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Microbial carbon use efficiency is governed by site-level soil and climate factors and does not explain soil carbon gains under diversified crop rotations

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ABSTRACT

Soil microbial carbon use efficiency (CUE) is an important parameter governing the formation of soil organic carbon (C). We hypothesized that increased CUE could explain higher soil C with diversified crop rotations, which do not necessarily have higher C inputs or reduced soil disturbance — traditional drivers of soil C. Across five long-term experiments, crop rotational diversity increased microbial biomass C but did not affect microbial CUE or its components. CUE was marginally higher when the crop grown the year prior was a legume vs. a grain, though soil C did not differ. Site-level soil and climate factors governed CUE far more than management. Higher soil C in more diverse rotations thus likely results from mechanisms other than increasing microbial CUE.

Soil microbial physiology plays a fundamental role in soil organic carbon (C) accrual (Tao et al., 2023). Heterotrophic soil microorganisms take up organic C, which is partitioned between catabolic respiration and anabolic growth, with the C allocated to biomass production having the potential to be stabilized on soil minerals (Kallenbach et al., 2016). The fraction of anabolic C, i.e. carbon use efficiency (CUE; Geyer et al., 2019), depends on both intrinsic traits of soil microbes at individual and community levels as well as environmental factors, such as abiotic conditions and resource quality, that affect microbial physiology (Manzoni et al., 2012, 2017; Domeignoz-Horta et al., 2020; Pold et al., 2020). Substantial variation in CUE across ecosystem types and biomes reflects the impact of these interacting factors, partially accounted for by differences in soil and climate (He et al., 2023; Hu et al., 2025; Zhang et al., 2025). Management within ecosystems can also influence these factors and thus possibly CUE, including foundational agricultural practices like crop rotation (Mooshammer et al., 2022).

Crop rotational diversity can increase soil C (McDaniel et al., 2014) but the proposed mechanisms behind this do not fully explain the process (Kallenbach et al., 2015). For example, traditional soil C concepts and models suggest building soil C in agricultural systems requires increasing C inputs through additions of slowly decomposing crop residues, or reducing C loss by minimizing soil disturbance to slow decomposition (Parton et al., 1994; Paustian et al., 1997). Yet soil C can be higher in more diversified rotations even when C inputs are lower and disturbance higher (Kallenbach et al., 2015), suggesting alternative explanations are likely, including CUE. Currently, the limited number of

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Table 1
Characteristics of the long-term experimental corn-based cropping system studies. The five sites were located in Colorado (CO), South Dakota (SD), Nebraska (NE) and Ohio (OH) in the Central U.S. and Ontario (ON) in Canada. Cropping systems at all sites were no-till and received synthetic N fertilizer. Fertilization application rate is given for the corn year of the rotation. 'Variable' indicates that N fertilizer is applied based on soil tests. Samples were collected from three different crop rotations at each site: the simplest (Rot1), intermediate (Rot2) and the most complex rotation (Rot3), except at site SD. At SD, Rot2 and Rot3 have the same diversity level. For data analysis, crop rotations were grouped by number of crops: one crop (C1), two crops (C2) and three or more crops (C3+).

Site	Lat/long	MAP (mm y^{-1})	Duration[a] (yr)	Fertilization (kg N ha^{-1})	Rot1	Rot2	Rot3
CO	40.2, −103.1	406	28	Variable	C–F–W[c]	C-M-W[d]	C-M-P-W[d]
SD	44.4, −96.8	582	18	~73	C–S[c]	C–P–W–S[d]	C–O–W–S[d]
NE	41.1, −96.5	777	35	180	C[b]	C–S[c]	C–O/RC-Sorg-S[d]
ON	43.6, −80.4	927	38	160-180	C[b]	C–C–S–S[c]	C–C–O/RC-B/RC[d]
OH	40.8, −81.9	947	56	202	C[b]	C–S[c]	C-A-A[d]

A: alfalfa; B: Spring barley; C: corn; F:fallow; M: millet; O: oats, P: pea; RC: red clover; S: soybean; Sorg: sorghum; W: winter wheat.
[a] Experimental duration between establishment of the study and sampling in 2018.
[b] C1.
[c] C2.
[d] C3+.

studies on crop rotation and microbial CUE show contrasting responses—both higher microbial CUE in diversified cropping systems with fewer C inputs (Kallenbach et al., 2015) and no effect of cropping system diversity on CUE (Judd et al., 2025).

We hypothesized that crop diversity would increase microbial CUE and help explain observations of higher soil C. More diverse crop rotations could influence CUE through shifts in soil microbial community composition (Venter et al., 2016; Mooshammer et al., 2022) and/or microbial interactions (Domeignoz-Horta et al., 2024), as well as higher resource quality of plant inputs (e.g. lower C:N ratios) (Kallenbach et al., 2019). We alternately hypothesized that the presence of legumes may instead be the primary management influence on CUE, rather than crop diversity per se, driven by resource quality of recent organic matter inputs. Finally, we compared the relative influence of crop rotation vs. soil-climate factors on microbial CUE.

To assess effect of crop rotation on microbial community CUE, we analyzed microbial CUE and its components, based on incorporation of ^{18}O–H_2O into microbial DNA, in maize-based crop rotations at five long-term experiments in the Central U.S. and Canada across a soil-climate gradient (Table 1). In this set of five long-term experiments, surface soil organic C stocks are significantly higher in the most diverse rotations (C3+), and similarly lower in monocultures (C1) and two-crop rotations (C2) (Fig. S1a and Mooshammer et al., 2022).

By working across multiple sites, we avoided limitations of single-site experiments that do not vary in soil-climate conditions. Experimental designs were standard (e.g., randomized complete block design) and details can be found in Mooshammer et al. (2022) as well as the Supplement and site references. Briefly, we collected soil samples (0-15 cm) during the maize vegetative growth phase of three maize-based crop rotations (the lowest, intermediate, and most complex rotation at each site; Table 1, Supplement), with similar tillage and fertilizer practices (i.e., no tillage, synthetic N fertilizer). To estimate microbial CUE and microbial biomass turnover, we measured microbial growth using an ^{18}O technique that quantifies the incorporation of ^{18}O into newly formed microbial dsDNA (Schwartz, 2009; Spohn et al., 2016) (Supplement). We also measured microbial biomass C by the chloroform fumigation extraction method (Vance et al., 1987).

To test our hypotheses, we used a mixed effects model including both rotational diversity (C1, C2, C3+) and prior year crop (legume vs. grain) as fixed effects, with site as a random effect. This approach tests the partial effect of each predictor while controlling for the other, addressing the partial nesting between rotational diversity and prior year crop (all C1 rotations had maize as the prior year crop; C2 rotations were preceded mostly by soybean; C3+ rotations had more a balanced split of grains and legumes). Adjusted generalized variance inflation factors were modest (1.35 for crop rotation and 1.83 for prior year legume), confirming that the partial effects were reliably estimable (Fox and Monette, 1992).

Contrary to our hypothesis, soil microbial community CUE did not show a statistically clear response to crop rotational diversity, nor did its components, i.e., microbial growth and respiration (Table 2 and Fig. 1). This suggests that differences in microbial CUE during the maize phase of the rotation cannot explain the higher soil C in the most diverse rotation. Yet CUE can fluctuate substantially within and across seasons (Schnecker et al., 2023), so point-in-time measurements likely do not represent the cumulative metabolic conditions under which soil C accrued. Our study was designed to capture whether a long-term history of crop rotation affected CUE during the maize phase, and does not rule out changes during other crop phases that could help explain higher soil C.

Rotational diversity did significantly affect MBC, increasing by 1.87 μmol C g^{-1} (29.7%) from C1 to C3+ with C2 intermediate. The increase in MBC with rotational diversity, without a corresponding shift in CUE, suggests that greater substrate availability rather than more efficient metabolism sustains a larger microbial biomass whose turnover could generate more necromass available for stabilization on soil minerals (Mooshammer et al., 2022). This and other stabilization mechanisms (Xiao et al., 2024; King and Sokol, 2025), rather than shifts in CUE, may instead explain higher soil C in these diversified cropping systems.

Turning to the second hypothesis, CUE was marginally higher when legumes vs. grains preceded maize ($p = 0.052$), driven by reduced respiration per unit of microbial biomass rather than increased growth

Table 2
Effect of crop rotational diversity and prior year crop on microbial biomass C, CUE, MBC turnover, respiration, and growth. Shown are the results of mixed-effect analysis of variance (ANOVA) using crop rotational diversity groups (C1, C2, C3+) and prior year crop (legume vs. grain) as fixed factors and site as a random effect. Marginal R^2 (R^2_m) reports the proportion of variance explained by the fixed effects, and conditional R^2 (R^2_c) reports proportion of variance explained by both fixed effects and site, as the random effect.

	Crop Rotation (C1, C2, C3+)		Prior year crop (legume vs. grain)		R^2_m	R^2_c
	F-value	p-value	F-value	p-value		
Microbial biomass C	4.0	0.027	1.0	ns	0.10	0.76
CUE	1.0	ns	4.0	0.052	0.07	0.78
MBC turnover	0.2	ns	0.0	ns	0.01	0.66
Per g soil d.w.						
Growth	0.9	ns	0.2	ns	0.02	0.72
Respiration	1.0	ns	0.5	ns	0.06	0.20
Per microbial biomass C unit						
Growth	1.0	ns	0.0	ns	0.02	0.80
Respiration	0.8	ns	5.6	0.022	0.22	0.56

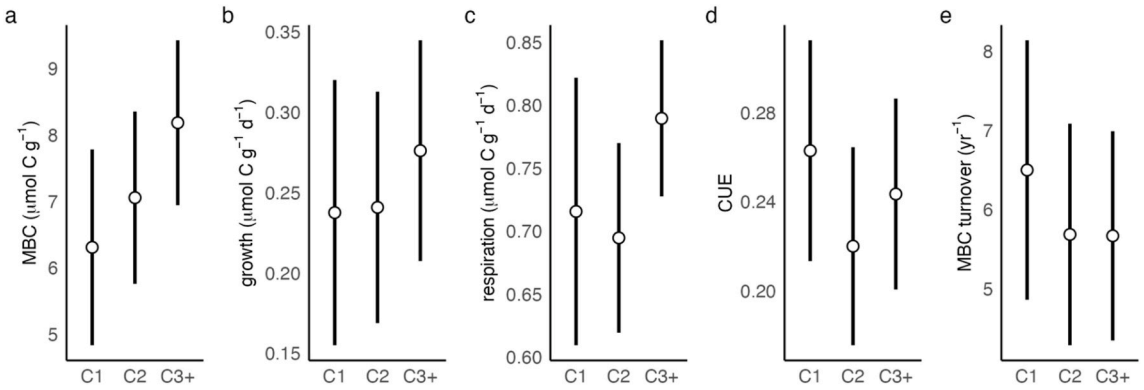

Fig. 1. Soil microbial biomass carbon (MBC) and microbial community physiological characteristics in rotation with one (C1), two (C2) or three or more (C3+) crop and cover crop species in rotation, in maize-based crop rotations across five long-term experiments in the Central U.S. and Canada: a) microbial biomass carbon (MBC); b) microbial growth; c) microbial respiration; d) microbial carbon use efficiency (CUE); and e) MBC turnover. Shown are estimated means and standard errors from mixed effects models. Rotational diversity significantly affected MBC ($p = 0.027$) but not other response variables (Table 2).

(Table 2; Fig. 2). The effect was stronger when prior year crop was modeled alone ($p < 0.05$), indicating that part of the apparent prior-year legume effect reflects correlated differences in rotation structure (Table S1). Subset analyses corroborated this pattern: the legume effect was significant when restricted to C1+C2 rotations (driven by the continuous-maize vs. corn-soybean contrast), marginal in C2+C3+, and absent within C3+ alone (Table S1). Soil C did not differ by prior year crop (Fig. S1), consistent with recent evidence that microbial growth rate may predict soil C better than CUE because growth directly quantifies biomass — and thus necromass — production (He et al., 2026).

Beyond the limited effect of management on CUE, long-term experimental sites accounted for substantially more variation in microbial community CUE, and its components, compared to rotational diversity, as indicated by the much higher values of conditional R^2 (R^2_c, including fixed effects and site random effects) compared to marginal R^2 (R^2_m, including only fixed effects) (Table 2, Fig. S2). This is consistent with global patterns showing that abiotic conditions are primary drivers of microbial physiology (He et al., 2026; Hu et al., 2025; Zhang et al., 2025). Site-level random intercepts of microbial CUE and growth from mixed effects models were marginally, positively correlated with increasing mean annual precipitation ($p = 0.08$ and $p = 0.05$, respectively), whereas mean annual temperature and mean surface soil clay content were not. While this should be considered exploratory due to the small number of sites, this could indicate that soil microbial communities adapted to drier conditions at the more arid sites (Hawkes et al., 2017) come with the tradeoff of lower intrinsic CUE (Lennon et al., 2012; Allison and Goulden, 2017). The same site-level factors that shape CUE also govern downstream stabilization capacity through controls on mineral surface availability and saturation deficit (King and Sokol, 2025), suggesting that pedoclimatic context sets the primary controls on both microbial physiology and soil C stabilization in these systems, with management a secondary control.

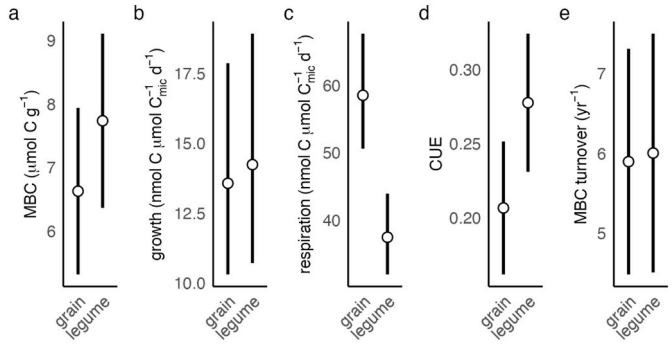

Fig. 2. Microbial biomass carbon (MBC) and microbial community carbon use efficiency (CUE), and its components when grains vs. legumes preceded the year of sampling, in maize-based crop rotations across five long-term experiments in Central U.S. and Canada: a) microbial biomass carbon (MBC); b) microbial growth; c) microbial respiration; d) microbial carbon use efficiency (CUE); and e) MBC turnover. Shown are estimated means and standard errors from mixed effects models. Prior year crop significantly affected biomass-specific respiration ($p = 0.022$) and was marginally associated with CUE ($p = 0.052$) (Table 2).

We conclude that microbial CUE does not account for higher soil C in diversified crop rotations across this set of long-term experiments. Although prior-year legumes marginally increased CUE, the effect operated through reduced respiration rather than enhanced growth, limiting its relevance for soil C accrual. Instead, the capacity of diversified rotations to build soil C likely operates through greater necromass inputs from a larger microbial biomass and their stabilization on soil minerals — processes strongly modulated by site-level soil and climate conditions. Management strategies aimed at increasing soil C will likely be more effective when they target microbial biomass and necromass production within the pedoclimatic constraints of a given site, rather than CUE per se.

CRediT authorship contribution statement

Timothy M. Bowles: Conceptualization, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing. **Maria Mooshammer:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **A. Stuart Grandy:** Conceptualization, Funding acquisition, Writing – review & editing. **Kevin Geyer:** Investigation, Writing – review & editing. **Serita D. Frey:** Methodology, Writing – review & editing. **Francisco Calderón:** Resources, Writing – review & editing. **Steve Culman:** Resources, Writing – review & editing. **Bill Deen:** Resources, Writing – review & editing. **Kari Dunfield:** Resources, Writing – review & editing. **Virginia L. Jin:** Resources, Writing – review & editing. **R. Michael Lehman:** Resources, Writing – review & editing. **Shannon L. Osborne:** Resources, Writing – review & editing. **Marty Schmer:** Resources, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Timothy Bowles reports financial support was provided by US Department of Agriculture. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2026.110230.

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