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Important constraints on soil organic carbon formation efficiency in subtropical and tropical grasslands

Elaine Mitchell[1] | Clemens Scheer[1] | David Rowlings[1] | Francesca Cotrufo[2] | Richard T. Conant[2] | Peter Grace[1]

[1]Queensland University of Technology, Brisbane, Queensland, Australia
[2]Colorado State University, Fort Collins, Colorado, USA

Correspondence
Elaine Mitchell, Queensland University of Technology, 2 George Street, Brisbane, 4000 Qld, Australia.
Email: E5.mitchell@qut.edu.au

Funding information
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Abstract

More than 10% of Australia's 49 M ha of grassland is considered degraded, prompting widespread interest in the management of these ecosystems to increase soil carbon (C) sequestration—with an emphasis on long-lived C storage. We know that management practices that increase plant biomass also increase C inputs to the soil, but we lack a quantitative understanding of the fate of soil C inputs into different soil organic carbon (SOC) fractions that have fundamentally different formation pathways and persistence in the soil. Our understanding of the factors that constrain SOC formation in these fractions is also limited, particularly within tropical climates. We used isotopically labelled residue (^{13}C) to determine the fate of residue C inputs into short-lived particulate organic matter (POM) and more persistent mineral-associated organic matter (MAOM) across a broad climatic gradient (ΔMAT 10°C) with varying soil properties. Climate was the primary driver of aboveground residue mass loss which corresponded to higher residue-derived POM formation. In contrast, MAOM formation efficiency was constrained by soil properties. The differential controls on POM and MAOM formation highlight that a targeted approach to grassland restoration is required; we must identify priority regions for improved grazing management in soils that have a relatively high silt+clay content and cation exchange capacity, with a low C saturation in the silt+clay fraction to deliver long-term SOC sequestration.

KEYWORDS
carbon sequestration, climate, fractionation, mineral-associated organic matter, particulate organic matter, soil carbon, soil fertility, soil management practices, soil properties

1 | INTRODUCTION

More than 10% of Australia's 49 M ha of grassland is considered degraded (Conant & Paustian, 2002) prompting widespread interest in the management of these ecosystems to increase soil carbon (C) sequestration, while improving ecosystem services (Asner et al., 2004; Conant et al., 2017; Lipper et al., 2010; Ryals et al., 2014). We know that management practices that increase plant biomass (e.g. reduction in grazing intensity) also increase C inputs to the soil (Conant & Paustian, 2002) but we lack a quantitative understanding of the fate of soil C inputs into different SOC fractions (long-lived vs. short-lived SOC) that have fundamentally different formation pathways and persistence in the soil (Cotrufo et al., 2015). Our understanding of the factors that constrain SOC formation from increased C inputs, such as climate and soil properties, is also inadequate—particularly within tropical climates. A lack of studies at tropical latitudes limits our ability to inform management strategies for SOC sequestration in these unique environments, while also restricting the modelling precision of global and regional C dynamics under a changing climate.

At a global, as well as broad (sub)regional scales, climate is considered to be the key driver of SOC formation, with warmer and wetter conditions increasing both C input and SOC decomposition through their control on net primary productivity and microbial decomposition respectively (Wiesmeier et al., 2019). Once C input is incorporated within the SOC pool, the drivers of SOC decomposition become more complex due to the interaction of C with the mineral soil matrix (Cotrufo et al., 2010). The properties of the soil matrix, reflected by mineralogy and physical structure, can 'protect' SOC from the soil microbial community, which reduces the probability and therefore the rate of decomposition (Dungait et al., 2012; Lehmann & Kleber, 2015; Schmidt et al., 2011). An established hypothesis is that silt and clay content (i.e. the mineral fraction) principally determines SOC 'protection' or stabilization by promoting the sorption of organic matter to mineral surfaces and aggregate formation (Baldock & Skjemstad, 2000; Kögel-Knabner et al., 2008; Krull et al., 2003; Six & Paustian, 2014). While some mineral-associated organic matter (MAOM) can turnover on short timescales (Jilling et al., 2018), the majority of MAOM persists for hundreds or thousands of years before turning over (Lützow et al., 2006), thereby forming a functionally important pool for long-term SOC sequestration. While long-term SOC sequestration is preferable in terms of greenhouse gas mitigation, short-lived or labile fractions of SOC (with residence times of months to years) are also essential for the provision of energy and nutrients to microbiota and plants (Lavallee et al., 2020). Labile SOC largely exists as particulate organic matter (POM), which remains unprotected in the mineral soil and readily lost from the soil system as CO_2 via microbial respiration.

In this study, we evaluate the effect of climate and soil properties on residue decomposition and 'new' residue-derived MAOM and POM formation in tropical grasslands. Residue placement was manipulated (surface applied vs. incorporated within soil) to provide a greater process-level understanding of how the placement of residue effects decomposition and stabilization processes through greater proximity to reactive mineral surfaces. Embedding residue within the soil can also potentially mimic the impact of animal trampling which has been reported to enhance the physical break down and incorporation of plant residue in the mineral soil—thereby increasing plant allocation belowground (Sanjari et al., 2008; Schuman et al., 1999; Southorn, 2002; Wei et al., 2021). In turn, grazing management strategies such as time-controlled grazing can affect the distribution and intensity of trampling (Teague et al., 2008).

We hypothesized that climate would dominate residue decomposition, with greater decomposition occurring at warmer wetter sites. We expected greater residue decomposition to translate into greater 'new' residue-derived SOC formation from physical fragmentation and incorporation of residue, and the leaching of soluble plant components (sensu Cotrufo et al., 2015). In contrast, the fate of residue C inputs in MOAM vs. POM will depend on the properties of the mineral soil matrix, with finer textured soils (with a greater surface area and charge density) promoting greater efficiency of MAOM formation. Residue incorporation within the soil will compound the effect of soil properties to increase MAOM formation due to the greater proximity of substrate to the soil microbial community and reactive mineral surfaces (Mitchell et al., 2018). An understanding of the constraints on POM and MAOM formation in tropical grasslands will help to identify priority regions for grassland restoration efforts that will have the greatest impact on long-lived SOC.

2 | MATERIALS AND METHODS

The study was conducted along a 3600 km north–south transect spanning ~15° latitude in north-eastern Australia. From north to south, the following sites were used: (1) Kidman Springs, a semi-arid site in the Northern Territory and four subtropical sites; (2) Brigalow; (3) Samford; (4) Crows Nest; and (5) Tamworth (Table 1). We characterized all soils as per Mitchell et al. (2020).

Annual precipitation and mean annual temperature (MAT) were used as climatic indicators. Climate (temperature and precipitation) varied along a gradient from semi-arid in the north (Kidman) to subtropical in the south (Tamworth). MAT ranged from 28°C (Kidman Springs) to 16°C (Tamworth). There was a difference of ~650 mm in annual precipitation between the site of highest (Samford, 1102 mm) and lowest annual precipitation (Tamworth, 448 mm). Soil C concentration ranged from 1.3% to 3.8% and soil sand content ranged from 22% to 70%.

Surface air temperature and soil temperature (at a depth of 10 cm) were measured using a data logger (Onset; HOBO) over 12 months. Rainfall data were used from the nearest weather station, with rain gauge collection at the Crows Nest and Samford sites. Soil bulk density was determined on four replicates at each site by the soil core (10 cm) method.

2.1 | Isotopically labelled residue production and analyses

'New' residue-derived C in soils was traced using ^{13}C-labelled Rhodes grass tops (*Chloris gayana*). The grass was grown within a continuous labelling chamber under controlled conditions, detailed in the study by Mitchell et al. (2016). Once the Rhodes grass had reached maturity, the aboveground biomass was cut at 10 cm from the soil surface. This biomass was then air-dried, cut to 10 cm pieces, homogenized and used for the decomposition experiment as described below. Residue moisture content was measured on three oven-dried (60°C) subsamples for dry weight correction. The oven-dried subsamples were mill-ground and used for the determination of C (44%) and N (3.1%) concentrations and the stable C isotope composition (^{13}C = 3.8 atom %) by elemental analysis and isotope ratio mass spectrometry (EA-IRMS; Sercon Limited).

2.2 | Experimental design

This experiment used a well-established design (Mitchell et al., 2016, 2018, 2020). Briefly, the air-dried isotopically labelled residue was

TABLE 1 Selected site and soil (0–10 cm) properties for the study sites distributed along a north–south temperature transect from Kidman Springs, NT (16°S) to Tamworth, NSW (31°S)

Site							Soil					
Name	Biome[a]	Latitude	Longitude	Annual precipitation (mm)	Mean annual temperature (°C)	Climate decomposition index (CDI)	Type[b]	Silt+clay (%)	Sand (%)	Total C (%)	CEC (cmol/kg)	pH
Kidman, NT	Semi-arid tropical	16.07°S	130.55°E	946	27	0.63	Vertosol	57	43	1.2 (±0.16)	34	7.1
Brigalow, QLD	Subtropical	24.34°S	149.58°E	628	22	0.74	Vertosol	36	64	2.4 (±0.31)	16	6.6
Samford, QLD	Subtropical	27.22°S	152.54°E	1102	20	0.71	Chromosol	30	70	1.5 (±0.13)	9	5.4
Crows Nest, QLD (clay)	Subtropical	27.16°S	152.02°E	665	17	0.65	Vertosol	81	19	3.7 (±0.68)	24	5.3
Crows Nest, QLD (loam)	Subtropical	27.16°S	152.02°E	665	17	0.65	Dermosol	69	31	3.3 (±0.12)	19	5.1
Crows Nest, QLD (sand)	Subtropical	27.16°S	152.02°E	665	17	0.65	Chromosol	41	59	1.9 (±0.14)	11	5.1
Tamworth, NSW	Subtropical	31.05°S	150.55°E	448	16	0.6	Vertosol	75	25	2.7 (±0.12)	51	6.7

Abbreviation: CEC, cation exchange capacity.

[a] Köppen Climate Classification System.

[b] The Australian Soil Classification (Isbell, 1996).

placed on the soil surface at each site (Spring 2014 before the onset of summer wet conditions), inside plastic collars (10 cm in diameter, 15 cm height) which were inserted to a depth of 10 cm (with 5 cm remaining above the soil surface). Aboveground vegetation was previously removed from inside the collars by clipping. Collars were covered by a 2-mm polyethylene mesh to prevent the loss of labelled residue or input of external plant material. Residue was added to the microcosms at a rate of 10 t ha^{-1} and was either applied to the soil surface (SUR) or incorporated within the top 10 cm of soil (MIX). A Control was established where no residue was added.

2.3 | Residue and soil collection

After 12 months, all recognizable residue remaining on the soil surface was removed by hand, dried at 60°C, weighed and pulverized for further analyses. Soil was sampled by excavating the intact plastic cores to a depth of 10 cm and by sampling further to a depth of 20 cm below the plastic core. All soil cores (0–10, 10–20 cm) were placed in plastic bags and kept (4°C) until processed within a few days from sampling. Surface soils (0–10 cm) were fractionated, while bulk soil measurements were conducted on the 10–20 cm soil samples.

Surface soils (0–10 cm) were sieved to 2 mm prior to fractionation. Any organic matter >2 mm in the 0–10 cm layer was removed and analysed as part of the residue fraction (i.e. residue remaining on the soil surface in SUR and within the soil profile for MIX). A representative subsample from each soil sample was dried in an oven at 60°C, pulverized and used for elemental and isotopic analyses.

Soils were fractionated by size and density to separate its primary components, using the same process described in the study by Mitchell et al. (2018), following the approach of Zimmermann et al. (2007). SOM was partitioned into (1) POM, and (2) mineral associated organic matter (MAOM). Mineral-associated organic matter consisted of two fractions: (i) OM encapsulated within microaggregates (SA >53μm), and (ii) silt and clay-associated OM (SC <53 μm).

Briefly, 30 g of soil (<2 mm) was added to 150 ml water and dispersed using a weak ultrasonic treatment (output energy of 22 J ml^{-1}) to disrupt macroaggregates, leaving more stable microaggregates intact (Amelung & Zech, 1999). This procedure is based on the assumption that low-energy sonication should act to preserve fragile POM from fragmenting and spreading within the different size fractions (Stemmer et al., 1999). The dispersed suspension was then wet sieved over a 53-μm mesh sieve until the rinsing water was clear. The fraction >53 μm, containing the sand and microaggregates (SA) together with POM, was dried at 40°C and weighed. POM was isolated by stirring the fraction >53 μm with sodium polytungstate (SPT) at a density of 1.8 g cm^{-3}. The mixture was centrifuged at 1000 *g* for 15 min and the light fraction (POM) was decanted, washed with deionised water to remove all SPT, dried at 40°C and weighed. The suspension <53 μm was filtered through a 0.45-μm aperture nylon mesh and the material >0.45 μm (silt and clay fraction, SC) was dried at 40°C and weighed. All fractions were pulverized and analysed for C and N elemental and isotopic concentrations by EA-IRMS, as stated above for residue. In this study, we analysed the SA and the SC fraction together as MAOM. They were analysed together as MAOM as we assumed both fractions contributed to long-lived SOC; the SA fraction contained POM fragments occluded within microaggregates, while the SC fraction contained OM associated with mineral surfaces.

2.4 | Data analysis and statistics

The residue-derived C contribution to the bulk soil and SOM fractions was assessed for the residue-added plots and compared to the control plots, following the same procedure established in the study by Mitchell et al. (2018). The isotopic mixing model was applied as follows:

$$f_{\text{residue}} = \frac{(\delta_{\text{soil}} - \delta_{\text{control}})}{(\delta_{\text{residue}} - \delta_{\text{control}})},$$

where f_{residue} is the fraction of the residue-derived C contributing to the bulk soil or SOM fraction. The δ_{soil} is the δ^{13}C of the specific bulk soil or SOM fraction. The δ_{control} is the δ^{13}C of the bulk soil or SOM fraction from the control plots (average value across all respective bulk soil or SOM fractions used). The δ_{residue} is the δ^{13}C of the initial applied residue. The amount of residue-derived C in all C pools was obtained by multiplying the f_{residue} values to corresponding C pools.

ANOVA was used to determine the statistical significance of residue-derived C recovery in different C pools, with significance determined as $p < 0.05$. The efficiency of MAOM formation was determined as a percentage of residue C decomposed relative to the amount of MAOM-C formed (MAOM-C formation/residue C decomposed *100; Cotrufo et al., 2015). The saturation deficit was determined as the difference between the theoretical SOC saturation value and the measured SOC in the fine fraction (g silt+clay C kg^{-1} soil). The theoretical value of C saturation in grasslands was calculated according to the upper C limit in grassland soils defined by Six et al. (2002).

A multiple linear regression model was used to determine the relationship between explanatory variables for: (1) climate (annual precipitation and MAT); (2) soil properties (pH, %C, cation exchange capacity [CEC] and % silt and clay); and (3) residue placement, and dependent variables. Dependent variables were residue-derived C in different C compartments (residue C, POM, MAOM). The percentage of the model variance of the dependent variable explained by each explanatory variable was determined using the Relative Importance Test, using '*relaimpo*' package in R 3.3.1 (R Core Team, 2016). This approach deconstructs the r^2 value in the multiple regression which contains correlated regressors. All residuals were checked for normality and homogeneity of variance. Statistical significance was determined at $p < 0.05$.

A structural equation model was used to identify the relationship between the explanatory and dependent variables. The three latent variables of climate, soil properties and placement represent the observed variables (or indicators) described above. The loading of each latent variable was calculated as the correlation between a latent variable and its indicators. An iterative algorithm was used to estimate the loadings until the convergence of loadings was reached to maximize the explained variances of the dependent variables. A non-parametric bootstrapping was used to estimate the precision of the parameter estimates. The significant pathway coefficients were determined using 95% bootstrap confidence intervals, with non-significant pathways removed. The following three potential pathways were considered in a hypothesis-oriented model (as presented in the introduction): firstly, that climate (temperature and precipitation) will accelerate the transfer of C from the residue to SOM; secondly, that soil properties will primarily influence MAOM formation; and, thirdly that residue placement within the mineral soil will accelerate residue decomposition and increase C content in all SOC pools.

3 | RESULTS

3.1 | Residue C mass loss

The greatest amount of residue C mass loss occurred at the warmest site with a relatively high rainfall (Figure 1). When residue was placed on the surface (SUR), only 12% (±1.4) of residue C remained on the soil surface after 12 months of in situ decomposition at Kidman, in comparison to a significantly greater amount ($p < 0.01$) (58% ± 3.7) at Tamworth (the coldest and driest site; Figure 1a). Residue incorporated within the soil profile (MIX) resulted in a significantly greater amount of residue C loss ($p < 0.05$; ~35% greater in MIX in comparison to SUR; Figure 1b). Kidman (semi-arid site) was the only site where residue C mass loss in MIX was not significantly greater than SUR treatment.

Examining the relative importance of predictor variables in determining residue C mass loss revealed that residue placement (SUR vs. MIX) was the most important predictor (accounting for 54% of model variance; Figure 2a,d). Climatic factors (precipitation and temperature) together accounted for 39% of model variance. In contrast, soil properties were not significant in determining residue C mass loss. Across all seven experimental sites, there were variations of up to 2.5-fold in soil texture, fourfold in CEC and 2 pH units, but these variables had little discernible effect on residue C remaining. The overall model fit is shown in Figure 2d (model explained 83% of variance, $r^2 = 0.82$).

3.2 | Residue-derived SOC formation

The greatest amount of residue-derived SOC (% of added residue found in the SOC pool) was at the warmest site of Kidman (MAT = 27°C; 24% residue-derived SOC in SUR, 37% of residue-derived SOC in MIX). This was significantly greater ($p < 0.05$) than SOC formation at a relatively cooler and drier site (MAT ~17°C) with a relatively high sand content where there was only 5% of residue-derived SOC.

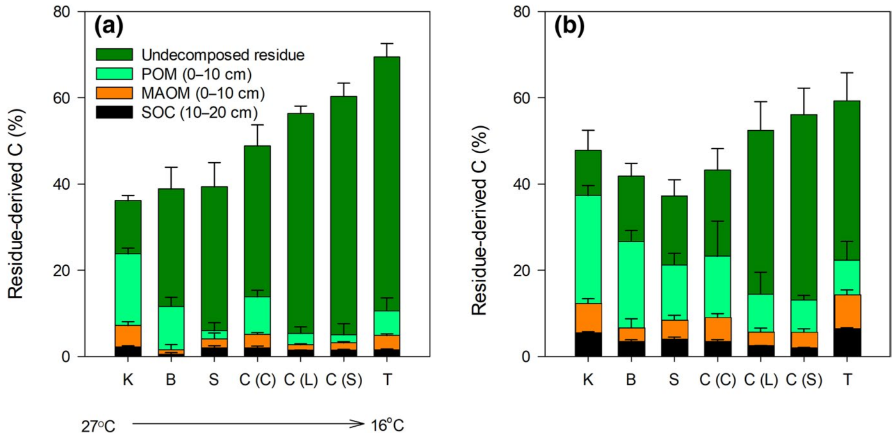

FIGURE 1 Per cent recovery of initial residue C incubated either (a) on the soil surface or (b) mixed within the top soil. Recovery is separated for the top soil (0–10 cm) in undecomposed residue >2 mm, particulate organic matter (POM) and mineral-associated organic matter (MAOM), while for the subsoil (10–20 cm) is in bulk soil organic carbon (SOC). Sites are displayed along the temperature gradient: Kidman (K, mean annual temperature [MAT] 27°C), Brigalow (B, MAT 22°C), Samford (S, MAT 20°C), Crows Nest (C = clay), Crows Nest (L = loam), Crows Nest (S = sand; MAT 17°C) and Tamworth (T, MAT 16°C). Data are averages with standard errors as bars (*n* = 4)

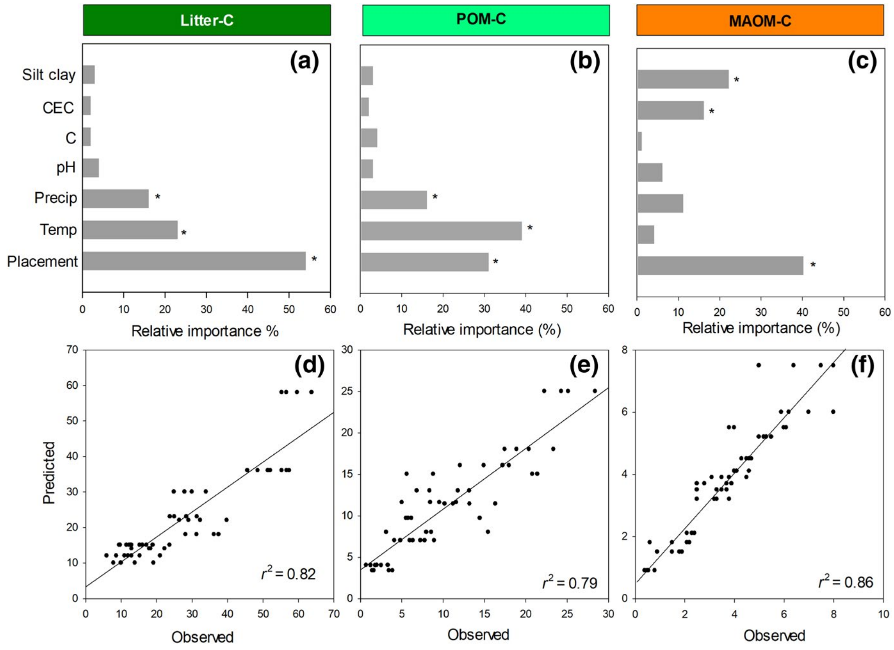

FIGURE 2 The relative importance of predictor variables (% silt clay, cation exchange capacity, C, pH, Precip [precipitation], Temp [temperature] and placement) in explaining (a) residue C remaining, and new residue-derived C in (b) POM and (c) MAOM after 12 months of incubation at seven study sites. The relative importance of each variable is represented as a % contribution to the model fit. The model fit (predicted values vs. observed values) are shown in (d)–(f) with the overall model fit reported as r^2 value. *indicates significant contribution of variable to model fit ($p < 0.05$)

When SOC content was fractionated for POM and MAOM content, it revealed that the warmest and wettest sites, with the greatest residue-derived SOC, also corresponded to the sites with the greatest residue-derived POM. The greatest residue-derived POM accrual occurred at the warmest site of Kidman, where 21% (±2.1) of residue C was recovered in POM (average across MIX and SUR treatment) compared with only 7% (±0.8) at the coldest and driest site. At the warmest and wettest site, residue-derived POM accumulation accounted for the greatest *amount* of residue-derived SOC accrual, as well as for the greatest *proportion* of residue-derived SOC accrual. For example, residue-derived POM accumulation accounted for 70% and 87% of residue-derived SOC at Kidman and Brigalow respectively (the two warmest sites), in comparison to only 53% of residue-derived SOC accumulation at the coldest driest site.

The relative importance of regression model revealed that climate was the dominant factor determining the amount of residue-derived POM, accounting for 55% of model variance (Figure 2b). The placement of residue was also a dominant predictor (accounting for 31% of model variance), with the incorporation of residue resulting in an average ~threefold increase in the amount of residue-derived POM accumulation (Figures 1b and 2b,c).

In contrast to the POM and residue C remaining undecomposed, MAOM formation did not display an obvious trend along the climatic gradient, with no significant difference in MAOM formation between the extremes of the climatic gradient. The placement of residue was the strongest predictor of residue C recovered in MAOM (40% of model variance), followed by soil properties (45% of model variance), with silt+clay and CEC being the significant predictors (Figure 2c,f).

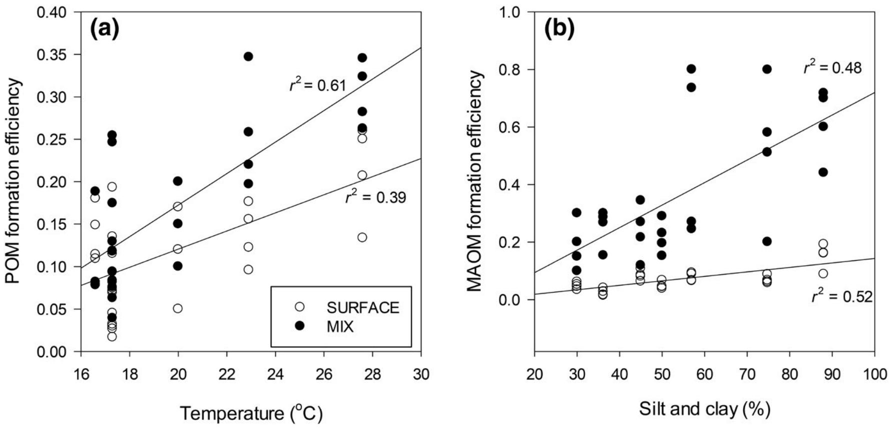

FIGURE 3 The relationship between the efficiency of mineral-associated organic matter (MAOM) formation (residue-derived C in MAOM/residue C mass loss) and (a) silt and clay content (%) and (b) soil saturation deficit (g silt+clay C/theoretical maximum of silt+clay C) as defined by Six et al. (2002)

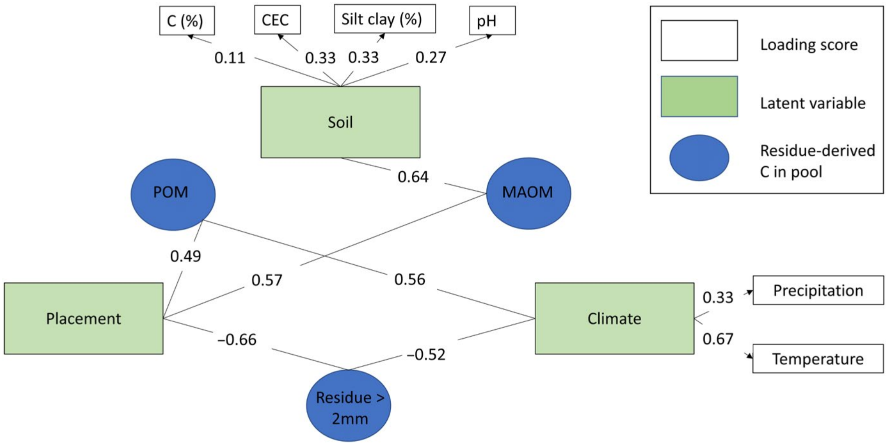

FIGURE 4 A schematic representation of the path analyses used to identify the controls on the fate of residue-derived C in different C pools (blue circles: residue, particulate organic matter [POM] and mineral-associated organic matter [MAOM]). Latent variables (green rectangles) were constructed for soil (%C, cation exchange capacity [CEC], silt and clay%, pH) and climate (temperature and precipitation) using loading scores (clear rectangles) to account for the range of measured indicators. Only significant pathways ($p < 0.05$) are shown

The efficiency of MAOM formation (MAOM-C formation/residue C decomposed) was used to examine the efficiency by which residue C loss was converted to stable SOC (in effect normalizing data for the amount of residue decomposed). The relationship between residue placement, silt+clay content and MAOM formation can be seen in Figure 3a. The efficiency of MAOM formation significantly increased ($p < 0.05$) with greater silt+clay content and with residue incorporation. To further analyse the effect of silt+clay content on 'new' residue-derived MAOM formation, we calculated the saturation deficit of the silt+clay fraction (i.e. the amount of existing C in the silt+clay fraction in comparison to its potential C storage given its silt+clay content; Six et al., 2002). The soils with the greater saturation deficit displayed a significantly greater ($p < 0.05$) efficiency of MAOM formation (Figure 3b).

3.3 | Drivers of the distribution of residue-derived SOC in POM and MAOM

We used structural equation modelling to test the overall relationship between climate, soil properties and residue placement on residue C dynamics (Figure 4). Two latent variables were established for climate (indicators: temperature and rainfall) and soil properties (indicators: pH, silt and clay%, CEC, C) and residue placement was the third variable (surface vs. incorporated). Non-significant pathways were removed to identify the dominant drivers. The model demonstrates that climate dominates the residue mass loss and residue-derived POM (pathway coefficients = 0.52 and 0.56 respectively), while soil properties dominate residue-derived MAOM (pathway coefficients = 0.64; Figure 4). Residue placement was significant in determining the outcomes in all C pools.

4 | DISCUSSION

Our findings highlight that soil properties act as a major constraint on the formation of long-lived MAOM in tropical grassland soils. Therefore, we must prioritize SOC restoration efforts in areas that have a high long-lived C accumulation potential, namely areas with a high silt+clay content, a high CEC and a low existing C saturation in the silt+clay fraction.

A warmer and wetter climate resulted in greater residue mass loss and SOC formation, which is consistent with findings across gradients in other climatic zones (temperate to subarctic; e.g. Doetterl et al., 2015; Gregorich et al., 2017). Greater residue mass loss was correlated with greater POM formation, which formed the majority (~60%) of 'new' residue-derived SOC. In contrast, residue-derived MOAM formation (~40% of 'new' residue-derived SOC) was primarily determined by soil physical properties (silt+clay content and CEC), presumably due to the sorption of C to reactive mineral surfaces.

The C saturation of the silt+clay fraction also affected the accumulation of SOC as MAOM. MAOM formed with greater efficiency in soils with a greater saturation deficit. This means MAOM accumulated more efficiently in soils where there was a greater difference between measured MAOM-C content and the potential MAOM-C content derived from modelling (see Six et al., 2002). We were cautious in the interpretation of upper limit of C accumulation as these values were derived from temperate grassland soils meaning that further research is required to define these limits in tropical soils. Greater MAOM formation occurred in soils with a greater saturation deficit presumably due to the greater availability of mineral surfaces for sorptive protection of organic matter, which can protect C from decomposition, even if some of the C compounds are labile or young in age (Cotrufo et al., 2013; Schmidt et al., 2011). In short, there is limited potential for SOC restoration efforts in soils close to C saturation in the silt +clay fraction as there is a greater probability that C inputs—particularly as labile dissolved organic C—will be mineralized as they percolate down the soil column due to lack of available mineral surfaces for sorptive protection (Abramoff et al., 2021).

Although this study did not analyse mineralogical properties, an in-depth study at the Crow Nest site (using the same experimental set-up) demonstrated the importance of mineralogical properties in sorptive protection of SOC. Soils with a similar clay content (~30%) but contrasting mineralogical properties (2:1 smectite dominated vs. 1:1 kaolinite dominated) displayed significantly different MAOM accumulation; 2:1 smectite-dominated clays accumulated a significantly greater amount of residue-derived SOC in the initial 3 months—which was attributed to the leaching of labile C components and adsorption to mineral surfaces in the early stages of decomposition (Mitchell et al., 2018, 2020).

The study confirmed that aboveground inputs contribute a relatively small amount to SOC, and that SOC restoration efforts should focus more on belowground inputs via incorporation or root inputs. After 1 year of in situ decomposition, ~4% (±1.3) of initial residue C was converted to MAOM-C and ~11% (±3.6) to POM, highlighting that aboveground inputs preferentially supply the shorter lived POM pool. Research has demonstrated the primacy of living root inputs (root exudates) in particular for SOC stabilization (e.g. Rasse et al., 2005), due to their favourable labile chemical composition, as well as their unique pattern of entry to the mineral soil, that is belowground C inputs are in closer proximity to microbes and reactive mineral surfaces (e.g. Sokol et al., 2019). The primacy of the belowground pathway for SOC formation was demonstrated by the fact that the MIX treatment significantly increased SOC formation at all sites (~threefold greater than surface applied residue). Given the likely primacy of the belowground pathway for SOC formation, sequestration efforts should focus on measures that increase the allocation of biomass belowground, for example crop genotypes that have a high amount of root biomass and/or rhizodeposition (Kell, 2012; Poirier et al., 2018), while more research is required on the role of grazing management in increasing the incorporation of aboveground biomass via hoof action.

This study has also highlighted some unique controls of residue decomposition in tropical climates that must be considered in the future SOC modelling efforts. The semi-arid site of Kidman was the only site where the decomposition of surface applied (SUR) and incorporated residue (MIX) progressed at similar rates, that is similar amounts of residue remaining after 12 months of decomposition. A similar rate of decomposition suggests that other factors were acting to accelerate the decomposition of surface residue which was most likely due to the enhanced operation of photodegradation, whereby relatively prolonged dry conditions combined with relatively higher doses of solar radiation acted to breakdown organic material, particularly plant structural components, for example lignin (Brandt et al., 2010). This promoted the direct loss of C to the atmosphere without being incorporated into the SOC pool (Austin et al., 2016) and resulted in a significant decline in SOC formation efficiency for the surface applied residue (39% of decomposed residue was converted to SOC in MIX, whereas only 25% of decomposed residue was converted to SOC in SUR). These findings illustrate the need for more data collection and model calibration within semi-arid tropical environments for C cycling estimates.

In conclusion, this study demonstrates that we should not adhere blindly to the principle that increasing C inputs will achieve gains in long-term SOC storage, as encoded in most computational models of terrestrial ecosystems. Long-lived SOC accumulation will be most effective in soils with a relatively high silt+clay content, a high CEC and that have the capacity to accumulate long-lived C in the silt+clay fraction in addition to the existing background C already stored as MAOM (i.e. high C saturation deficit). Decision-makers should target these soils as a priority in SOC restoration efforts. This will require the continued development of cost-effective approaches to soil C measurement and the identification of priority areas at a landscape level using a combination of remote sensing and modelling.

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CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

ORCID

Elaine Mitchell https://orcid.org/0000-0002-5210-8836
David Rowlings https://orcid.org/0000-0002-1618-9309
Francesca Cotrufo https://orcid.org/0000-0002-6191-8953
Richard T. Conant https://orcid.org/0000-0001-7315-2476

REFERENCES

Abramoff, R. Z., Georgiou, K., Guenet, B., Torn, M. S., Huang, Y., Zhang, H., Feng, W., Jagadamma, S., Kaiser, K., Kothawala, D., Mayes, M. A., & Ciais, P. (2021). How much carbon can be added to soil by sorption? *Biogeochemistry*, *152*(2–3), 127–142. https://doi.org/10.1007/s10533-021-00759-x

Amelung, W., & Zech, W. (1999). Minimisation of organic matter disruption during particle-size fractionation of grassland epipedons. *Geoderma*, *92*(1–2), 73–85. https://doi.org/10.1016/S0016-7061(99)00023-3

Asner, G. P., Elmore, A. J., Olander, L. P., Martin, R. E., & Harris, T. (2004). Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, *29*(1), 261–299. https://doi.org/10.1146/annurev.energy.29.062403.102142

Austin, A. T., Méndez, M. S., & Ballaré, C. L. (2016). Photodegradation alleviates the lignin bottleneck for carbon turnover in terrestrial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(16), 4392–4397. https://doi.org/10.1073/pnas.1516157113

Baldock, J. A., & Skjemstad, J. O. (2000). Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry*, *31*(7–8), 697–710. https://doi.org/10.1016/S0146-6380(00)00049-8

Brandt, L. A., King, J. Y., Hobbie, S. E., Milchunas, D. G., & Sinsabaugh, R. L. (2010). The role of photodegradation in surface litter decomposition across a grassland ecosystem precipitation gradient. *Ecosystems*, *13*(5), 765–781. https://doi.org/10.1007/s10021-010-9353-2

Conant, R. T., Cerri, C. E. P., Osborne, B. B., & Paustian, K. (2017). Grassland management impacts on soil carbon stocks: A new synthesis. *Ecological Applications*, *27*(2), 662–668. https://doi.org/10.1002/eap.1473

Conant, R. T., & Paustian, K. (2002). Potential soil carbon sequestration in overgrazed grassland ecosystems. *Global Biogeochemical Cycles*, *16*(4), 90-1–90-9. https://doi.org/10.1029/2001GB001661

Cotrufo, M., Del Galdo, I., & Piermatteo, D. (2010). Litter decomposition: Concepts, methods and future perspectives. In *Soil carbon dynamics: An integrated methodology* (January, pp. 76–90). https://doi.org/10.1017/CBO9780511711794.006

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, *8*(10), 776–779. https://doi.org/10.1038/ngeo2520

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology* *19*(4), 988–995. https://doi.org/10.1111/gcb.12113

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., Zagal Venegas, E., & Boeckx, P. (2015). Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geoscience*, *8*(10), 780–783. https://doi.org/10.1038/ngeo2516

Dungait, J. A. J., Hopkins, D. W., Gregory, A. S., & Whitmore, A. P. (2012). Soil organic matter turnover is governed by accessibility not recalcitrance. *Global Change Biology*, *18*(6), 1781–1796. https://doi.org/10.1111/j.1365-2486.2012.02665.x

Gregorich, E. G., Janzen, H., Ellert, B. H., Helgason, B. L., Qian, B., Zebarth, B. J., Angers, D. A., Beyaert, R. P., Drury, C. F., Duguid, S. D., May, W. E., McConkey, B. G., & Dyck, M. F. (2017). Litter decay controlled by temperature, not soil properties, affecting future soil carbon. *Global Change Biology*, *23*(4), 1725–1734. https://doi.org/10.1111/gcb.13502

Isbell, R. F. (1996). The Australian soil classification. *Geoderma*, *75*(1–2), 152–153. https://doi.org/10.1016/S0016-7061(96)00096-1

Jilling, A., Keiluweit, M., Contosta, A. R., Frey, S., Schimel, J., Schnecker, J., Smith, R. G., Tiemann, L., & Grandy, A. S. (2018). Minerals in the rhizosphere: Overlooked mediators of soil nitrogen availability to plants and microbes. *Biogeochemistry*, *139*(2), 103–122. https://doi.org/10.1007/s10533-018-0459-5

Kell, D. B. (2012). Large-scale sequestration of atmospheric carbon via plant roots in natural and agricultural ecosystems: Why and how. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1595), 1589–1597. https://doi.org/10.1098/rstb.2011.0244

Kögel-Knabner, I., Guggenberger, G., Kleber, M., Kandeler, E., Kalbitz, K., Scheu, S., Eusterhues, K., & Leinweber, P. (2008). Organo-mineral associations in temperate soils: Integrating biology, mineralogy, and organic matter chemistry. *Journal of Plant Nutrition and Soil Science*, *171*(1), 61–82. https://doi.org/10.1002/jpln.200700048

Krull, E. S., Baldock, J. A., & Skjemstad, J. O. (2003). Importance of mechanisms and processes of the stabilisation of soil organic matter for modelling carbon turnover. *Functional Plant Biology*, *30*(2), 207–https://doi.org/10.1071/FP02085

Lavallee, J. M., Soong, J. L., & Cotrufo, M. F. (2020). Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Global Change Biology*, *26*(1), 261–273. https://doi.org/10.1111/gcb.14859

Lehmann, J., & Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*, *528*(7580), 60–68. https://doi.org/10.1038/nature16069

Lipper, L., Dutilly-Diane, C., & McCarthy, N. (2010). Supplying carbon sequestration from West African rangelands: Opportunities and barriers. *Rangeland Ecology & Management*, *63*(1), 155–166. https://doi.org/10.2111/REM-D-09-00009.1

Lützow, M. V., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., & Flessa, H. (2006). Stabilization of organic matter in temperate soils: Mechanisms and their relevance under different soil conditions – A review. *European Journal of Soil Science*, *57*(4), 426–445. https://doi.org/10.1111/j.1365-2389.2006.00809.x

Mitchell, E., Scheer, C., Rowlings, D., Conant, R. T., Cotrufo, M. F., & Grace, P. (2018). Amount and incorporation of plant residue inputs modify residue stabilisation dynamics in soil organic matter fractions. *Agriculture, Ecosystems & Environment*, *256*, 82–91. https://doi.org/10.1016/j.agee.2017.12.006

Mitchell, E., Scheer, C., Rowlings, D. W., Conant, R. T., Cotrufo, M. F., van Delden, L., & Grace, P. R. (2016). The influence of above-ground residue input and incorporation on GHG fluxes and stable SOM formation in a sandy soil. *Soil Biology and Biochemistry*, *101*, 104–113. https://doi.org/10.1016/j.soilbio.2016.07.008

Mitchell, E., Scheer, C., Rowlings, D., Cotrufo, M. F., Conant, R. T., Friedl, J., & Grace, P. (2020). Trade-off between 'new' SOC stabilisation from above-ground inputs and priming of native C as determined by soil type and residue placement. *Biogeochemistry*, *149*(2), 221–236. https://doi.org/10.1007/s10533-020-00675-6

Poirier, V., Roumet, C., & Munson, A. D. (2018). The root of the matter: Linking root traits and soil organic matter stabilization processes. *Soil Biology and Biochemistry*, *120*, 246–259. https://doi.org/10.1016/j.soilbio.2018.02.016

Rasse, D. P., Rumpel, C., & Dignac, M. F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, *269*(1–2), 341–356. https://doi.org/10.1007/s11104-004-0907-y

Ryals, R., Kaiser, M., Torn, M. S., Berhe, A. A., & Silver, W. L. (2014). Impacts of organic matter amendments on carbon and nitrogen dynamics in grassland soils. *Soil Biology and Biochemistry*, *68*, 52–61. https://doi.org/10.1016/j.soilbio.2013.09.011

Sanjari, G., Ghadiri, H., Ciesiolka, C. A. A., & Yu, B. (2008). Comparing the effects of continuous and time-controlled grazing systems on soil characteristics in Southeast Queensland. *Australian Journal of Soil Research*, *46*(4), 348. https://doi.org/10.1071/SR07220

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., & Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, *478*(7367), 49–56. https://doi.org/10.1038/nature10386

Schuman, G. E., Reeder, J. D., Manley, J. T., Hart, R. H., & Manley, W. A. (1999). Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. *Ecological Applications*, *9*(1), 65–71. https://doi.org/10.1890/1051-0761(1999)009%5B0065:IOGMOT%5D2.0.CO;2

Six, J., Conant, R. T., Paul, E. A., & Paustian, K. (2002). Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. *Plant and Soil*, *241*(2), 155–176. https://doi.org/10.1023/A:1016125726789

Six, J., & Paustian, K. (2014). Aggregate-associated soil organic matter as an ecosystem property and a measurement tool. *Soil Biology and Biochemistry*, *68*, A4–A9. https://doi.org/10.1016/j.soilbio.2013.06.014

Sokol, N., Kuebbing, S., Karlsen-Ayala, E., & Bradford, M. (2019). Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. *New Phytologist*, *221*(1), 233–246. https://doi.org/10.1111/nph.15361

Southorn, N. J. (2002). The soil structure component of soil quality under alternate grazing management strategies. *Advances in Geoecology*, *35*, 163–170

Stemmer, M., Von Lutzow, M., Kanderler, E., Pichlmayer, F., & Gerzabek, M. H. (1999). The effect of maize straw placement on mineralisation of C and N in soil particle size fractions. *European Journal of Soil Science*, *50*, 73–85.

Teague, R., Provenza, F., Norton, B., Steffens, T., Barnes, M., Kothmann, M., & Roath, R. (2008). Benefits of multi-paddock grazing management on rangelands: Limitations of experimental grazing research and knowledge gaps. In *Grasslands: Ecology, management and restoration* (pp. 41–80). Nova Science Publishers.

Wei, Y., Zhang, Y., Wilson, G. W. T., Guo, Y., Bi, Y., Xiong, X., & Liu, N. (2021). Transformation of litter carbon to stable soil organic matter is facilitated by ungulate trampling. *Geoderma*, *385*, 114828. https://doi.org/10.1016/j.geoderma.2020.114828

Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., von Lützow, M., Marin-Spiotta, E., van Wesemael, B., Rabot, E., Ließ, M., Garcia-Franco, N., Wollschläger, U., Vogel, H. J., & Kögel-Knabner, I. (2019). Soil organic carbon storage as a key function of soils – A review of drivers and indicators at various scales. *Geoderma*, 149–162. https://doi.org/10.1016/j.geoderma.2018.07.026

Zimmermann, M., Leifeld, J., Schmidt, M. W. I., Smith, P., & Fuhrer, J. (2007). Measured soil organic matter fractions can be related to pools in the RothC model. *European Journal of Soil Science*, *58*(3), 658–667. https://doi.org/10.1111/j.1365-2389.2006.00855.x

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