase in residual soil N due to symbiotic N fixation in the soybean plant (Green and Blackmer 1995; Gentry et al. 2001). Conversely, decreased net N mineralization explains the "yield penalty" often observed under continuous corn (Gentry et al. 2013). Expanding on this work, our data suggest that increased N mineralization linked to accelerated decomposition of extant soil organic matter and recent corn litter inputs-not simply lower soil N immobilization and faster N release from decaying soybean residue-may also contribute to the soybean N credit. Empirical estimates of the soybean N credit vary tremendously, e.g. from -22 to 210 kg N ha y⁻¹ among Wisconsin cropping systems (Bundy et al. 1993), with enormous implications for N fertilizer use in the Corn Belt. Some long-term corn-soybean cropping systems appear to have net negative N balances (Jaynes and Karlen 2008; Gentry et al. 2009; David et al. 2010),

which may contribute to a regional trend of lower soil N stocks (Tomer et al. 2017). Our data suggest that better prediction of the magnitude of the soybean N credit, and its long-term sustainability, may require an explicit consideration of the dynamics of decomposition priming under field conditions.

Our findings are also consistent with observations of decreased soil C retention in corn-soybean rotations even after accounting for lower C inputs from soybean residues. Poffenbarger et al. (2017) observed that cornsoybean rotations required more than 30% greater C input to maintain equivalent soil C stocks as compared with a continuous corn system (4.2 vs 3.2 Mg residue C $ha^{-1} y^{-1}$) over a 14–16 y field trial. Similarly, Russell et al. (2009) observed that soil C at one long-term experimental site in Iowa (Nashua) was 12% lower under long-term corn-soybean rotations than continuous corn, despite the fact that mean residue C inputs were only 3% lower. Conversely, a continuous corn-oatsalfalfa rotation had slightly greater soil C than continuous corn despite lower residue C inputs in that study. Huggins et al. (2007) found similar stocks of C₃-derived C in surface soils under continuous corn and cornsoybean rotations, despite the absence of contemporary inputs of C₃-C in the former treatment—implying increased decomposition of legacy soybean C inputs under corn-soybean rotations than continuous corn.

Our laboratory study demonstrates the plausibility of enhanced litter and SOC decomposition under soil from corn-soybean rotations vs. continuous corn, controlling for climate-a hypothesis that bears further testing under field conditions. This is an important finding in that previous work has often focused on decreased net primary productivity of soybean as a primary driver of observed differences in SOC stocks between these systems (e.g. Russell et al. 2009). Other factors may also contribute to shifts in SOC dynamics under cornsoybean rotations as compared with continuous corn, such as greater early-season soil temperature following soybean due to lower residue cover (Huggins et al. 2007), or differences in the physical and chemical partitioning of residues during decomposition (Tiemann et al. 2015). Mahal et al. (2019) recently demonstrated that N fertilizer addition could directly suppress SOC decomposition in continuous corn, presumably by inhibiting microbial decomposition activity related to N acquisition. Further evaluation of these mechanisms is critical, as even small changes in decomposition rates within and among cropping systems have key implications for soil C and N cycling and related environmental impacts in one of the dominant agroecosystems of North America.

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Author's contributions AER, ARM, and SJH conceived the research and designed and performed the experiment. SJH analyzed data and wrote the paper, with contributions from AER.

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