Title: Constraints on mineral-associated and particulate organic carbon response to regenerative management: carbon inputs and saturation deficit

Authors

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Abstract

Regenerative management has potential to increase soil organic carbon (SOC), which will be crucial for mitigating climate change and improving soil health. Distinct fractions of SOC, particulate organic carbon (POC) and mineral-associated organic carbon (MAOC), have been posited as having contrasting responses to regenerative management. The POC response has been proposed as a leading indicator of total SOC response, whereas MAOC response has been seen as eventually limiting SOC response due to its saturation behavior. We explored these and linked expectations of SOC, POC and MAOC response by leveraging multiple datasets of regenerative management with cover crops or perennial crops as contrasted with conventional management (n = 45 sites). Across sites, POC as a percentage of SOC was on average 19%. Regenerative management increased both POC and MAOC but increases in POC were smaller and narrower (0.78 ± 0.26 g C kg soil^{-1}) than increases in MAOC (1.41 ± 0.80 g C kg soil^{-1}). Changes in POC were only weakly correlated with changes in SOC ($p < 0.001$ but $R^2 = 0.11$), revealing that absolute changes in POC at any timepoint should not be taken as indicative of total SOC responses. The MAOC response made up the majority of SOC response at 58% of sites. Changes in POC and MAOC with regenerative management were also not related ($p = 0.72$), indicating that comprehensive assessment of POC and MAOC is needed to understand SOC accumulation under regenerative management. Increases in POC were explained by annual average of increase in root C inputs with regenerative management, suggesting a limited ability for the current portfolio of regenerative management practices to increase POC, even when implemented over decadal time scales. In contrast, increases in MAOC were partially explained by cumulative-for-the-trial increases in root C inputs and

were not clearly constrained by silt + clay-estimated saturation deficit. Our results indicate that the increase of MAOC storage in agricultural soils is not limited by saturation but rather by the extent to which root C inputs can be augmented, and that increasing POC storage will require novel practices to overcome current limitations on POC accumulation.

1. Introduction

Increasing soil organic carbon (SOC) in agricultural lands is a key solution for mitigating climate change and improving soil health (Bossio et al., 2020; Minasny et al., 2017; Paustian et al., 2016). Regenerative agricultural practices are designed to accumulate SOC, often by increasing C inputs to soil (King and Blesh, 2018), as a means to improve soil functioning (Schreefel et al., 2020). Increases in SOC can either be in the form of particulate organic carbon (POC) or mineral-associated organic carbon (MAOC). These pools of SOC have distinct formation pathways and mechanism of protection. Inputs of structural compounds primarily form POC (Cotrufo et al., 2015; von Lützow et al., 2007), which receives minimal protection from the soil matrix (King et al., 2023), and generally has a fast turnover rate compared to MAOC (Lutzow et al., 2006; Poeplau et al., 2018). Inputs of low-molecular weight compounds primarily form MAOC, which is protected from decomposition by the soil matrix (Cotrufo et al., 2015; Kleber et al., 2015). Each of these pools of SOC has received research attention from somewhat divergent standpoints, but increasingly there is an awareness that effective SOC management depends on accurate, holistic understandings of how both POC and MAOC respond to management (Angst et al., 2023; Cotrufo and Lavallee, 2022).

Mineral-associated organic carbon has been the focus of an abundance of work elaborating its empirical properties and theoretical controls (Cotrufo et al., 2013; Feng et al., 2013; Hassink and Whitmore, 1997). As MAOC receives protection from soil mineral surfaces, and the availability of soil mineral surfaces varies between soils but is necessarily finite, the concept of a soil-specific upper limit of MAOC storage has been termed ‘saturation’ (Hassink, 1997; Six et al., 2002; Stewart et al., 2007). An assumption that saturation dynamics govern MAOC behavior has since proliferated (Angst et al., 2023; Castellano et al., 2015; Just et al., 2023) and has legitimized soil-texture-derived MAOC saturation levels being used to estimate MAOC storage capacity regionally (Beare et al., 2014) and globally (Georgiou et al., 2022). It reasonably follows from current theory of MAOC saturation that resources to promote regenerative management should target soils farther from MAOC saturation, which could have major logistic and economic consequences for SOC storage initiatives. While an emerging understanding of controls on MAOC accumulation indicate soil matrix properties such as exchangeable calcium and amorphous iron and aluminum are stronger determinants of MAOC storage capacity than silt + clay (King et al., 2023; Rasmussen et al., 2018; Rowley et al., 2018), there remains insufficient data on these properties to test any updated formula for determining MAOC saturation level. Even with respect to the long-standing silt + clay-defined MAOC saturation, there has been little investigation whether a silt + clay-defined MAOC saturation deficit influences responsiveness of MAOC to regenerative management specifically in agricultural soils. If soils under annual agriculture are consistently far enough from MAOC saturation given loss of SOC under agricultural land use (Sanderman et al., 2017), it may be that factors other than MAOC saturation deficit influence MAOC response to regenerative management.

Studies focusing on POC response to regenerative management (Janzen et al., 1992; Liu et al., 2022; Mi et al., 2016; Mirsky et al., 2008) have emerged in part because observing a response to management in SOC is expected to be challenged by several barriers. The SOC pool is large compared to annual inputs and outputs, so any improvements in agricultural management usually require multiple seasons of implementation to realize measurable SOC changes (Smith, 2004). It is also unclear whether hard-won increases in total SOC are necessary or sufficient for improvements in soil functioning (Gregorich et al., 1994). These challenges in studying SOC have inspired research seeking to identify measurable quantities of soil that enable sensitive detection of fractions relevant to SOC functioning (Cantero-martı et al., 2014; Gregorich and Janzen, 1996; Haynes, 2005), or early indicators of SOC change (Culman et al., 2012). Amongst this suite of SOC fractions, POC is often included, having been described in early work as a management-responsive fraction (Hussain et al., 1999; Wander et al., 1994). Given this research, POC change is often described as an indicator of SOC change (Eze et al., 2023), although relationship between absolute POC change and SOC change under regenerative management has received limited synthesis across agricultural soils broadly, which could help to determine the utility of POC assessments as indicators of SOC change. Another expectation motivating the study of POC is that POC response to management, not being constrained by inherent soil properties, is instead limited only by C inputs (Castellano et al., 2015; Six et al., 2002).

Carbon inputs to soil are recognized as crucial for maintenance of SOC levels in the face of on-going SOC decomposition and turnover (Gregorich et al., 1995; Luo et al., 2017). A central pathway through which regenerative practices increase SOC is therefore by increasing the quantity of C inputs to soil (King and Blesh, 2018; Kong et al., 2005). Regenerative practices such as cover cropping and perennial cropping can extend plant growth to the shoulders of traditional growing seasons to increase total plant productivity and C inputs (King and Blesh, 2018). Replacing annual crops with perennial crops also increases belowground (root) inputs compared to most annual crops (Anderson-Teixeira et al., 2013). Root inputs are particularly important for SOC accumulation and maintenance due to their preferential retention compared to shoot inputs (Austin et al., 2017; Kong and Six, 2010; Rasse et al., 2005; Sokol et al., 2018) and can lead to either formation of MAOC through rhizodeposition or formation of POC due to persistence of root structural tissues (Fulton-Smith and Cotrufo, 2019; Poirier et al., 2018). Differences in root or shoot C inputs between a regenerative and conventional practice can be assessed in terms of either an average annual change (Wooliver and Jagadamma, 2023), or a cumulative-for-the-trial change (Das et al., 2014), where responsiveness to the latter would indicate longer residence times of C inputs. Despite the demonstrated importance of C inputs for SOC, it is currently unclear whether increases in C inputs under regenerative practices similarly affect POC and MAOC, given differences in turnover time and protection from decomposition between the two fractions. If it were the case that MAOC accumulation is primarily saturation-limited but that POC is primarily C input limited, we could expect to see little or no signal of C inputs in increasing MAOC in soils close to saturation while POC accumulation would align with long-term increases in C inputs.

We leveraged datasets from King et al. (2023), Prairie et al. (2023) and Rui et al. (2022) to ask: 1) What is the response size of SOC, POC and MAOC to regenerative management practices of cover cropping and perennial cropping, broadly across agricultural soils? We also asked: 2) What are the relationships between POC, MAOC and SOC response to these forms of regenerative management, and, finally, 3) Can the expected variability in POC and MAOC response to regenerative management be explained by soil properties or C inputs? Previous studies have examined the role of climate and other soil properties (silt + clay; soil pH) in mediating the effect of regenerative management on SOC and found minimal influence (Jian et al., 2020; Poeplau and Don, 2015), however we also investigated these variables to corroborate the absence of their influence in our dataset. Our overarching hypothesis was that the response sizes and the controls on response sizes of POC and MAOC to regenerative management would differ. Specifically, we hypothesized that POC response was more likely to be influenced by C inputs whereas MAOC was more likely to be influenced by saturation deficit. We focused on cover cropping and perennial cropping as regenerative practices that have a larger effect on SOC throughout tillage layer than changing tillage regime alone (Nunes et al., 2020) and can increase SOC via modifying C inputs (King and Blesh, 2018).

2. Methods

2.2 Use of multiple datasets

We extracted data from a meta-analysis on the effect of regenerative agricultural management on SOC, POC and MAOC (Prairie et al., 2023). From this global dataset, we selected paired observations from sites that compared cover cropped to non-cover cropped studies, and studies that compared rotations with a perennial forage to rotations without either a perennial forage or a cover crop (n = 26 studies, 109 paired comparisons, SI Table 1). We included only observations from topsoil (< 20 cm depth, SI Table 1), and if multiple soil increments were reported for this depth, we used a depth-weighted average to arrive at a single observation for topsoil C concentration in our analyses. Depth-weighted averages (C_{av}) were calculated as follows:

$$C_{av} = C_{upper}\left(\frac{length\ upper}{length\ total}\right) + C_{lower}\left(\frac{length\ lower}{length\ total}\right) \qquad \text{Eq. (1)}$$

where C_{upper} and C_{lower} are the concentration of soil C in an upper and lower depth increment, respectively, *length upper* is the length in cm of the upper soil increment, *length total* is the length in cm of the entire sampling depth above 20 cm, and *length lower* is the length in cm of the lower sampling depth. *Length upper* and *length lower* were determined by the sampling depths reported in each study. We also included data from the site of Rui et al. (2022), which matched criteria for inclusion in the Prairie et al. 2023 meta-analysis, but was published too recently to be included; this site is included in SI Table 1. Rui et al. (2022) is reported at 0-15 cm and 15-30 cm, but we use only the 0-15 cm depth in this study for greatest consistentency with other soil depth reports.

We also used data on soils collected from 15 long-term agricultural sites in the United States (King et al., 2023). We analyzed these soils at our Soil Innovation Laboratory at Colorado State University, and the availability of crop yield data from these sites enabled estimation of C inputs. Sites, sampling strategies, and soil processing for these 15 sites are described in the subsequent methods. For all three studies (King et al., 2023; Prairie et al., 2023; Rui et al., 2022) we extracted published information on climate (mean annual temperature, MAT; the difference between mean annual precipitation and potential evapotranspiration, MAP-PET) and available soil properties (silt + clay; soil pH).

2.3 Site selection and soil sampling

For the U.S. measured data (King et al., 2023), soils were sampled in the fall of 2020 from 15 agricultural sites (SI Table 2). Sites were chosen to include paired comparisons of regenerative management (cover crop, perennial forage, or perennial bioenergy) compared to conventional cropping systems without perennial or perennial bioenergy; at one site, the conventional cropping system included a cover crop (SI Table 2). All treatments were replicated 3-5 times and had been in place at least 5 years, with maximum study duration of 57 years (SI Table 3). With few exceptions, plots received agronomically realistic rates of synthetic N fertilizer, most were under no-till, and no plots received exogenous organic amendments.

Soils were sampled from 0 - 20 cm with multiple composited cores as necessary to achieve approximately 600 g dry mass equivalent per plot. Where crop management was based on annual crop rotations with corn or wheat, soils were sampled following harvest (October – November), and conventional and regenerative treatments were sampled concurrently. Location of soil cores was standardized with respect to in-row vs. between-row cores in conventional and regenerative treatments when both were in row crop at the time of sampling and was randomized in perennial-cropped plots. After sampling, soils were transported to Colorado State University campus on ice and transferred to a 4° C walk-in refrigerator upon arrival. All soils were passed through an 8 mm sieve while fresh, then 2 mm sieved, each time removing roots and rocks that remained on the soil surface before soils were allowed to air-dry.

2.4 Soil fractionation into POC and MAOC

For the U.S. measured data (King et al., 2023), soils were separated by size into sand + POC (> 53 µm) and silt + clay + MAOC (<53 µm) following Cambardella & Elliott (1992). These fractions are hereafter referred to as simply 'POC' and 'MAOC', respectively. Briefly, 5.75 – 6.25 g of 2-mm sieved bulk soil dried at 60° C was shaken for 18 hours with 12 glass beads in 30 mL 0.5% sodium hexametaphosphate to disrupt all aggregates. The resulting soil slurry was rinsed with DI water over a 53-µm sieve to isolate POC and remove the glass beads. Soil solution passing through the sieve was deemed MAOC. Both the POC and MAOC fractions were dried at 60° C until reaching constant mass. Recoveries of the initial soil masses in the summed fractions were between 95 and 103% for all samples, with a mean recovery of 100.5%. Soils containing carbonates (identified by effervescence after addition of 5% HCl, 18 samples) were treated to remove inorganic carbon via HCl fumigation (Harris et al., 2001). Bulk soil, MAOC, and POC were ground using a mortar and pestle before analysis on a Costech elemental analyzer to quantify organic C (Costech ECS4010, Analytical Technologies, Inc., Milano, Italy). The average recovery of SOC in POC and MAOC fractions was 92%.

Across all sites, bulk density values were not available with sufficient consistency to justify calculating C stocks. Therefore, changes in SOC, POC, and MAOC under regenerative management vs. conventional management are reported as changes in concentration (g C kg soil^{-1}):

$$\Delta C = \text{C regenerative} - \text{C conventional} \qquad \text{Eq. (2)}$$

2.5 Crop C inputs to soil

For all the sites in King et al. (2023), the best available crop yield data from each site were used to estimate C inputs from crops to soil (SI Table 4). Allometric equations (Bolinder et al., 2007) were used to estimate shoot and root + exudate inputs for each crop; belowground inputs were only considered to the soil sampling depth (0-20 cm) and were truncated using crop-specific root distributions (Fan et al., 2016). For perennial crops grown multiple years, annual root inputs were estimated as 62% of root inputs from the initial year, following an assumption of partial root turnover (King and Blesh, 2018). Shoot inputs were reduced by the proportions of shoots that were removed for stover production, if any, and rotation-average crop inputs were calculated (Mg C ha^{-1} yr^{-1}).

We conducted an additional search of sites reported in the meta-analysis of Prairie et al. (2023) for additional data to relate C inputs to changes in soil C pools. From this search, we identified Poffenbarger et al., (2020), with who also reported C inputs separately by shoot and root for two sites, which we also included, noting possible differences in method of C input calculations. For the dataset of Rui et al. (2022), we leveraged C input calculations from Sanford et al., (2012) at the same site. Root C inputs were estimated to the depth of soil sampling using coefficients representative of the cropping system (Fan et al., 2016).

2.6 Estimation of MAOC saturation and MAOC saturation deficit

We used the dataset of Georgiou et al. (2022) to estimate the theoretical C saturation of the MAOC fraction in our soils. Given our interest in comparing observed MAOC levels to a *theoretical maximum*, we relied on the dataset of Georgiou et al. (2022) for its strong representation of native vegetation, which typically has higher MAOC levels that agricultural soils. As soils in the global database (Prairie et al., 2023) did not consistently report soil order, which has previously been used to coarsely categorize soils by ‘high activity’ or ‘low activity’ minerals (Georgiou et al., 2022), we adopted a global slope of MAOC ~ silt + clay across all observations. To derive the boundary line analysis from the data of Georgiou et al. (2022), we used the observations for g MAOC kg $soil^{-1}$ as a function of silt + clay, and first identifying observations in the 95^{th} percentile or higher MAOC concentration in each of 10 segments of silt + clay content (i.e., the first segment of observations with < 10 % silt + clay, the next segment of observations with greater than or equal to 10% silt + clay and < 20%, etc.). Using simple linear regression of these boundary points with intercept forced through zero, on the assumption that soils without silt + clay have no MAOC, we estimated the boundary line slope of MAOC ~ silt + clay to be 0.7323. To calculate theoretical MAOC saturation in g MAOC kg $soil^{-1}$ for all observations across the datasets used in this study, we multiplied silt + clay by 0.7323 (our boundary line slope). We then took two approaches to estimate C saturation deficit of measured soils: 1) *absolute C saturation deficit* was calculated by subtracting observed g MAOC kg $soil^{-1}$ from theoretical g MAOC kg $soil^{-1}$ at saturation; and 2) *percent C saturation* was calculated by dividing observed g MAOC kg $soil^{-1}$ by theoretical g MAOC kg $soil^{-1}$ and multiplying by 100.

2.7 Statistical methods

To test for the effect of regenerative vs. conventional management on SOC, POC, and MAOC within the U.S. measured dataset (King et al., 2023), we used t-tests comparing replicated plots (n=3-5, SI Table 2) of treatments within sites. Additional tests of linear relationships between change in POC, MAOC, and SOC and change in POC and MAOC with change in C inputs were leveraged. Regressions were checked for assumptions of normality and homoscedasticity of residuals using Breusch-Pagan and Shapiro-Wilk tests, respectively. Relationships between SOC, POC and MAOC change (Figure 2) met assumptions of homoscedasticity of residuals but did not meet assumptions of normality of residuals.

For relationships between change in POC or MAOC with change in root C inputs (Figure 5), all tests met these assumptions, except for change in POC ~ change in cumulative root C inputs, which returned $p = 0.016$ in the Shapiro-Wilk. For the relationships described above that did not meet assumptions of normality and homoscedasticity, data transformations (logarithmic and square root) did not improve Breusch-Pagan and Shapiro-Wilk test results, therefore we used raw data in subsequent regressions.

To compare fixed effects of increases in cumulative root C input and MAOC silt + clay saturation deficit for their influence over change in MAOC with regenerative vs. conventional management, we used multiple regression ($n = 18$ sites). The limited number of observations reporting POC, MAOC, and root C inputs prevented a more elaborate model with an interaction term between root C input and silt + clay saturation deficit. All analyses were carried out in R version 4.2.3.

3. Results

Our combined data sets encompassed a range of agricultural SOC concentrations spanning an order of magnitude (from 5.1 to 64.1 g C kg soil^{-1}, Fig. 1). Soils were dominated by MAOC, with 90% of observations containing 74% or greater MAOC as a constituent of SOC. The average MAOC level was 8 times that of POC (interquartile range: 4 – 11 times).

3.1 Changes in POC, MAOC and SOC with regenerative vs. conventional management

Regenerative management resulted in smaller absolute increases in POC (0.78 ± 0.26 g C kg soil^{-1}) compared to MAOC (1.41 ± 0.80 g C kg soil^{-1}). The mean and range of POC management response was even lower if five high values, all on either an Andisol with a highly active soil matrix (Zagal et al., 2013) or measured only to 2.5 cm (Dieckow et al., 2006), were excluded (0.49 ± 0.14 g C kg soil^{-1}). Measurements of very shallow soil (to 2.5 cm) may not reflect processes occurring throughout the topsoil. The range of MAOC response to management was much wider than that of POC, with some sites showing a slight MAOC decrease (-2.38 g C kg soil^{-1}) but, overall, the magnitude of MAOC increase exceeded that of POC in 58% of the cases.

The relationship between POC and SOC response was evaluated after the removal of 2 outliers of POC response greater than 8 g C kg soil^{-1} change, as these points had an outsize influence on test results and were sampled to only 2.5 cm. Using the cleaned dataset, the relationship between POC and SOC was weak (Fig 2a, $R^2 = 0.11$), but, due to high number of observations available for the test, returned a low p-value ($p < 0.001$). Increases in POC were not related to increases in MAOC ($p = 0.72$, Fig. 2b).

3.2 Moderators of regenerative management effect on POC, MAOC, and SOC

All soils had theoretical MAOC saturation deficit (Fig. 3), determined by difference from a theoretical maximum (saturation) based on silt + clay content (Georgiou et al., 2022, SI Figures 3). In our dataset, 69% and 88% of management comparisons were implemented on soils with at least 20 and 10 g C kg soil^{-1}, respectively, of MAOC saturation deficit. These capacities were 2-4 times larger than the measured MAOC gains due to regenerative management (Fig. 2). The MAOC saturation deficit explained little of the variability in MAOC accumulation rates (Fig. 3, $R^2 < 0.09$; SI Fig. 2). Climate, soil pH, and silt + clay also had minimal detectable effects in moderating SOC, POC and MAOC responses to regenerative management (SI Figures 6-8).

We investigated changes in C inputs with regenerative vs. conventional management, which were only available in the U.S. measured data and completed with data from Poffenbarger et al. (2020), Rui et al. (2022), and Sanford et al. (2012). At most sites, regenerative management increased root inputs and decreased shoot inputs compared to conventional management (Fig. 4), with larger increases in root inputs associated with larger decreases in shoot inputs (R^2= 0.4, p = 0.004). Most soils also received greater shoot C inputs than root C inputs (SI Fig. 4), and increases in root C inputs appeared to be constrained by MAP-PET (SI Fig. 5c). We explored relationships between change in C inputs and change in POC and MAOC for both cumulative-for-the-trial change in C inputs (i.e., long-term) and annual average change in C inputs (i.e., short-term, Fig. 5), Long-term change in C inputs was most closely related to observed MAOC, while short-term change in C inputs was more closely related to change in POC (Fig. 5). When long-term change in root C inputs was compared to the theoretical MAOC saturation deficit as a predictor of MAOC change with regenerative management, cumulative root C inputs emerged as a stronger driver of MAOC change (Table 1).

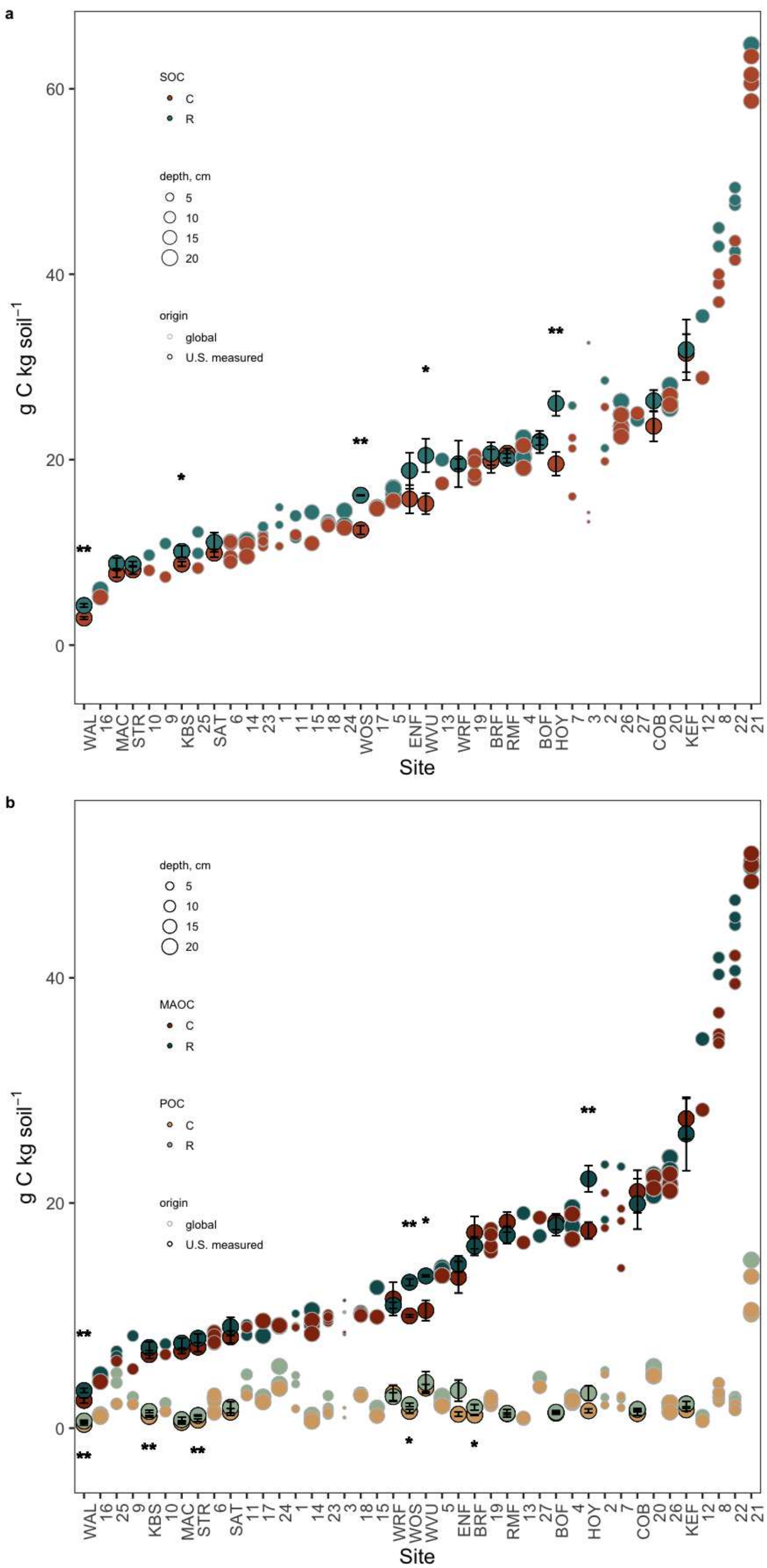
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Figure 1. Concentrations of a) soil organic carbon (SOC) and b) particulate organic carbon (POC) and mineral-associated organic carbon (MAOC). Both panels show C across sites, as influenced by conventional (C) or regenerative (R) management from two datasets. Site information corresponding to site identifiers for the global dataset (Prairie et al., 2023), supplemented with Rui et al. (2022), is shown in SI Table 1. Site identifiers for the U.S. measured dataset is shown in SI Fig. 1 and SI Table 2. Sites are ordered by increasing values of SOC concentration (a) or MAOC concentration (b). For U.S. measured sites, points represent means of each C fraction by treatment; error bars represent standard error of the mean. For each treatment, n = 3-5 plots. Asterisks represent pair-wise comparisons between sites (unadjusted): * = $p < 0.1$ and ** = $p < 0.05$. Pair-wise statistical comparisons of observations from global dataset and Rui et al. (2022) were not conducted due to only treatment-average observations being consistently available.

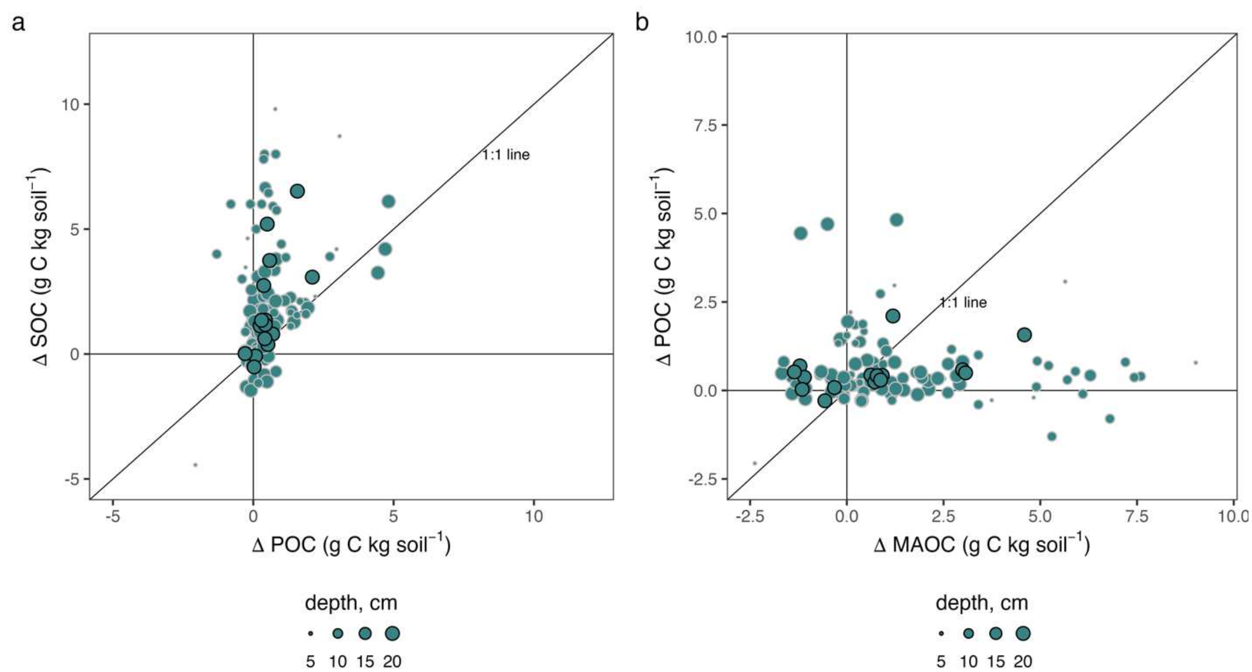

Figure 2. Change (Δ; g C kg soil $^{-1}$) in soil organic carbon (SOC), particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) due to regenerative compared to conventional management. For panel (a), linear regression (not plotted) returned $p < 0.001$ and $R^2 = 0.12$. For panel (b), a linear regression (not plotted) returned $p = 0.61$ and $R^2 < 0.01$. Size of symbol corresponds to sampled depth. Global dataset (gray symbol outlines, Prairie et al., 2023) includes 109 comparisons across 25 sites, supplemented with Rui et al. (2022). One study (Dieckow et al., 2006), sampled 0 – 2.5 cm, was removed from Prairie et al. 2023 due to extreme Δ POC. While U.S. measured dataset (black symbol outlines, King et al., 2023) includes 15 comparisons across 15 sites.

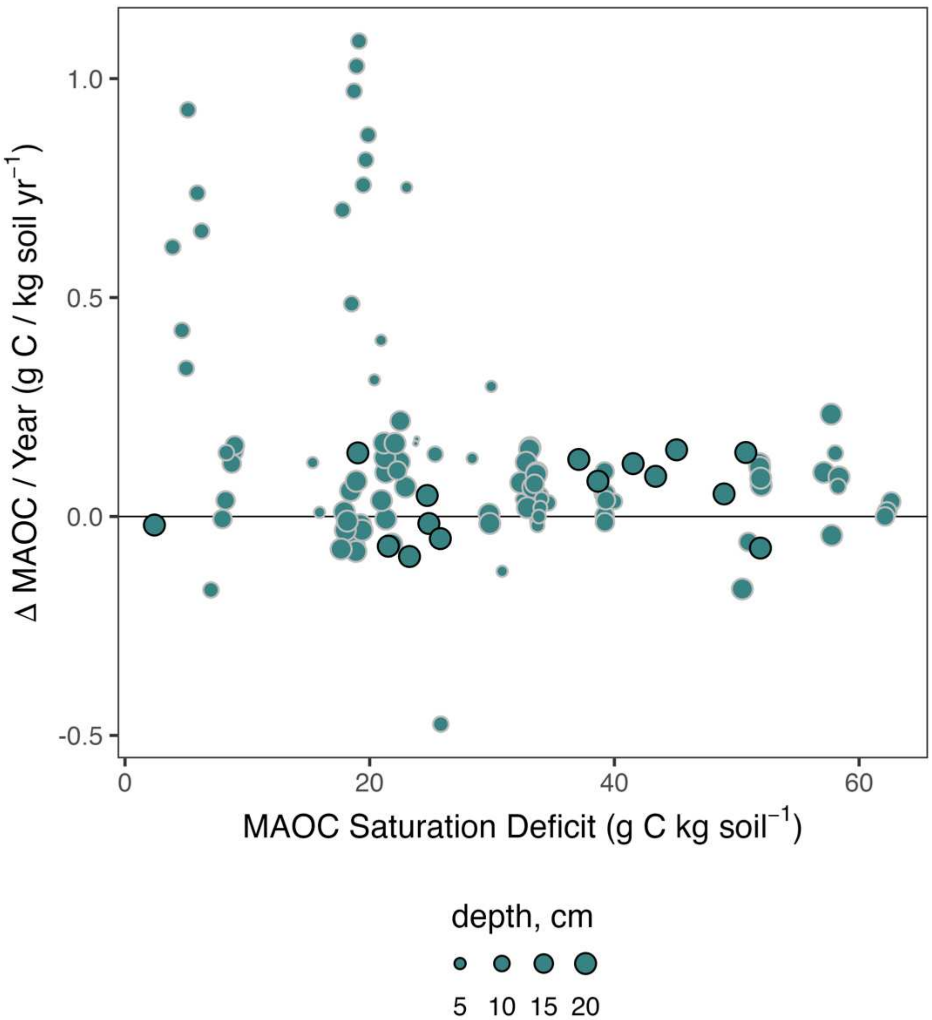

Figure 3. Yearly rates of MAOC change (Δ) in regenerative vs. conventional management, plotted against the corresponding estimated mineral-associated organic carbon (MAOC) saturation deficit. The MAOC saturation deficit is determined by silt + clay saturation deficit (Georgiou et al., 2022). Linear regression (not plotted) returned $R^2 < 0.09$. Size of symbol corresponds to sampled depth. Global dataset (gray symbol outlines, Prairie et al., 2023) includes 111 comparisons across 26 sites, supplemented with Rui et al. (2022), while U.S. measured dataset (black symbol outlines, King et al., 2023) includes 15 comparisons across 15 sites.

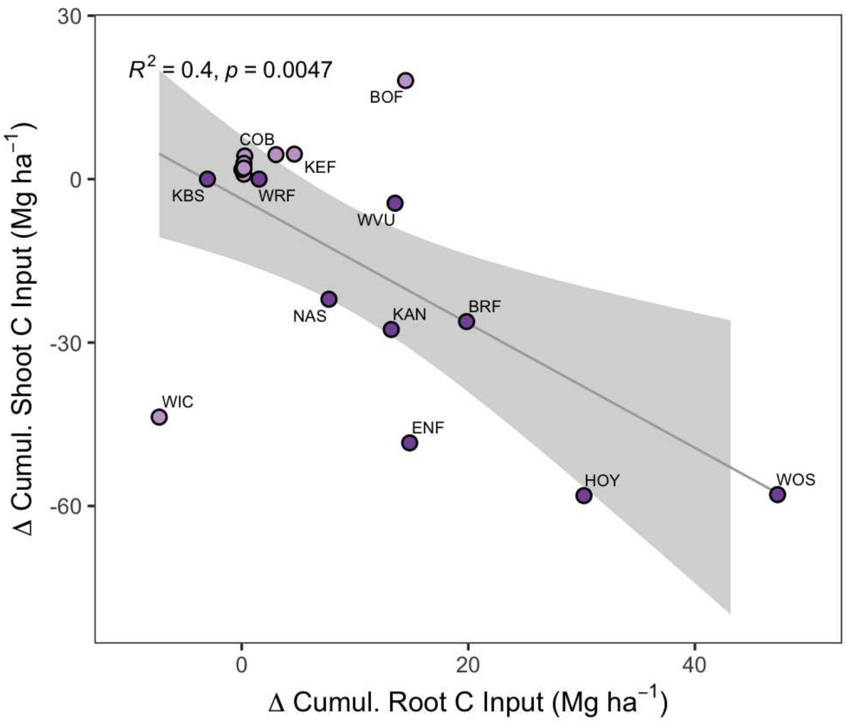

Figure 4. Change (Δ) in cumulative difference in root carbon (C) inputs with change in cumulative shoot C inputs in regenerative vs. conventional treatments across U.S. measured sites (King et al., 2023), supplemented with Poffenbarger et al., (2020) and Sanford et al., (2012), (n = 18 sites, 0-20 or 0-15 cm depth). Regenerative treatments are cover cropped (lighter purple symbols) and perennial cropped (darker purple symbols) compared to conventional cropping. Gray line represents simple linear regressions with a 95% confidence interval. Site information presented in SI Tables 1-2.

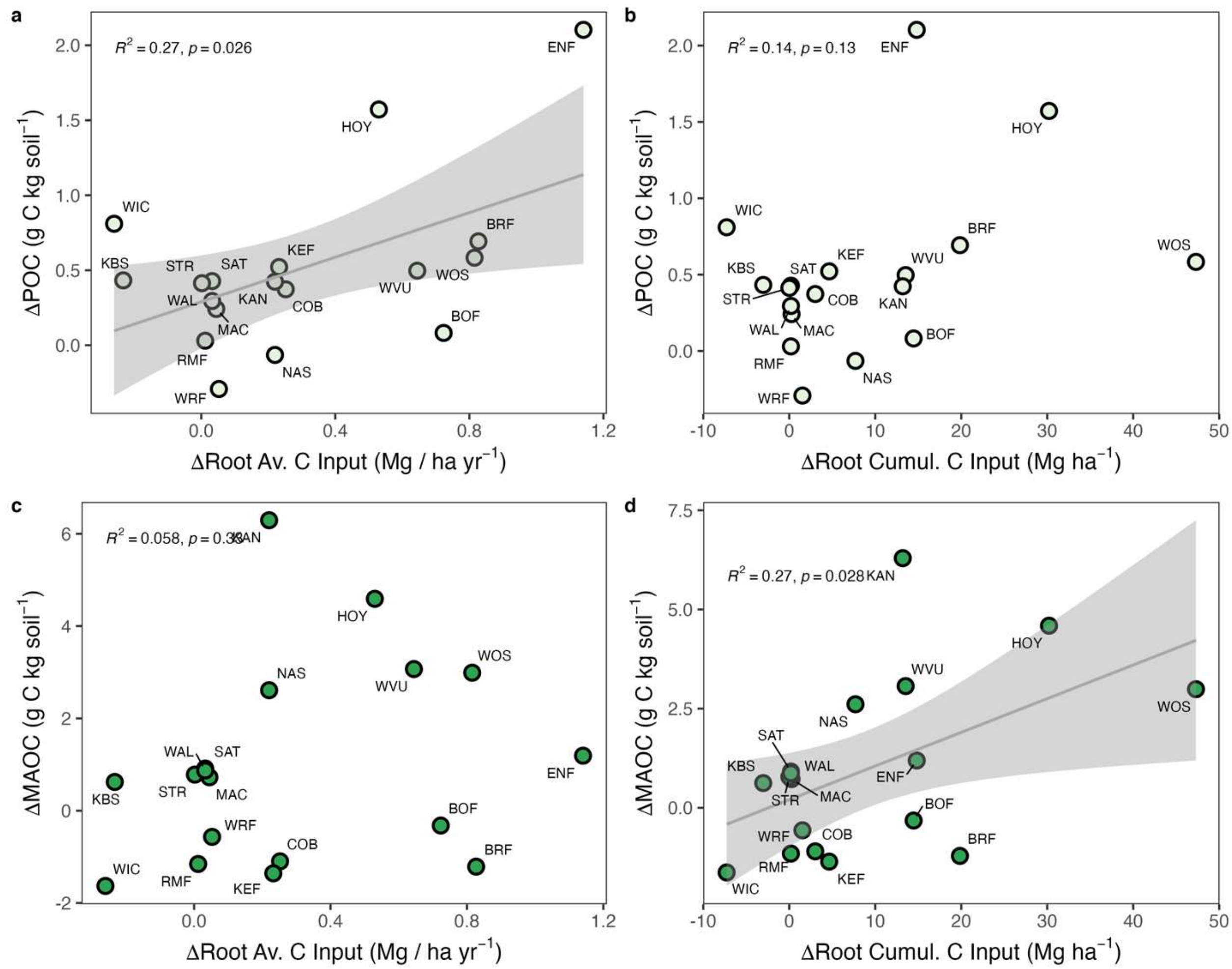

Figure 5. Effect of change (Δ) in root C inputs on Δ particulate organic carbon (POC; a,b) and Δ mineral associated organic carbon (MAOC; c,d) under regenerative vs. conventional management, for 0-20 or 0-15 cm (only WIC) soil depth. Panels a and c: Δ root C inputs expressed as cumulative for the trial (Mg / ha). Panels b and d: Δ root C inputs as annual averages (Mg / ha yr^{-1}). Gray lines represent simple linear regressions with 95% confidence interval; lines not plotted if p-value for the regression was greater than 0.05. Details for sites for NAS, KAN and WIC provided in SI Table 1; details for site all other site IDs (King et al., 2023) correspond to those in SI Table 2.

	Dependent variable: Δ MAOC (g C kg soil^{-1})
Δ Root Cumul. C Input	1.067*
	(0.51)
MAOC Sat. Def.	0.226
	(0.51)
Constant	0.962*
	(0.471)
Observations	18
R^2	0.275
Adjusted R^2	0.179
Residual Std. Error	1.998 (df = 15)
F Statistic	(df = 2; 15)
Note:	*p<0.1

Table 1. Multiple regression model of change (Δ) in mineral-associated organic carbon (MAOC) with regenerative vs. conventional management as mediated by Δ root C inputs or site-average MAOC saturation deficit. Both predictor variables scaled before regression.

4. Discussion

4.1 POC at any given time does not clearly relate to SOC change at that same time

Although POC has often been positioned as a leading indicator of change in SOC (Culman et al., 2012; Eze et al., 2023), the data in this study showed that absolute increases in POC are not proportional to absolute increases in SOC (Fig. 2a). Instead, increases in POC were constrained around a narrower range while SOC change varied more widely due to variability in MAOC change (Fig. 2b). These results demonstrate that absolute change in POC at any given time cannot be translated to a change in SOC at the same time, thereby limiting the utility of POC as an indicator of SOC change. An alternate interpretation of POC as indicator of SOC change, however, would be that measuring POC within a short time frame after regenerative management is implemented could predict SOC change over the longer term. This 'early indicator' interpretation of POC change could not be conclusively evaluated by the data available for this synthesis, which lacked the necessary temporal resolution across multiple studies. Nevertheless, the possibility that early changes in POC may predict eventual changes in SOC with consistent management cannot be ruled out by these data. As we discuss below, changes in POC were proportional to short-term increases in C inputs, and changes in MAOC were proportional to long-term changes in C input. It would therefore be consistent with these findings that a management system with a larger increase in C inputs could affect a larger initial increase in POC, which if implemented consistently could align over time with larger increases in MAOC than under regenerative management with smaller increases in C inputs. We emphasize that this hypothesis requires further testing to evaluate.

4.2 Average annual C inputs drive POC accumulation in response to regenerative management

Increases in POC with regenerative management were explained by average annual increases in root C inputs to soil (Fig. 5). This finding aligns with known importance of root C inputs for POC formation (Austin et al., 2017; Poirier et al., 2018; Puget and Drinkwater, 2001) and adds important nuance to the emerging understanding that POC is mediated more by drivers of decomposition than by C inputs across climatic gradients, as shown by limited relationships between C inputs and POC pools (Hansen et al., *in review*; King et al., 2023). When comparing within research sites, as in this study, however, climatic controls on decomposition are more similar than across global or regional comparisons (Famiglietti et al., 2008). When these climatic controls on decomposition are held constant, the significance of C inputs for POC accumulation emerges (Fig. 5, $p < 0.05$). Thus, while a positive relationship between C inputs and change in POC was observed for roots, we also observed a negative relationship between change in POC and change in shoot C inputs, likely due to a negative correlation between root and shoot C inputs (Fig. 4). This correlation was due to aboveground biomass removal in perennial forage and bioenergy systems that also increased root inputs (Anderson-Teixeira et al., 2013; Bolinder et al., 2007; Masters et al., 2016). Despite a clear signal of root C inputs increasing POC pools within sites, this change was constrained in magnitude (Fig. 2).

The causes of a limited, if distinct, accumulation of POC under regenerative agricultural management remain open to speculation. Natural grasslands may be considered a point of comparison, as they generally maintain larger POC levels (Cambardella and Elliott, 1992). Regenerative practices generally effect a modest increase in root C inputs compared to natural grasslands: in this study, average increase in root C was 0.34 Mg C ha yr^{-1}. In comparison, a grassland may increase root C by more than 1 Mg C ha^{-1} yr^{-1} compared to conventional annual grain systems (Dietzel et al., 2015; DuPont et al., 2014). Some perennialized systems in this study approached this magnitude of increase (Masters et al., 2016) but nevertheless showed little increase in POC. This limited POC increase despite some increase in root C inputs, combined with the response of POC to short-term rather than cumulative-for-the-trial increases in root C, together indicate a high rate of POC decomposition preventing its accumulation. Constraints on the accumulation of POC are further suggested by the non-response of POC fraction to extended duration of regenerative management (Hu et al., 2023). The rapid decomposition of POC in agricultural systems may arise from lower soil moisture than in native vegetation promoting decomposition, e.g., in tile drained systems (Schultz et al., 2007), or from a lack of aggregate protection (King et al., 2019); even in the largely no-till systems from King et al. (2023), aggregation would be expected to be lower than in native vegetation due to correspondingly lower SOC (King et al., 2019). Although agricultural systems receive greater inorganic N inputs than native vegetation, N fertilizer is generally reported to suppress mineralization of SOC (Mahal et al., 2019; Zang et al., 2016), although this effect may be moderated by other factors (Averill and Waring, 2018). The precise mechanisms causing low POC in agricultural soils require further testing.

4.3 Carbon inputs, not saturation deficit, limit MAOC accumulation in response to regenerative management

The concept of MAOC saturation has been used to explain a limited effect of management on MAOC pools at some sites (Antonio et al., 2022; Chung et al., 2008). Here, however, we observed that increases in MAOC with regenerative compared to conventional management were not clearly constrained by MAOC saturation deficit (Fig. 3, SI Fig. 2). This absence of influence of MAOC saturation deficit on MAOC accumulation may be due to all soils, regardless of management, having MAOC saturation deficits, determined by difference from a theoretical maximum (saturation) based on silt + clay content (Georgiou et al., 2022). Soils with a saturation deficit have previously been posited as being less influenced by saturation dynamics than soils at saturation (Stewart et al., 2007). Our results indicate that the response of MAOC to cover cropping and perennial cropping is constrained instead by crop C inputs, specifically by root C inputs. The importance of C inputs for SOC has been shown before, both between sites (King et al., 2023; Luo et al., 2017) and within sites (King and Blesh, 2018; Kong et al., 2005; Novelli et al., 2017; Virto et al., 2012). Here, we offer the first distinction of C inputs into root and shoot and simultaneous fractionation of SOC into POC and MAOC across a regional collection of sites. Using these data, we show that quantifying C inputs as cumulative increase in root C for the trial due to management allows the effect of C inputs on MAOC to be discerned (Fig. 5, Table 1).

Previous reports of the non-response of MAOC to regenerative management may be explained by lack of root C inputs. For instance, Rui et al. (2022) emphasize that regenerative management practices did not increase soil C stocks. Based on total C input estimations from the same site (Sanford et al., 2012), we find that the regenerative grain + cover crop treatment decreased C inputs compared to a conventional continuous corn (Fig. 4), a probable cause for the lack of MAOC response at this site. The variability observed in our study for the relationship between cumulate-for-the-trial increases in root C inputs and increases in MAOC could be attributable to several factors, including differences in C input quality or microbial communities, which were not assessed in this study, or to differences in soil matrix protective capacity that were not described by a traditional silt + clay-based MAOC saturation deficit.

Increasing evidence demonstrates that features of the soil matrix including calcium, magnesium, aluminum, and iron more closely reflect MAOC storage capacity than soil texture alone (King et al., 2023; Rasmussen et al., 2018; Rowley et al., 2021). Future work may examine how these features of the soil matrix can be synthesized to describe a maximum MAOC storage capacity. At the U.S. sites in this study, we demonstrated the potential of a matrix capacity index (MCI) that synthesized oxalate-extractable iron, aluminum, and exchangeable calcium and magnesium to predict MAOC. However, we chose not to use this MCI to calculate an MCI-based saturation deficit, given limitations in available data. Normally when calculating a saturation deficit, as with silt + clay, sites with natural vegetation are used to demonstrate optimum MAOC levels at a given level of silt + clay (Feng et al., 2013; Georgiou et al., 2022). As sites in our King et al., (2023) study included agricultural systems and not native vegetation, we did not calculate an MCI-based saturation deficit. Additional study is necessary to explore the concept of an MCI-based saturation deficit and the extent to which it can illuminate MAOC response to regenerative management.

4.4 Strategies for managing and studying MAOC and POC

The analyses presented here highlight the need for approaches we think will accelerate our ability to understand and manage SOC:

- *Focusing on C inputs for MAOC accumulation.* When identifying fields as targets for regenerative management, the data presented here do not justify seeking out soils having MAOC levels further below a silt + clay-defined saturation, as the MAOC response was not clearly constrained by a silt + clay-defined saturation deficit. In fact, in the arable soils studied here, even soils under long-term regenerative management were often far from the silt + clay-defined MAOC saturation. Given this 'saturation deficit' in MAOC even under regenerative management, the data shown here do not clearly support the use of silt + clay defined saturation maxima to delineate a level of MAOC that can be achieved in primarily arable systems. Instead, the data indicate an imperative to increase cumulative C inputs over time for MAOC accumulation. Although studying saturation deficit alone may provide insights, investigating the upper limit of increases in C inputs, especially root C inputs, in agricultural systems may more accurately constrain MAOC accumulation potentials.

- *Blue-sky thinking about POC accumulation strategies*. There may be specific features of regenerative management and environment that could enhance POC accumulation: larger, consistent increases in root C inputs or ligneous C inputs, combined with periodic restrictions on decomposition through flooding (as in some native grasslands (Schultz et al., 2007)); amending soils to recreate the highly active soil matrix in volcanic soils (Zagal et al., 2013), or the cultivation of fungal-dominated microbial communities (Malik et al., 2016). Investigating these strategies further may aid in developing agricultural systems able to accrue both MAOC and POC.

- *Towards a comprehensive understanding of POC and MAOC dynamics*. Our work indicates several avenues of needed study to accelerate our understanding of POC and MAOC responses to regenerative management. Linking updated concepts of soil matrix C storage capacity with C input quantification will likely be needed to further resolve the accumulation of MAOC in agricultural systems. Understanding mechanisms of root C retention in MAOC and the influence of C input chemistry (Zhang et al., 2022) on POC and MAOC retention will also be valuable. Studying additional regenerative practices, such as conversion from conventional tillage to no-tillage, use of manure or compost inputs, livestock integration, or intercropping will provide a more complete view of moderators of regenerative management. Time-resolved, and subsoil measurements of SOC will also accelerate our understanding of the dynamics of SOC response to regenerative management.

5. Conclusions

The absolute response size of the POC pool to management was usually less than that of MAOC and did not clearly correspond to changes in the SOC pool. The response of MAOC to management was highly variable across sites and the silt + clay-defined MAOC saturation deficit did not clearly constrain MAOC response to management. Instead, MAOC response to management was mediated by cumulative-for-the-trial increases in root C inputs. In contrast, POC response to management was mediated by average annual increases in root C inputs, reinforcing our understanding of this fraction as a fast-turnover SOC pool but also highlighting limited potential for accumulation of POC under current portfolio of regenerative management practices.

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