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Residue- and nitrogen-induced carbon mineralization varies with soil fertility status

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Abstract

By increasing the input of corn (*Zea mays* L.) residues, synthetic nitrogen (N) fertilization is often assumed to enhance soil storage of organic carbon (C), which could be especially beneficial for improving the fertility of depleted soils. To ascertain whether such a strategy can be effective, C mineralization was compared for two soils with different indigenous N contents by conducting a 60-day laboratory incubation experiment that involved continuous monitoring of CO_2 emissions with periodic sampling for atmospheric $\delta^{13}C$ analysis and for determination of soil microbial biomass and cellulolytic enzyme activities. The addition of exogenous N had a stimulatory effect on cumulative CO_2 production that was greater for the low than high N supplying soil and more prominent in the first than in the second month of incubation. During residue decomposition, microbial activities were maximized by incubating the low N soil with exogenous N, whereas cellulolytic enzyme activities were greater for the high N soil. Although intensive N fertilization can substantially increase the productivity of low-fertility soils, the additional residue inputs thereby generated are more effective for promoting C mineralization than sequestration.

1 | INTRODUCTION

Intensive nitrogen (N) fertilization in modern cereal production is motivated by the economic importance of high grain yields that are also beneficial for increasing residue inputs. These inputs are essential to agricultural sustainability, due in part to their significance as the major substrate for the synthesis of soil organic matter (SOM) that improves water availability, aggregate stability, and macroporosity; supplies mineralizable and exchangeable nutrients; and serves as the source of carbon (C) and energy for the heterotrophic microflora. The transformation of residue C to SOM is necessarily reduced by carbon dioxide (CO_2) production during microbial utilization, which depends on climatic conditions, the type of residue, microbial community composition, and soil physicochemical properties (Grzyb et al., 2020; Swift et al., 1979; Zhou et al., 2008).

The availability of N is also important for residue decomposition as this element occurs in all C-degrading enzymes; however, contrasting results have been obtained in numerous studies examining the effect of N addition on residue C mineralization, which can be positive (Green et al., 1995; Moran et al., 2005), negative (Henriksen & Breland, 1999; Lueken et al., 1962; Wang et al., 2004), or nonexistent (Al-Kaisi et al., 2017; Foereid et al., 2004; Recous et al., 1995). Many of the inconsistencies can be attributed to the use of residues varying in chemical composition (most commonly characterized in terms of C:N ratio and cellulose and lignin contents) or particle size, or to other differences in experimental design, such

Abbreviations: AS, ammonium sulfate; CEC, cation-exchange capacity; HNS, high N supplying soil; IRMS, isotope ratio mass spectrometer; LNS, low N supplying soil; MBC, microbial biomass C; PN, potassium nitrate; SOC, soil organic C; SOM, soil organic matter; TOC, total organic C; WHC, water-holding capacity.

as residue placement with or without incorporation (Parr & Papendick, 1978). Disparities can further arise due to variations in the quantity and/or form of N applied by fertilization and in the supply of fertilizer N relative to mineralizable soil N (Anderson, 1926; Niklewski, 1912; Rice & Tiedje, 1989).

Besides the N supplied by residues and fertilization, soil fertility, and particularly soil N availability, has important effects on the decomposition of cellulosic substrates (Schmidt & Ruschmeyer, 1958; Stewart et al., 2015), as would be expected in view of evidence that the input of mineral N promotes the activity of cellulose-degrading enzymes such as cellulase and β-glucosidase (Henriksen & Breland, 1999; Keeler et al., 2009). Such activities tend to be greater for highly productive soils that are well structured and nearly neutral in pH, which is conducive to an increase in microbial biomass (Blesh & Ying, 2020; Xu et al., 2019). In contrast, C mineralization can be impeded in low-fertility soils due to limited N availability that triggers a shift toward 'microbial N mining' whereby N is scavenged from recalcitrant SOM (Chen et al., 2014). The input of exogenous C and/or N can thereby cause negative as well as positive priming effects depending on soil fertility status, the result being either SOM accrual or loss (Kuzyakov et al., 2000; Paterson & Sim, 2013).

Intensive N fertilization is generally more effective for increasing the productivity of low- than high-fertility soils (Mulvaney et al., 2006), and a further benefit arises because higher yields generate more residues. The latter benefit is often assumed to be especially important for marginal soils under corn (*Zea mays* L.) production; however, to our knowledge, no studies have been reported to compare the dynamics of cellulosic residue decomposition in soils of contrasting fertility. With the aim of clarifying how these dynamics depend upon soil properties, a laboratory incubation experiment was conducted to ascertain whether (1) indigenous and exogenous N will be more effective for promoting C mineralization in a high N soil (HNS) than a low N soil (LNS), and (2) microbial activities and C-degrading enzyme production will be greater in the HNS due to the stimulatory effect of N.

Core Ideas

- Without fertilizer N, corn residue decomposition was unaffected by the supply of indigenous soil N.
- Addition of NH_4^+ or NO_3^- stimulated cellulosic residue decomposition.
- With N input, the mineralization of C was more rapid for a low- than high-N-supplying soil.
- Active biomass was greater in the low N soil and cellulolytic enzyme activities in the high N soil.
- Increasing residue inputs to low-fertility soils by intensive N fertilization enhances C mineralization.

TABLE 1 Physicochemical properties of soils studied.

Property	Soil HNS	Soil LNS
pH (1:1)	6.9	6.3
TOC (g kg^{-1})	16.8	10.2
$\delta^{13}C_{V\text{-}PDB}$ (‰)	−17.9	−19.7
Total N (g kg^{-1})	1.5	1.0
C:N	10.6	9.1
PMN (mg kg^{-1})[c]	197	133
Bioavailable P (mg kg^{-1})	53.7	124.8
CEC (cmol$_c$ kg^{-1})	16.4	12.1
Aggregate stability (%)	94.8	58.4
Sand (g kg^{-1})	64	31
Silt (g kg^{-1})	644	700
Clay (g kg^{-1})	292	269
WHC (g kg^{-1})	580	552

Note: Analytical data reported as a mean of duplicte or triplicate determinations. Abbreviations: CEC, cation-exchange capacity; HNS, high N soil; LNS, low N soil; PMN, potentially mineralizable N estimated by the Illinois soil N test; TOC, total organic C; V-PB, international standard for $\delta^{13}C$ values; WHC, water-holding capacity.

2 | MATERIALS AND METHODS

2.1 | Soils

Both soils studied were from agricultural sites mapped as the Birkbeck series (fine-silty, mixed, superactive, mesic Oxyaquic Hapludalfs) under a corn–soybean (*Glycine max* L. Merr.) rotation near Farmer City, IL (40°14′40″ N, 88°38′33″ W). One of the soils, designated hereafter as the HNS, had been in continuous row cropping since conversion from grazed pasture in 1992, whereas the other soil, subsequently referred to as the LNS, had been under continuous cultivation and cropping for 72 years. At each site, a bulk sample of surface (0–20 cm) soil was collected in early April of 2020, transferred to the laboratory in a 38-L polyethylene tote box, and stored in a refrigerator at 4°C. Before use, macro residues from the 2019 corn crop were removed, and the field-moist soil was sieved (2-mm screen) and then thoroughly mixed. A subsample was air-dried, and the physicochemical properties reported in Table 1 were determined by measuring pH with a glass electrode (soil:water ratio, 1:1) (Peters et al., 2015), organic C by dichromate oxidation (Mebius, 1960), total N by Kjeldahl digestion using a pretreatment with Fe and $KMnO_4$ (Bremner, 1996) followed by diffusion with NaOH (Stevens et al., 2000), potentially mineralizable N by the alkaline diffusion technique of Khan et al. (2001), Bray and Kurtz

P-1 using the Fiske–Subbarow colorimetric method (Frank et al., 2015), cation-exchange capacity (CEC) by the rapid saturation–diffusion method of Nunes and Mulvaney (2021), aggregate stability by a modification of the wet sieving technique of Kemper and Rosenau (1986), soil texture by the hydrometer method (Bouyoucos, 1962), and water-holding capacity (WHC) according to Bremner and Shaw (1958). For $\delta^{13}C$ analysis, soil used for physicochemical characterization was further crushed with a mortar and pestle to pass through a 0.25 mm screen, prior to dry combustion using a Carlo Erba NC2500 elemental analyzer interfaced to a Thermo Fisher Delta V Advantage isotope ratio mass spectrometer (IRMS) (Thermo Finnigan). The $\delta^{13}C$ values were expressed relative to the international V-PDB standard (Coplen, 1995).

2.2 | Residue

Following harvest, corn leaves, stalks, husks, and cobs were collected from a production field under a corn–soybean rotation located near Farmer City, IL. The residue samples were placed in a forced-air oven and allowed to dry at 50°C for at least 1 week, ground to <2 mm using a Model 4 Wiley mill (Thomas Scientific), and then transferred to Mason jars for air-tight storage at room temperature. Following Pordesimo et al. (2004), the four residual plant parts were combined and the resulting mixture was characterized using a Carlo Erba NC2500 elemental analyzer for determination of C (444 g kg^{-1}) and N (3.4 g kg^{-1}), from which the C:N ratio (130) was also obtained. Major organic fractions estimated by proximate analysis (Harper & Lynch, 1981) gave the following results: water-soluble fraction, 160 g kg^{-1}; lignin, 119 g kg^{-1}; cellulose + hemicellulose, 493 g kg^{-1}. Analyses for $\delta^{13}C_{V\text{-}PDB}$ performed using the combustion system mentioned previously gave a value of −12.1‰ for the residue mixture.

2.3 | Incubation technique

For each soil studied, 168 field-moist samples (50 g dry weight equivalent) were weighed into 120-mL specimen containers, and the moisture content was brought to 40% WHC by adding deionized water with a Metrohm 665 Dosimat. To minimize moisture loss while maintaining aerobic conditions, Parafilm (Alcan Packaging) was affixed to the mouth of each container and punctured to form 8–10 pores using a syringe needle. All samples were subsequently transferred to a constant-temperature room maintained at 25°C and preincubated for 7 days in darkness.

After preincubation, the following treatments were randomized among six sets of replicate samples of each soil: (1) no amendment (control), (2) KNO_3 (potassium nitrate [PN]), (3) $(NH_4)_2SO_4$ (ammonium sulfate [AS]), (4) residue (R), (5) residue + KNO_3 (R + PN), and (6) residue + $(NH_4)_2SO_4$ (R + AS). Residue was added at the rate of 10 mg dry weight g^{-1} soil, roughly representing modern corn production in the Midwestern United States, and then incorporated by thorough mixing. To supply 0.1 mg NO_3^-- or NH_4^+-N g^{-1} soil, the Dosimat was used to uniformly dispense 2 mL of a solution containing 2.5 mg N mL^{-1}. Soil moisture content for all treatments was subsequently adjusted to 50% WHC using the Dosimat, 3 treatment-specific specimen containers for each soil (total of 28) were weighed to allow periodic addition of water to replace evaporative losses, and the entire set of specimen containers was transferred to 336 1.9-L wide-mouth Mason jars. A total of 36 of these jars, selected to obtain triplicate samples representing each soil-treatment combination, and 3 empty jars used for determination of ambient CO_2, were sealed using lids modified for atmospheric sampling with a pair of ball valves (Jesmin et al., 2021), and the remaining 300 jars were sealed with standard lids. A 60-day incubation in darkness was initiated after returning all jars to the constant-temperature room noted previously.

After 7, 14, 30, 45, and 60 days, five samples per treatment of each soil were combined and thoroughly homogenized, and the composite samples were analyzed for the following microbial indicators: active biomass, microbial biomass C (MBC), and cellulase as well as β-D glucosidase activities. In addition, soil pH measurements were made (soil:water ratio, 1:1) after incubation for 7, 30, and 60 days.

2.4 | Atmospheric analyses

2.4.1 | Sample collection

Following daily sampling for gas analysis during the first 5 days of incubation, atmospheric collections were performed at 2- or 3-day intervals using the circulating system illustrated in Figure 1. All incubating jars were left open for 1 h of aeration after each sampling, deionized water was added as needed to maintain soil moisture content, and the jars were then returned to the constant temperature room.

After atmospheric sampling on days 6, 12, 28, and 58 of the incubation study, the 36 jars sampled were aerated with a flow of room air drawn through the circulating pump, which was equipped with an Ascarite trap to remove ambient CO_2 so the following incubation interval could be utilized for isotopic as well as quantitative CO_2 analyses.

2.4.2 | Gas chromatographic analyses

Atmospheric samples were analyzed for CO_2 and O_2 + Ar using a Hewlett-Packard Model 5790A gas chromatograph

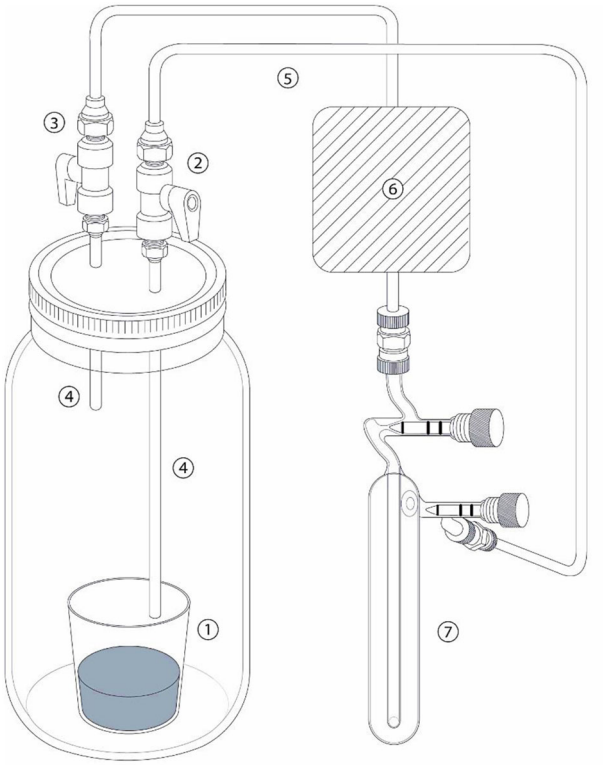


FIGURE 1 Diagrammatic representation of the circulating system used for atmospheric sampling. This system consisted of a specimen container with the incubating soil sample (1) inside a 1.9-L Mason jar sealed with a lid having inlet (2) and outlet (3) ball valves (Grainger 38EF92) connected via 6.4 mm O.D. brass (4) and polyethylene (5) tubing to a diaphragm pump (Cole-Parmer EW-07532-40) (6) and a 60-mL gas collection tube with two high vacuum stopcocks (7). After connecting the components and opening all valves and stopcocks, pumping was performed for 1 min.

(GC) (Agilent Technologies) equipped with an eight-port sampling valve (Valco Instruments Co.) having dual 0.5-mL sample loops, a Tracor U-90 ultrasonic detector, and a Hewlett-Packard Model 3390A reporting integrator. For this purpose, ultrahigh-purity He was used as the carrier gas, Porapak Q for separation of CO_2 at 50°C, and molecular sieve 5A for separation of O_2 + Ar at 25°C. Calibration standards were analyzed with every set of samples using certified mixtures of CO_2 in He (Matheson) and of O_2 in N_2 (Airgas).

2.4.3 | C isotopic analyses

Determinations of $\delta^{13}C_{V\text{-}PDB}$ were performed on atmospheric samples collected for CO_2 measurement after incubation for 7, 14, 30, and 60 days. Following gas chromatographic analysis, the sample tube was connected to the dual-inlet system of a Nuclide 3-60-RMS IRMS, and the tube was frozen in liquid N_2 and then evacuated to remove N_2, O_2, and Ar. Residual CO_2 was subsequently transferred via a dry ice–methanol cold trap to remove H_2O, for $\delta^{13}C$ analysis relative to a CO_2 isotopic standard obtained from Oztech Trading Corp.

For the R, R + PN, and R + AS treatments, the percentage of CO_2–C derived from residue (% R_d) was calculated following the approach described by Liang et al. (1999) as given below:

$$\%R_d = 100 \times (\delta_t - \delta_c) / (\delta_r - \delta_c) \quad (1)$$

where the variables represent $\delta^{13}C$ measured for CO_2 produced during incubation of the treated (t) or control (c) soil or for the residue mixture used ($\delta_r = -12.1‰$). For the C, PN, and AS treatments, the percentage of soil-derived CO_2–C (% S_d) was obtained as

$$\%S_d = 100 \times (\delta_t - \delta_r) / (\delta_s - \delta_r) \quad (2)$$

where δ_s is the $\delta^{13}C$ value for the soil used (as reported in Table 1), and the other variables are as defined previously.

2.5 | Microbial analyses

2.5.1 | Active biomass assay

A modified version of the biokinetics method described by Van de Werf and Verstraete (1987) was used to estimate active microbial biomass. In the modified method, 5 g (dry weight) of soil in a 50-mL polypropylene beaker was brought to 60% WHC with or without the addition of glucose medium, and incubation was performed at 25°C for 6.67 h after transferring the beaker to a 250-mL straight-sided glass jar equipped with a gas-tight lid having a ball valve for CO_2 analysis using the GC system previously described. The equation given by Van de Werf and Verstraete (1987) was used to calculate active biomass from the increase in CO_2 produced by glucose-treated samples.

2.5.2 | Microbial biomass C

To measure soil MBC by chloroform fumigation/extraction, 0.5 M K_2SO_4 extracts obtained as described by Vance et al. (1987) were analyzed for organic C by dichromate oxidation (Mebius, 1960). The equation proposed by Vance et al. (1987) was used to calculate MBC as F_c/0.45, where F_c is the difference in extractable organic C between fumigated and non-fumigated soil.

2.5.3 | Enzyme assays

Two major enzymes involved in soil C cycling—cellulase (EC 3.2.1.4) and β-glucosidase (EC 3.2.1.21)—were assayed by *para*-nitrophenol (*p*NP) methods described by Margenot et al. (2018). Briefly, triplicate 1-g soil samples (dry weight equivalent) were treated with 5 mL of 12 mM substrate solution prepared by dissolving *p*NP-β-D-cellobioside (cellulase) or *p*NP-β-D-glucopyranoside (β-glucosidase) in modified universal buffer (pH 6.0), and the mixture was vortexed for 30 s before a 2-h incubation at 37°C. For terminating hydrolysis of the added substrate following incubation, samples were immediately treated with 4 mL of 0.1 M Tris buffer (pH 12) and 1 mL of 2 M $CaCl_2$. A 1-mL aliquot of the supernatant was clarified by centrifugation at 14,000 *g* for 4 min, and *p*NP was determined by measuring absorbance at 405 nm.

2.6 | Statistical analyses

Means and standard deviations were computed from replicate data. After evaluating data for homogeneity (Levene's test) and normality (Shapiro–Wilk's test), the significance of treatment effects was determined by one-way and two-way analyses of variance using PAST version 3.22 (https://past.en.lo4d.com/windows), and mean comparisons were performed by Tukey's procedure ($p < 0.05$–0.001) or by the Wilcoxon test using RStudio version 1.3.1056 for paired enzymatic analyses.

3 | RESULTS AND DISCUSSION

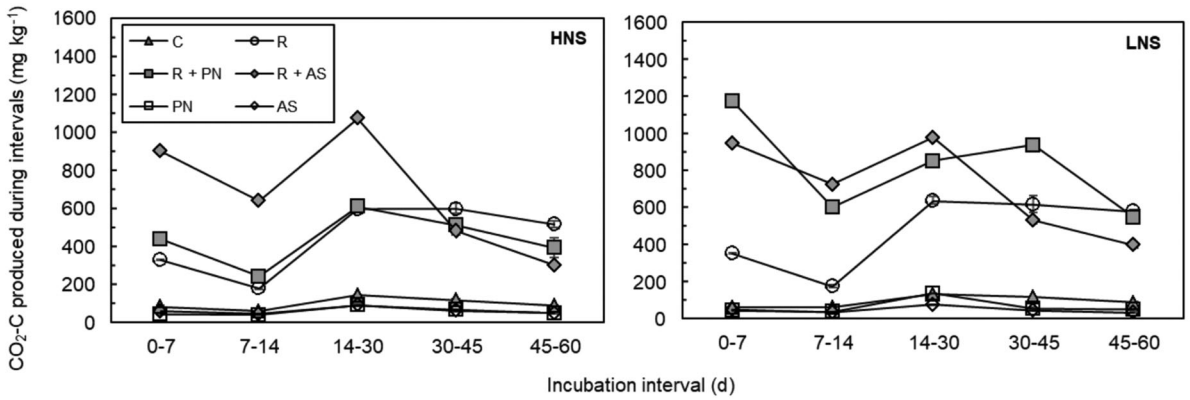
3.1 | C mineralization and origin of CO_2

The two soils used in this study differed widely in total N concentrations and potentially mineralizable N (Table 1). Owing to these differences, the use of a residue dominated by cellulose and hemicellulose (Johnson et al., 2007), and the importance of N availability on the decomposition of these constituents (Alexander, 1977; Bonanomi et al., 2017; Henriksen & Breland, 1999; Waksman & Starkey, 1924), we hypothesized that CO_2 production would be more rapid for the HNS than LNS. Yet no such trend is apparent from the temporal dynamics in CO_2–C measurements during the 60-day incubation period adopted (Figure 2) or from the cumulative amounts of CO_2 generated (Figure 3) under aerobic conditions with O_2 concentrations that always exceeded 0.20 kPa kPa^{-1}. On the contrary, a significant soil × treatment interaction was observed such that CO_2 production was significantly greater for the LNS than HNS following addition of exogenous N with residue, although the two soils did not differ significantly in C mineralization when incubated with residue alone (Figures 2 and 3).

As expected, measured concentrations of CO_2–C were much lower for the control treatment than for residue-amended soils, although no difference was observed between the HNS and LNS. The latter finding was somewhat surprising because total organic C content, which is predictive of C mineralization when air-dried soils are rewetted (Franzluebbers et al., 2000), was substantially greater for the HNS than LNS; however, neither soil was air-dried before use, and CO_2 measurements were initiated following a 1-week preincubation period. Based on $\delta^{13}C_{V\text{-}PDB}$ data collected periodically (Table S1), soil organic C (SOC) was the dominant source of CO_2–C for the control treatment during incubations of the LNS, whereas micro residues from the previous corn crop were comparable to SOC for CO_2 production by the HNS (Table 2). Greater SOC mineralization is consistent with less aggregate stability in the LNS (Table 1), which would have enhanced the microbial utilization of indigenous C pools (Tisdall & Oades, 1982).

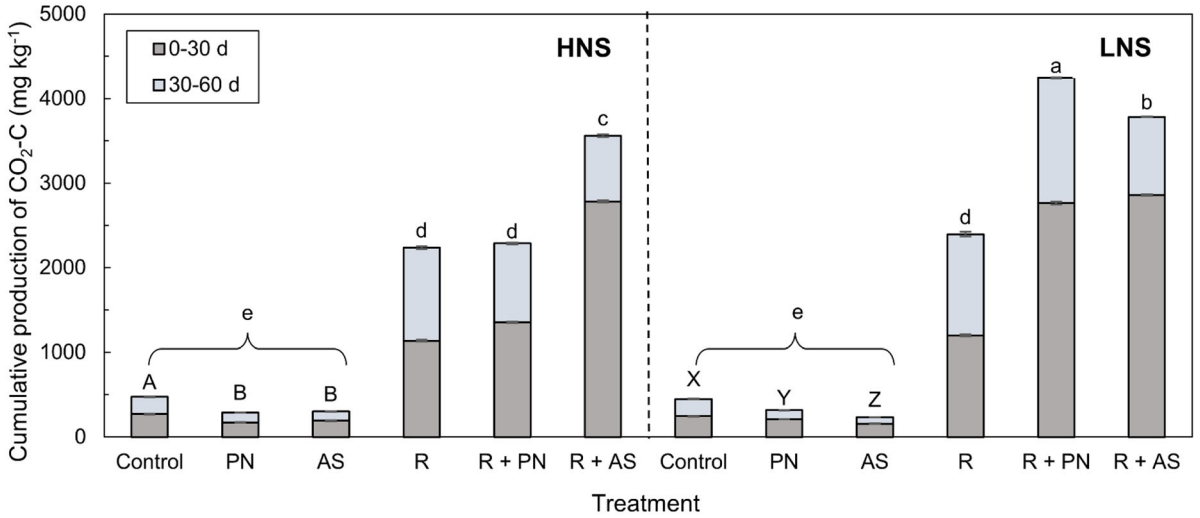
A further decline in CO_2–C production was observed when both soils were treated with PN or AS in the absence of residue addition, as documented in Figures 2 and 3. In the case of PN, such a reduction may be attributable to a high salt index (Elmajdoub & Marschner, 2013; Rader et al., 1943) that inhibits microbial activities due to osmotic pressure (Adviento-Borbe et al., 2006). The acidifying effect of AS (Pierre, 1928), clearly depicted in Figure 4, would have been a more important factor than salinization for microbial inhibition of heterotrophic C oxidation (Blagodatskaya & Anderson, 1999). Owing to a lower CEC (Table 1) that limited buffering capacity and exacerbated acidification, cumulative CO_2–C production by the LNS was reduced significantly for AS in comparison with PN, whereas no such difference occurred for the HNS (Figure 3). Regardless of the form of exogenous N applied, SOC mineralization in the absence of added residue tended to be more extensive for the LNS than HNS (Table 2). This finding is consistent with the 'microbial N mining' theory suggesting that when N is limiting, some microbes use labile C to decompose recalcitrant organic matter in order to acquire N (Berg & McClaugherty, 2003; Chen et al., 2014; Craine et al., 2007; Moorhead & Sinsabaugh, 2006).

The stimulatory effect of residue addition on CO_2–C emissions is readily apparent from Figures 2 and 3, which show that these emissions followed the same temporal pattern throughout the entire incubation with very similar cumulative CO_2 production for both soils. Such findings were unexpected because total and potentially mineralizable N were significantly lower for the LNS than HNS (Table 1), potentially limiting microbial activities. This limitation would have stimulated microbial demand for residue-derived N (Xu et al., 2019), presumably accounting for greater residue



Day	HNS						LNS					
	Control	PN	AS	R	R+PN	R+AS	Control	PN	AS	R	R+PN	R+AS
0-7	e	e	e	d	c	b	e	e	e	d	a	b
7-14	f	f	f	e	d	b	f	f	f	e	c	a
14-30	e	e	e	d	d	a	e	e	e	d	c	b
30-45	d	d	d	b	c	c	d	d	d	b	a	bc
45-60	c	c	c	a	b	b	c	c	c	a	a	b

FIGURE 2 Total quantity of CO_2–C produced by high and low N soils (HNS and LNS) in five sampling intervals during a 60-day aerobic incubation involving an unamended control and the following five treatments: potassium nitrate (PN), ammonium sulfate (AS), and residue (R) with or without PN (R + PN) or AS (R + AS). Data shown as a mean from triplicate incubations with standard error bars. Within a given incubation interval, the soil × treatment interaction was significant, and treatments followed by the same letter do not differ significantly at $p < 0.05$.



	HNS						LNS					
	Control	PN	AS	R	R + PN	R + AS	Control	PN	AS	R	R + PN	R + AS
0-30 d	e	e	e	d	c	ab	e	e	e	d	b	a
30-60 d	e	ef	ef	b	c	d	e	ef	f	b	a	c

FIGURE 3 Cumulative production of CO_2–C by high and low N soils (HNS and LNS) during a 60-day aerobic incubation involving an unamended control and the following five treatments: potassium nitrate (PN), ammonium sulfate (AS), and residue (R) with or without PN (R + PN) or AS (R + AS). Data shown as a mean from triplicate incubations with standard error bars and a table for mean comparisons within the first or second month of incubation that each showed a significant ($p < 0.05$) soil × treatment interaction. For all treatments from both soils, data do not differ significantly ($p < 0.05$) when bars are accompanied by the same lowercase letter. For soil-specific comparison of treatments without residue, data do not differ significantly when bars are accompanied by the same uppercase letter.

TABLE 2 Origin of CO_2 produced during soil incubations with and without the addition of residue.

	HNS			LNS		
Incubation period (days)	**R**	**R + PN**	**R + AS**	**R**	**R + PN**	**R+AS**
Percentage of CO2–C derived from residue						
7	49.1 ± 9.7^{C}	98.2 ± 0.2^{A}	98.6 ± 0.0^{A}	72.6 ± 3.2^{B}	98.7 ± 2.2^{A}	99.4 ± 0.0^{A}
14	60.1 ± 5.2^{C}	92.0 ± 2.1^{A}	93.8 ± 3.3^{A}	78.1 ± 1.9^{B}	95.1 ± 1.2^{A}	96.6 ± 2.8^{A}
30	69.8 ± 1.5^{C}	86.1 ± 4.6^{B}	76.2 ± 1.4^{BC}	93.5 ± 0.9^{A}	83.6 ± 0.3^{B}	93.0 ± 4.2^{AB}
60	53.7 ± 2.0^{BC}	59.3 ± 2.1^{B}	48.7 ± 5.3^{C}	80.4 ± 0.5^{A}	74.0 ± 2.1^{A}	75.1 ± 2.0^{A}
Percentage of CO_2–C derived from soil						
7	50.1 ± 0.8^{c}	62.0 ± 1.2^{b}	47.5 ± 3.9^{c}	84.9 ± 7.3^{a}	70.4 ± 1.9^{b}	61.0 ± 1.4^{b}
14	46.1 ± 2.5^{d}	69.9 ± 1.7^{c}	70.1 ± 0.8^{c}	82.3 ± 1.2^{a}	74.7 ± 1.6^{b}	73.6 ± 1.3^{bc}
30	46.3 ± 5.8^{d}	73.3 ± 3.1^{c}	76.1 ± 0.6^{bc}	85.5 ± 0.9^{a}	79.6 ± 2.3^{abc}	81.5 ± 0.6^{ab}
60	53.8 ± 2.4^{d}	77.7 ± 5.5^{c}	86.5 ± 1.5^{b}	94.7 ± 1.9^{a}	83.1 ± 2.8^{bc}	85.7 ± 1.2^{bc}

Note: Data reported as a mean ± standard deviation (three replicates). Within a given incubation period, treatments followed by the same upper- or lowercase letter do not differ significantly at $p < 0.05$. For residue-amended treatments, the percentage of residue-derived CO_2–C was calculated by Equation (1). In the absence of added residue, the percentage of soil-derived CO_2–C was calculated by Equation (2).

Abbreviations: AS, amended with ammonium sulfate; HNS, high N soil; LNS, low N soil; PN, amended with potassium nitrate; R, residue-amended; R + AS, amended with residue and ammonium sulfate; R + PN, amended with residue and potassium nitrate.

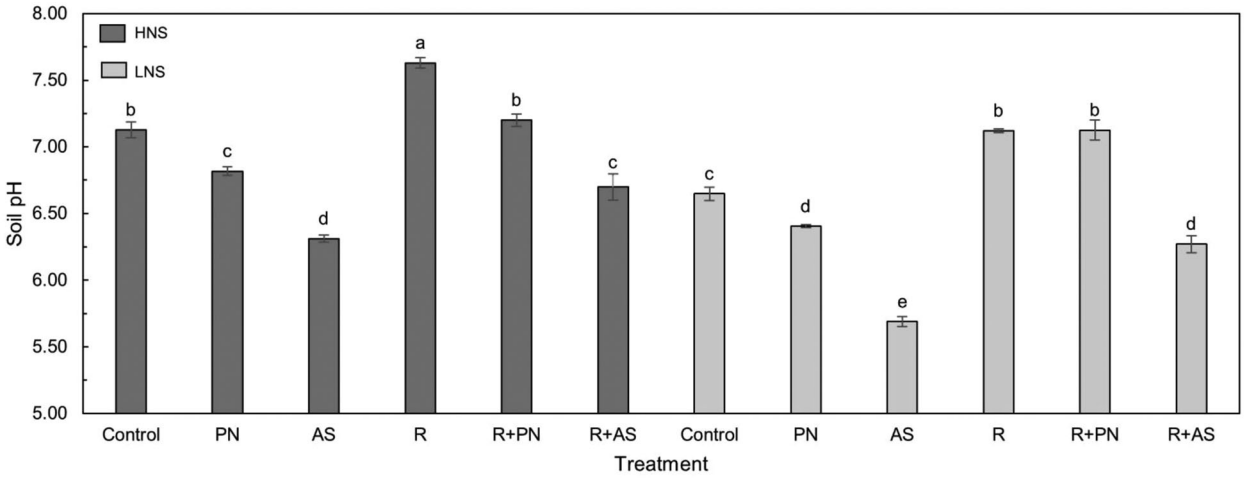


FIGURE 4 Soil pH measured for high and low N soils (HNS and LNS) during a 60-day aerobic incubation involving an unamended control and the following five treatments: potassium nitrate (PN), ammonium sulfate (AS), and residue (R) with or without PN (R + PN) or AS (R + AS). Data shown as a mean with standard error bars from triplicate incubations at three intervals (7, 30, and 60 days). For all treatments from both soils, the soil × treatment interaction was significant ($p < 0.05$), and data do not differ significantly when bars are accompanied by the same letter.

C mineralization that was observed for the LNS relative to the HNS (Table 2).

Considering the importance of N availability to corn stover decomposition, we hypothesized that residue C mineralization in the presence of exogenous N would be more extensive when augmented by a greater supply of endogenous N in the HNS than LNS. On the contrary, cumulative CO_2 production was significantly greater for the LNS when incubations were performed with either PN or AS, owing to the stimulating effect of substrate addition to a soil with limited availability of indigenous C and N. The driving factor for such stimulation was the input of highly carbonaceous residue (0.37 mmol C g^{-1} soil) amply supplied with mineral N (0.7 μmol N g^{-1} soil), which increased residue C mineralization during the initial stage of incubation (Table 2). Similar increases have been reported previously (Ekblad & Nordgren, 2002; Zhang et al., 2005) and can be explained by a shift from a population of specialized and slow-growing microorganisms (K-strategists) to one dominated by rapidly multiplying opportunists (r-strategists) (Chen et al., 2014). As compared to the LNS, mineral N addition was less effective for stimulating residue C mineralization in the HNS (Figure 3), presumably reflecting a greater supply of soil C and N that better satisfied microbial demand.

Of the two exogenous N sources used, PN was less effective than AS for promoting residue decomposition in the HNS but more effective when applied to the LNS. These opposing effects reveal the importance of soil N supply to the mineralization of a highly carbonaceous residue, as more extensive NO_3^- assimilation in the LNS due to limited NH_4^+ supply would have stimulated microbial C utilization as an energy source (Myrold & Posavatz, 2007). Owing to the microbial preference for NH_4^+ over NO_3^- (Jansson et al., 1955; Recous et al., 1990; Rice & Tiedje, 1989) and consistent with previous studies (Miller & Schmidt, 1963; Tesařová, 1971; Úlehlová, 1966), CO_2 production in the first month of incubation was significantly greater for both soils when residue was applied with AS instead of PN; however, the opposite trend was observed in the second month (Figure 3) due to substrate depletion (Jesmin et al., 2021).

3.2 | Microbial biomass

To quantify soil-specific treatment effects on the active fraction of biomass, periodic assays were performed by short-term measurements of soil respiration following the addition of glucose solution as a readily available substrate. Mean values obtained for the entire incubation are presented in Figure 5 and were strongly correlated ($p < 0.001$) with cumulative CO_2 production for the HNS ($r = 0.88$) and LNS ($r = 0.94$). Although a significant soil × treatment interaction was observed, active biomass increased significantly for both soils when residue addition was combined with the input of mineral N, NH_4^+ being more effective for the HNS and NO_3^- for the LNS. The latter disparity, and a parallel trend in cumulative CO_2–C production (Figure 3), can be explained by the inhibitory effect of soil acidity on cellulose decomposition (Ruschmeyer & Schmidt, 1958; Schmidt & Ruschmeyer, 1958; White et al., 1949). Owing to a lower organic matter content and CEC that reduced buffering capacity, acidification was more serious for the LNS than the HNS when treated with AS (Figure 4), which favored the utilization of NO_3^- in the presence of a highly carbonaceous residue.

Due to a lower rate of residue C mineralization, greater C assimilation was expected for the HNS than LNS, and

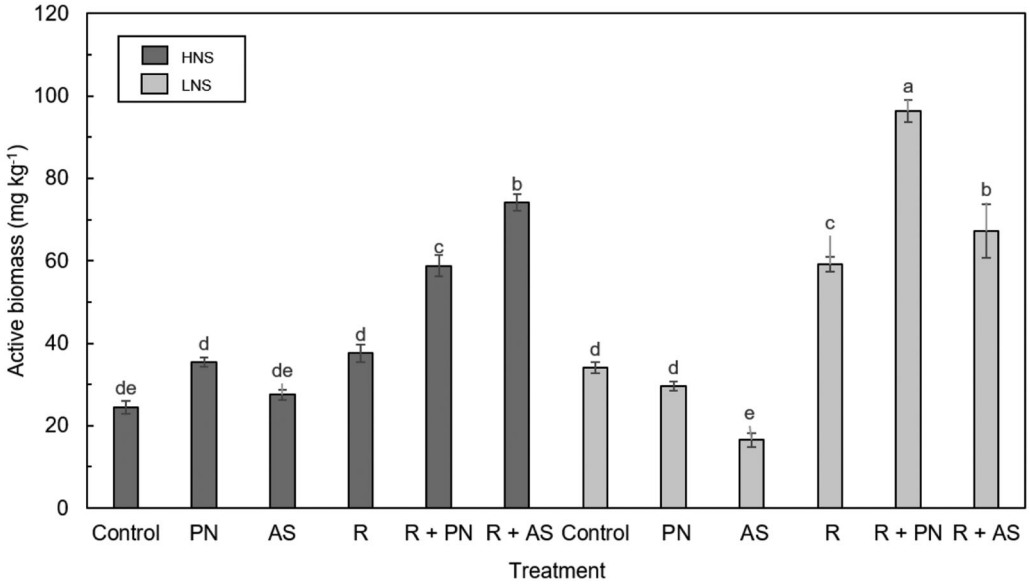


FIGURE 5 Active biomass measured for high and low N soils (HNS and LNS) during a 60-day aerobic incubation involving an unamended control and the following five treatments: potassium nitrate (PN), ammonium sulfate (AS), and residue (R) with or without PN (R + PN) or AS (R + AS). Data shown as a mean with standard error bars from triplicate incubations at five intervals (7, 14, 30, 45, and 60 days). For all treatments from both soils, the soil × treatment interaction was significant ($p < 0.05$), and data do not differ significantly when bars are accompanied by the same letter.

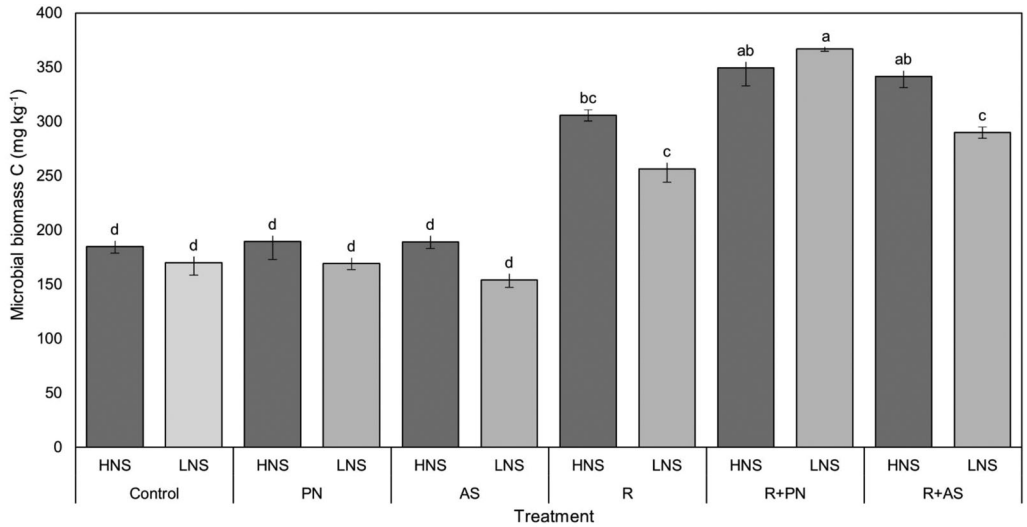


FIGURE 6 Microbial biomass C measured for high and low N soils (HNS and LNS) during a 60-day aerobic incubation involving an unamended control and the following five treatments: potassium nitrate (PN), ammonium sulfate (AS), and residue (R) with or without PN (R + PN) or AS (R + AS). Data shown as a mean with standard error bars from triplicate incubations at five intervals (7, 14, 30, 45, and 60 days). For all treatments from both soils, the soil × treatment interaction was significant ($p < 0.01$), and data do not differ significantly ($p < 0.05$) when bars are accompanied by the same letter.

a significant difference in MBC was indeed observed for incubations with R + AS but not R or R + PN (Figure 6). Despite a soil × treatment interaction, significant increases in MBC occurred for both soils when all three of these treatments were compared to those involving no addition of residue, which is consistent with previous findings that residue inputs increase the production of microbial biomass (e.g., Nicolardot et al., 2007; Tarafdar et al., 2001; Trinsoutrot et al., 2000). A strong correlation at $p < 0.0001$ was observed between MBC and cumulative CO_2 production for

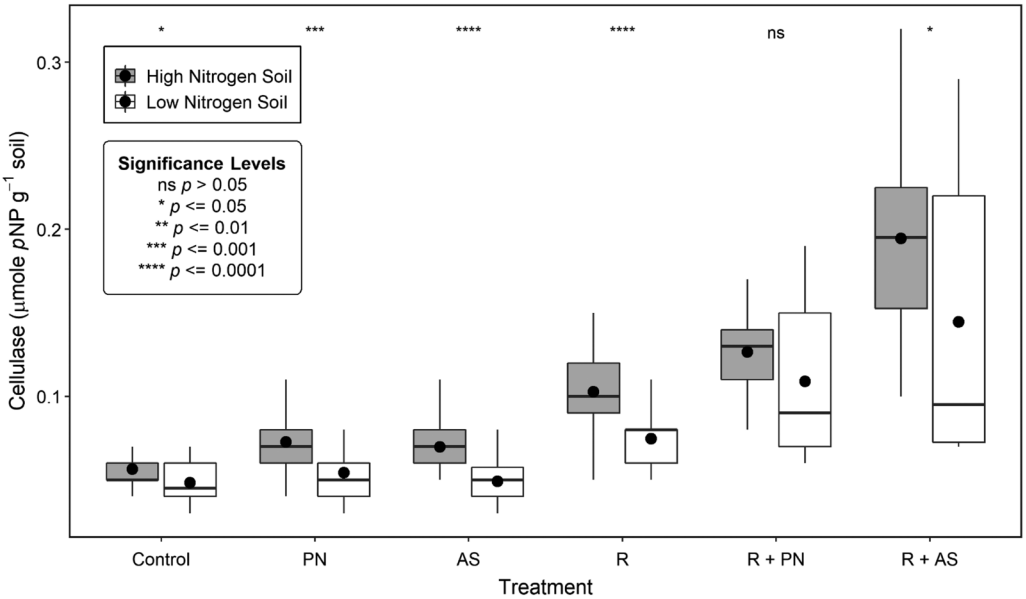


FIGURE 7 Box plot of cellulase activities measured for high and low N soils (HNS and LNS) during a 60-day aerobic incubation involving an unamended control and the following five treatments: potassium nitrate (PN), ammonium sulfate (AS), and residue (R) with or without PN (R + PN) or AS (R + AS). Data shown as a mean (●) from six replicate subsamples collected after incubation for 7, 14, 30, 45, or 60 days. For each treatment, statistical significance is indicated above box plots for comparison of the two soils studied.

both the HNS ($r = 0.92$) and the LNS ($r = 0.96$), demonstrating the essential involvement of microbial biomass in C mineralization.

3.3 | C-degrading enzymes

The fundamental role of cellulase in C mineralization is apparent from strong correlations between cellulase activity and CO_2 production that have been obtained in several incubation studies (e.g., Geissler & Horwath, 2009; Jesmin et al., 2021; Luo et al., 2019). Likewise, highly significant ($p < 0.0001$) correlations were found in the present investigation for the HNS ($r = 0.93$) and LNS ($r = 0.90$). In both cases, cellulase activity was increased by the addition of residue as an inducible substrate, in-line with previous reports by Suto and Tomita (2001) and Zengqiang et al. (2016). These increases are documented in Figure 7, which also shows a further increase occurred by the additional input of mineral N, with AS being more effective than PN. Stimulatory effects of N on cellulase activity have been observed previously (e.g., Carreiro et al., 2000; Luo et al., 2019) and can be attributed to the effects of N availability on the growth and activities of cellulolytic microorganisms during utilization of readily degradable substrates. Such effects most likely explain why cellulase activity tended to be greater for the HNS than the LNS (Figure 7).

Besides cellulase, periodic assays were performed during incubations to determine how residue and/or exogenous N inputs affect the activity of β-glucosidase, which is essential for catalyzing the final steps in the degradation of cellulose to simple sugars. For both soils studied, cellulase and β-glucosidase activities were strongly correlated ($r \sim 0.90$, $p < 0.0001$), as previously reported in several studies (e.g., Keeler et al., 2009; Zhang et al., 2020). Treatment effects on β-glucosidase are reported in Figure 8, which shows that activities for this enzyme were invariably greater for the HNS than the LNS and increased significantly in the presence of residue, and that further increases occurred when residue was applied with AS but not PN. The stimulatory effect of mineral N on β-glucosidase activity has been reported previously (e.g., Keeler et al., 2009; Liu et al., 2021) and can be attributed to enhanced microbial activities that promote the production of C-degrading enzymes by supplying an essential elemental constituent of all enzymes. The finding that NH_4^+ had a greater effect than NO_3^- (Figure 8) is consistent with microbial preferences for a source of mineral N that can be readily assimilated without the need for reduction. Despite strong positive correlations at $p < 0.0001$ between β-glucosidase activity and cumulative CO_2 production for the HNS ($r = 0.87$) and the LNS ($r = 0.81$), a disparity occurred between these two parameters when the latter soil was treated with R + PN. Such a discrepancy may be attributable to differences in sampling frequency, owing to continuous atmospheric analyses as opposed to periodic enzyme assays. Another contributing factor could have been a difference between the soils studied with respect to microbial community composition and their enzymatic strategies and

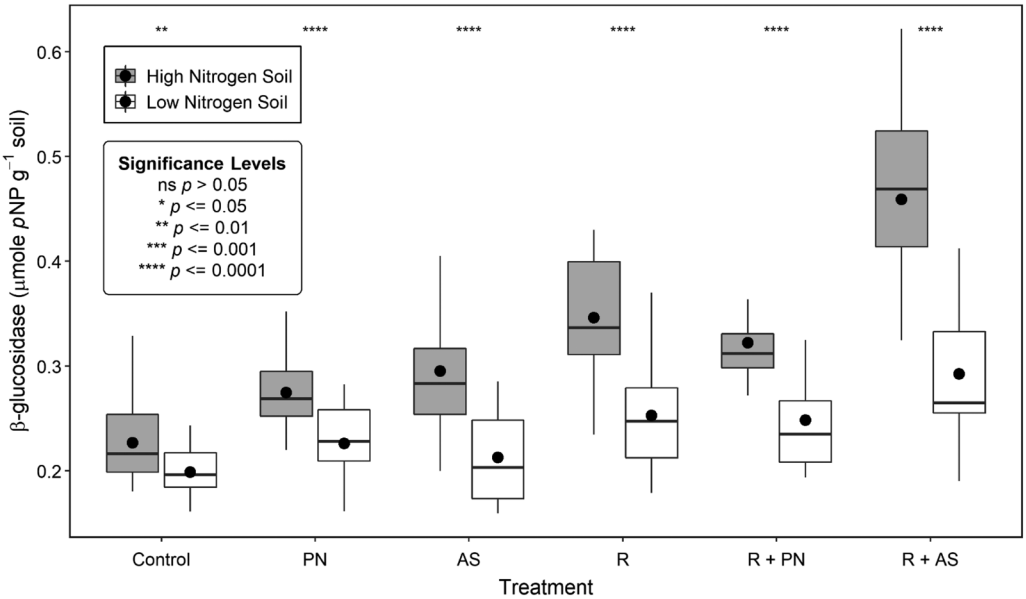


FIGURE 8 Box plot of β-glucosidase activities measured for high and low N soils (HNS and LNS) during a 60-day aerobic incubation involving an unamended control and the following five treatments: potassium nitrate (PN), ammonium sulfate (AS), and residue (R) with or without PN (R + PN) or AS (R + AS). Data shown as a mean (●) from six replicate subsamples collected after incubation for 7, 14, 30, 45, or 60 days. For each treatment, asterisks above box plots show statistical significance for comparison of the two soils studied.

capabilities for C mineralization (Alexander, 1977; Lo et al., 2009).

4 | CONCLUSIONS

Contrary to what was expected in a 60-day incubation study with two contrasting soils, corn residue decomposition was unaffected by differences in the supply of indigenous N. The stimulatory effect of exogenous N, however, was more evident for the LNS than HNS, with NO_3^- being the more effective N-form in the former case and NH_4^+ in the latter. The active fraction of microbial biomass was maximized by the presence of exogenous N during residue decomposition in the LNS, whereas cellulolytic enzyme activities were greater for the HNS.

The work reported herein raises questions about the feasibility of improving low-fertility soils under corn production by increasing residue inputs through intensive N fertilization, although this must be corroborated by field studies that collectively encompass different soil types, climatic conditions, and tillage practices, in relation to the management of both above- and belowground residues. The present findings are consistent with the absence of soil C sequestration in numerous long-term cropping experiments and suggest the need to minimize C mineralization in N-limited soils by reducing heterotrophic utilization of fertilizer N. Such a reduction becomes possible by avoiding excessive N fertilization and by synchronizing fertilizer N application with crop N demand.

AUTHOR CONTRIBUTIONS

Tanjila Jesmin: Conceptualization; data curation; formal analysis; investigation; methodology; writing—original draft; writing—review and editing. **Richard L. Mulvaney**: Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; writing—original draft; writing—review and editing. **Thomas W. Boutton**: Writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interests.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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