Journal of Environmental Management 365 (2024) 121657

Contents lists available at ScienceDirect



Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article



Simulating adaptive grazing management on soil organic carbon in the Southeast U.S.A. using MEMS 2

Rafael S. Santos^a, Emma K. Hamilton^b, Paige L. Stanley^b, Keith Paustian^{a,b}, M. Francesca Cotrufo^b, Yao Zhang^{a,*}

^a Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO, 80521, USA ^b Department of Soil and Crop Sciences, Colorado State University, Fort Collins, CO, 80521, USA

ARTICLEINFO

Keywords: Adaptive multi-paddock grazing Ecosystem model Soil organic carbon Particulate organic carbon Mineral-associated organic carbon

ABSTRACT

Grazing lands play a significant role in global carbon (C) dynamics, holding substantial soil organic carbon (SOC) stocks. However, historical mismanagement (e.g., overgrazing and land-use change) has led to substantial SOC losses. Regenerative practices, such as adaptive multi-paddock (AMP) grazing, offer a promising avenue to improve soil health and help combat climate change by increasing SOC accrual, both in its particulate (POC) and mineral-associated (MAOC) organic C components. Because adaptive grazing patterns emerge from the combination of different levers such as frequency, intensity, and timing of grazing, studying AMP grazing management in experimental trials and representing it in models remains challenging. Existing ecosystem models lack the capacity to predict how different adaptive grazing levers affect SOC storage and its distribution between POC and MAOC and along the soil profile accurately. Therefore, they cannot adequately assist decision-makers in effectively optimizing adaptive practices based on SOC outcomes. Here, we address this critical gap by developing version 2.34 of the MEMS 2 model. This version advances the previous by incorporating perennial grass growth and grazing submodules to simulate grass green-up and dormancy, reserve organ dynamics, the influence of standing dead plant mass on new plant growth, grass and supplemental feed consumption by animals, and their feces and urine input to soil. Using data from grazing experiments in the southeastern United States and experimental SOC data from two conventional and three AMP grazing sites in Mississippi, we tested the capacity of MEMS 2.34 to simulate grass forage production, total SOC, POC, and MAOC dynamics to 1-m depth. Further, we manipulated grazing management levers, i.e., timing, intensity, and frequency, to do a sensitivity analysis of their effects on SOC dynamics in the long term. Our findings indicate that the model can represent bahiagrass forage production (BIAS = 9.51 g C m⁻², RRMSE = 0.27, RMSE = 65.57 g C m⁻², $R^2 = 0.72$) and accurately captured the dynamics of SOC fractions across sites and depths (0–15 cm: RRMSE = 0.05; 15–100 cm: RRMSE =1.08-2.07), aligning with patterns observed in the measured data. The model best captured SOC and MAOC stocks across AMP sites in the 0-15 cm layer, while POC was best predicted at-depth. Otherwise, the model tended to overestimate SOC and MAOC below 15 cm, and POC in the topsoil. Our simulations indicate that grazing frequency and intensity were key levers for enhancing SOC stocks compared to the current management baseline, with decreasing grazing intensity yielding the highest SOC after 50 years (63.7–65.9 Mg C ha⁻¹). By enhancing our understanding of the effects of adaptive grazing management on SOC pools in the southeastern U. S., MEMS 2.34 offers a valuable tool for researchers, producers, and policymakers to make AMP grazing management decisions based on potential SOC outcomes.

1. Introduction

Grazing is an important process both agriculturally and biogeochemically. Grazing lands managed for agriculture currently span millions of acres, which collectively hold \sim 30% of all terrestrial soil organic carbon (SOC) on Earth (Dondini et al., 2023). Due to historically poor management, intensification, and land-use change, many grazing lands have lost large amounts of their original SOC stocks (Sanderman et al., 2017). Improved management of grazing lands holds potential as a tool for leveraging SOC sequestration as a climate change mitigation

* Corresponding author.

https://doi.org/10.1016/j.jenvman.2024.121657

Received 15 April 2024; Received in revised form 2 June 2024; Accepted 29 June 2024

Available online 3 July 2024

E-mail address: yao.zhang@colostate.com (Y. Zhang).

^{0301-4797/© 2024} Elsevier Ltd. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

strategy (Bai and Cotrufo, 2022; Conant et al., 2017). Recent evidence suggests that adaptive multi-paddock (AMP) grazing, a strategy which employs adaptive and frequent movement of animals at greater-than-average stocking densities and longer pasture rest periods, is associated with increased SOC along the soil profile, particularly in the mineral-associated organic matter (MAOM) fraction (Mosier et al., 2021). Despite the importance of grazing management as a control on SOC dynamics, no validated process-based ecosystem models exist to represent and predict how AMP grazing management affects SOC stock dynamics. Such ecosystem models can act as decision support tools at multiple levels, including helping to inform producers' grazing management strategies for sequestering SOC, helping researchers understand the potential for grazing to support climate change mitigation, and even helping policy makers and governing bodies design incentive structures for effective management practices. The need for these predictive ecosystem models is especially pressing for grazing lands, where gold-standard SOC measurements can be prohibitively time, labor, and cost-intensive (Stanley et al., 2023). Ecosystem models thus have the potential to greatly improve the understanding of grazing management on SOC by bridging the gap between expensive field measurements and scalable predictions.

Several ecosystem models currently simulate grazing but have important limitations. These limitations include only representing croplands, neglecting mechanistic controls on SOC (e.g., nitrogen (N) availability), simulating only topsoil SOC dynamics, oversimplifying grass responses to defoliation, or interpreting grazing simply as a mowing event (Ma et al., 2019). Grazing lands exhibit unique biogeochemical processes compared to croplands and often have plant communities with an evolutionary history of adaptation to grazing, which can drive distinct responses to defoliation (Oesterheld and Semmartin, 2011). Ecosystem models that attempt to simulate biogeochemical responses to grazing also tend to have large errors, on average, highlighting the need to improve modeling capabilities for these systems (Ehrhardt et al., 2018). Additionally, several models have been designed for hydrologic and biomass production purposes on grazing lands, but few have been developed specifically to also represent soil processes and SOC storage (Wang et al., 2020).

DayCent, one of the most widely used ecosystem models for assessing SOC dynamics, simulates grazing on grazing lands (Damian et al., 2021; Silva et al., 2022), but still falls short from representing important yet complex biogeochemical processes in these systems. Biogeochemically, DayCent models SOC components as conceptual pools empirically defined by assumed mean residence times rather than representing measurable SOC fractions that are defined mechanistically. This limits predictive capabilities under novel environmental conditions or management practices and makes it impossible to test hypotheses related to how specific processes produce patterns and outcomes. For example, rather than the "active," "passive," and "slow" SOC pools conceptually represented in DayCent, SOC is better understood when divided into the functionally distinct, measurable particulate organic matter (POM) and MAOM fractions (Lavallee et al., 2020). In fact, POM and MAOM form, persist, and turn over through different mechanisms (Cotrufo and Lavallee, 2022), which respond differently to environmental and management changes (Prairie et al., 2023; Rocci et al., 2021), including grazing management (Mosier et al., 2021), making their representation in models extremely critical (Rocci et al., 2024). Grazing lands generally contain a significant portion of SOC in MAOM, which is a persistent form of SOC important for long-term SOC storage but with the potential to eventually saturate (Cotrufo et al., 2019; Bai and Cotrufo, 2022). Alternatively, while POM appears to be a smaller pool of SOC in grazing lands, its formation may be favored under certain managements, climates, and soil textures (Hansen et al., 2024). As POM and MAOM form from structural and soluble inputs, respectively (Cotrufo et al., 2015), and N availability may affect their dynamics differently (Averill and Waring, 2017), with MAOM having a higher demand for N than POM (Cotrufo et al., 2019), the impact of grazing on plant and nutrient inputs

to soil might be critical to POM and MAOM formation. In sum, building SOC responses to grazing in terms of POM and MAOM into ecosystem models would improve alignment with experimental data and could inform grazing management practices favorable to accumulating POM and MAOM in a way that is more tailored to climatic change mitigation (Stanley et al., 2024). DayCent serves as the foundational soil biogeochemical module of many grazing models (e.g., APEX, SAVANNA, ISFM, and PaSim; Ma et al., 2019), which therefore face the same challenges.

To represent the state-of-the art understanding of SOC dynamics (Cotrufo et al., 2013, 2015; Kleber et al., 2015; Schrumpf et al., 2021; Sokol et al., 2019) and represent functionally different measurable SOC pools, i.e. particulate (POC) and mineral-associated (MAOC) organic C (Lavallee et al., 2020), we developed the process-based MEMS 2.0 ecosystem model (Zhang et al., 2021). Stemming from the SOC model, MEMS 1.0 (Robertson et al., 2019), MEMS 2.0 represents full ecosystem dynamics including plant growth, root inputs, N controls on plant and SOC dynamics through the depth profile, soil hydrology, and SOC transport (Zhang et al., 2021). In this study, we present our efforts to further develop the model into a new version - MEMS 2.34 (Cotrufo et al., 2013, 2015; Kleber et al., 2015; Schrumpf et al., 2021; Sokol et al., 2019) to represent perennial grasslands under AMP grazing and overcome many of the above-described challenges. This work was motivated by the several limitations which prevented MEMS 2.0 from simulating ecosystem outcomes from grazing management on grazing lands. For example, it treated annual and perennial grasses similarly despite their different growth strategies. Perennial grasses possess physiological structures that serve as reservoirs for storing carbohydrates and essential nutrients, commonly identified as the crown, stolon, or rhizome (White, 1973). Unlike annual plants that invest most of their energy into seed production, perennials invest in reserve organs (e.g., rhizome, stolon) (Herrmann and Schachtel, 2001; Jing et al., 2012; Rymph, 2004). These organs play an important role in facilitating the persistence of these grasses across seasons, enabling them to adapt to adverse environmental conditions and recover from defoliation events (i.e., grazing; Benot et al., 2019). Further, MEMS 2.0 could not accurately predict the phenological events of perennial grasses, particularly the timing of green-up (the onset of growth after dormancy) and the transition into dormancy. These critical phenological stages exert a large influence on the growth patterns and overall biomass production of perennial grasses (Piao et al., 2007).

Additionally, process-based ecosystem models developed to simulate grazing effects on SOC (including MEMS 2.0) have featured only rudimentary grazing aspects, which have limited their implications to inform realistic grazing management. Grazing management practices vary greatly and involve a complex series of ecological feedbacks that differ across a wide variety of climates (Stanley et al., 2024). For example, some producers may not rotate grazing animals across their land base at all, while others may choose to rotate based on a set schedule (e.g., 1x/month), and others may choose to rotate animals based on ecological cues (e.g., plant recovery, seasonality, etc.). Field studies have not well captured these unique management features of grazing systems, instead relying mostly on poorly-defined parameters of grazing intensity (Stanley et al., 2024). These limitations of grazing management parameters in experimental datasets have therefore translated into problematic representations of grazing management in models (Brilli et al., 2017; Ma et al., 2019; Wang et al., 2020). Instead, incorporating management levers typically manipulated by producers on grazing lands, including the timing, duration, frequency, and intensity of grazing (Stanley et al., 2024) could be more useful for end users to model the impact of realistic grazing decisions on SOC outcomes.

Ecosystem models representing the current understanding of controls on SOC accrual and persistence (Rocci et al., 2024), with the ability to predict the effects of grazing management practices on SOC are urgently needed by researchers, producers, and policy makers. To address this need, we modified the MEMS 2 model to expand its capabilities

with: 1) improved representation of perennial grass growth and biomass production dynamics, and 2) exploratory capacity to simulate ecosystem outcomes from grazing management. Our new grazing model, MEMS 2.34, includes two new main components: biomass removal by herbivores and the return of nutrients through feces and urine deposition. To make these model improvements, we used experimental data on perennial grass from various locations across the southeastern United States and SOC measurements from AMP-grazed and conventionally managed farms in Mississippi.

2. Material and methods

2.1. MEMS 2.34 - grazing model description

2.1.1. Green-up and dormancy

Green-up and dormancy are two critical phenology stages of perennial grasses. Similar to our annual crop submodel, we based phenology stage calculations on heat units. The heat units (or growing degree days) are the accumulation of heat within a certain temperature range, which could be modified by the effect of daylength (photoperiod) and/or abiotic stresses at certain growing stages in some species (Soltani et al., 2012).

The timing of grass green-up in the spring for temperate climates is driven by daylength and soil temperature. To adjust for this in our model, we followed the method described in Xin et al. (2015). We used a daylength threshold value to set the start of the heat unit accumulation using the temperature of the first soil layer (0-2 cm) internally defined in the model. At the completion of the accumulation of heat units, the grass is ready for green-up if the soil water potential meets the minimum requirement.

We designed dormancy in the model to be triggered by any of the following situations: completion of heat units accumulation (growth cycle completion), daylength falling below a specified threshold, frost kill temperature, or plant water stress. The threshold for daylength is an input parameter with a default value provided in Xin et al. (2015). The frost kill temperature is a user-defined value that the model compares to the daily minimum temperature. If the plant water stress (below a specified threshold and calculated based on the actual and potential transpiration) persists for over 14 days, the plant will enter dormancy. In tropical and other regions characterized by wet and dry seasons, the model can be configured to respond solely to soil moisture levels, regulating green-up and dormancy accordingly.

2.1.2. Perennial grass reserve organ

The perennial grass reserve organ in MEMS 2.34 comprises both a structural and a non-structural (predominantly carbohydrate) pool (White, 1973). The non-structural pool serves as a dynamic resource, which can be mobilized to meet the carbohydrate requirements of other organs as needed. The reserve organ maintains a balance between minimum and maximum N content. Nitrogen is translocated to the reserve organ post-seeding and before entering complete dormancy, facilitating its readiness for subsequent growth cycles (Rymph, 2004). Additionally, the translocation of N remains flexible, allowing plants to utilize it for growth when required.

The presence of the reserve organ required us to modify the allocation of net primary production (NPP) to account for its energy storage. In MEMS 2.0, the NPP allocation to plant organs (e.g., leaf and stem) is dynamic according to the stage of phenology, using predefined curves that were calibrated for different species and varieties (Zhang et al., 2021). For example, the calibrated allocation curves for Bahiagrass (*Paspalum notatum*), the dominant perennial grass species in our study region (Wang et al., 2021), were presented in Supplementary material – Figure S1.

Defoliation influences the allocation of NPP between aboveground and belowground components in grasses (Turner et al., 1993). To account for this effect, we modeled a critical live shoot-to-root ratio, below which NPP is preferentially allocated towards aboveground growth (Gong et al., 2015; Yin et al., 2005). The proportion of NPP allocated to aboveground biomass increases as the shoot-to-root ratio decreases. This mechanism operates in conjunction with the reserve organ pool to facilitate rapid aboveground recovery after defoliation events. As a result, the model simulates the plant's ability to replenish photosynthetic tissues and restore its capacity for C assimilation following defoliation.

2.1.3. Impact of standing dead on new plant growth

Standing dead material can hinder the growth of new leaves by shading, thus reducing access to sunlight (Knapp, 1984). The MEMS 2.0 model assumed a simple homogeneous canopy structure, where green tissues, senesced tissues, and standing dead litter from the previous growing season intercepted light equally based on their leaf area.

In MEMS 2.34, we used similar assumptions and methods presented in Spitters and Aerts (1983) who simulate grass species competition by dividing the canopy into multiple layers. We made three key assumptions to better reflect the impact of shading by standing dead plant material on new growth. First, recently senesced leaves are located at the bottom of the canopy (Yin, 2000). Second, based on the heights of green and standing dead tissues from the previous growing season, the canopy can be divided into two layers: a top layer consisting of a single component (green or standing dead) and a bottom layer that is a homogeneous mixture (Spitters and Aerts, 1983). Third, a rectangular leaf area density function was employed (Spitters and Aerts, 1983), simplifying the partitioning of leaf area index (LAI) into layers. The LAI of live and the standing dead biomass in each layer is proportional to their respective heights within that layer. We calculate light interception separately for each layer using the Beer-Lambert law (Monsi and Saeki, 2005). The top layer's light interception is determined by its LAI, while the bottom layer's light interception accounts for the total LAI of all components minus the top layer's contribution.

2.1.4. Grazing and supplemental feeding events

Grazing and supplemental feeding events were incorporated in MEMS 2.34, allowing users to schedule their management practices. These events trigger the calculation of daily biomass removal and the return of feces and urine to the field. For simplicity, we designed the animal forage intake rate (as a percentage of body weight) as a userdefined input.

Users create daily grazing events in the management schedule input file, defining: (1) the start and end dates of grazing periods (minimum of one day); (2) the animal type (e.g., cattle and sheep), and (3) the stocking density, i.e., the number of animals expressed in terms of animal units (AU; based on 500 kg) per area (m^2) of land being grazed at any one period (Allen et al., 2011). The users can add and define animal types according to the traits of specific herds. However, only one type of animal can be used for each period and mixed herds comprising animals of varying ages and genders can only be defined using one set of parameters that represent the average traits of that herd.

Supplemental feed can also be added as a management event when the animals remain in the field. We assumed that animals prioritize consuming the supplemental feed, turning to forage from the field (live or standing dead material) only if their demand isn't met. Users can create daily supplemental feed events in the management schedule input file, defining: (1) the start and end dates of supplemental feeding periods (minimum of one day); (2) supplemental feed amount (g m⁻²), and (3) feed quality, expressed as C and N content, soluble and acid unhydrolyzable fractions, and cellulose and hemicellulose fractions, which we describe further below. Like plant biomass, feed digestibility and Nexcreta returned to soil is calculated based on feed quality.

2.1.5. Digestible nutrient content

Forage quality (i.e., chemical composition) drives the digestible nutrient contents, which determines the partitioning of C and N

assimilated by the animals. This influences the quantity and composition of C and N returned into the soil organic matter pools through feces and urine (Fig. 1). This development is a key advantage of MEMS 2.34 to mechanistically represent grazing effects on SOC compared to other widely used ecosystem models (as they do not account for forage quality) (e.g., DNDC and DayCent; Saggar et al., 2004; Hartman et al., 2018).

In the original MEMS 2.0, plant biomass was separated into soluble, hydrolyzable, and acid unhydrolyzable pools (excluding ash; Zhang et al., 2021). In MEMS 2.34, the digestible nutrient content of each of these pools is calculated based on their chemical composition assessed through different methods. We defined the soluble pool as non-structural carbohydrates and amino acids extracted through hot water (Soong et al., 2015). The digestibility of non-structural carbohydrates is set to 0.98 following Heinke et al. (2023). Amino acids represent the only soluble N pool, and their mass is calculated from the %N of the soluble pool, assuming an average N content of amino acid of 16% (Heinke et al., 2023). The digestibility of amino acids is then calculated as for crude protein (described below). We did not include other minor soluble compounds for simplicity. The hydrolyzable pool is comprised of proteins, hemicelluloses, celluloses, fatty acids, and other minor constituents. For simplicity, the latter is grouped with and treated as fatty acids. Celluloses and hemicelluloses are grouped into a new plant input parameter measurable as the neutral detergent fiber (NDF) excluding lignin and ash (Van Soest et al., 1991). The digestibility of cellulose and hemicellulose is calculated using the equation from the National Research Council (2001) derived from a study conducted by Weiss et al. (1992). Proteins are assumed to contain all the N of the hydrolyzable pool, and their digestibility is calculated using the linear equations described in Wardeh (1981). The acid unhydrolyzable pool is mainly comprised of lignin. This constituent is obtained through the acid detergent fiber (ADF) digestion method, with the acid-unhydrolyzable residue (AUR) serving as a proxy for lignin (Rowland and Roberts, 1994). Because lignin has typically a negligible N content, it was

assumed to have zero digestibility (Heinke et al., 2023).

2.1.6. Feces and urine production and input to soil

The C and N returning to the fields as feces and urine are estimated from the digestibility, for the animal, of each of the biomass pools. The C and N in feces are the non-digestible C and N fractions of these pools. The N of urine is calculated based on the following mass balance equation (Heinke et al., 2023; Ruelle et al., 2018):

$$N_{urine} = N_{intake} - N_{feces}$$
 Equation 1

The components in the equation are the N weight in urine, total intake biomass, and feces. Note that the equation did not account for the N retention in the animal body weight which could be a significant proportion (Haynes and Williams, 1993). The C in urine is neglected in our model.

We created a new set of soil surface litter pools (i.e., soluble, hydrolyzable, and unhydrolyzable) for feces (Fig. 1). Because of a lack of data, the decomposition of feces is calculated in the same way as plant litter. We are carrying out field studies to determine if a different set of decay parameters should be used for feces. For simplicity, urine was added to the soil surface ammonium pool, as urine is primarily comprised of urea.

2.2. Observed data used for modeling

2.2.1. Study sites description and soil sampling

Based on the available literature (Apfelbaum et al., 2022; Mosier et al., 2021; Wang et al., 2021; White et al., 2023) and additional data collected from two paired farms under conventional grazing (CG) and AMP grazing management in Woodville, Mississippi (Supplementary material – Figure S1), we initialized and assessed the performance of MEMS 2.34. The CG farm has been managed under CG management for approximately 50 years, whereas the AMP farm has been under AMP



Fig. 1. Schematic representation of the MEMS 2.34 ecosystem model representing the inclusion of livestock grazing contributing to manure and mineral N inputs to soils. Figure adapted from Zhang et al. (2021) under the terms of the Creative Commons Attribution 4.0 License. Illustration by Dr. Jocelyn M. Lavallee. ANPP: above ground net primary productivity. BNPP: below ground net primary productivity. DOM: dissolved organic matter. POM: particulate organic matter. MAOM: mineral-associated organic matter (MAOM) consists of exchangeable and stable component pools (eMAOM and sMAOM, respectively). N: nitrogen.

management since 2007, preceded by 13 years of CG management. Conventional grazing involves leaving animals in an open area and continuously or infrequently moving them. In this approach, the stocking density is the main control of the forage availability (Mosier et al., 2021). The CG farm divides its total grazeable acres into five large pastures (e.g., 8.1 ha each). In a typical year under this management approach, animals (~62 AU) are left free to graze in an individual pasture for 5-10 days before being moved to another pasture, where this cycle is repeated. In contrast, AMP grazing management is characterized by short-duration rotational grazing (e.g., 1-2 days) at high stocking density across numerous temporary fenced paddocks. The number, size, and time of recovery varies according to many factors, including season, forage availability, precipitation, and temperature. In a typical year at the AMP farm, 250 AU are rotated across 216 ha of grazable land separated into 40-100 paddocks. At the start of the year, when forage is less available, fewer large paddocks (e.g., 8.1 ha) are used, while in late spring-early summer, when forage production is high, smaller paddocks (e.g., 0.8 ha) are used. Both farms primarily focus on beef cattle production.

In general, at the CG farm, the grazing period begins in early March and goes through November. At the AMP farm, this period is reportedly longer (e.g., from mid-February to mid-December). Bahiagrass is the most dominant grass on both farms, though the AMP farm has greater species diversity (Wang et al., 2021). During the winter, when grasses are dormant, both farms rely primarily on supplemental feed (e.g., bales of hay, protein supplement) as the forage available in the field is not enough to meet animal nutrition needs. The supplemental feed is spread out daily in the pasture or paddock during this period as animals are rotated across the farm. The amount of hay and the duration of the supplemental feed vary based on how weather conditions (i.e., frost, precipitation rate) affect the quantity and quality of the standing dead material at the end of the season. In a typical year, the supplemental period lasts for about 30–90 days, and 1361–2268 kg of hay is spread out on the field daily.

Soil sampling campaigns were performed by Resource Environmental Solutions LLC and Shell International Exploration and Production Inc. at different representative sites across both farms to capture the impact of CG and AMP management on soil organic matter dynamics. At the AMP farm, samples were collected at three sites: AMP-1 in 2019 (n = 25) and 2022 (n = 6), and AMP-2 and AMP-3 in 2022 (n = 6). At the CG farm, samples were collected at two sites: CG-1 and CG-2 in 2022 (n = 6) (Supplementary material – Figure S1). More samples were taken at the AMP farm in 2019 (following a grid pattern with 25 squared cells each having 25 \times 25 m); this field campaign was aimed to better understand SOC spatial heterogeneity, which is beyond our study's scope. However, we included this data in our simulations for robustness. In other years, six samples per site were collected.

An ATV-mounted Giddings hydraulic sampling unit was used to collect intact soil cores in plastic sleeves (5 cm in diameter x 1 m length). The intact cores were shipped in crates to Cquester Analytics LLC. These soil cores were kept refrigerated until segmented into depth intervals of 0–15, 15–30, 30–50, 50–70, and 70–100 cm, processed, and analyzed as described in Mosier et al. (2021). Briefly, soil samples were heat-treated (116 °C for 24–48 h) according to USDA APHIS protocol. Afterwards, bulk soils were 8-mm sieved, and then a subsample was 2-mm sieved for fractionation and elemental analyses.

2.2.2. SOC fraction analysis

Soil organic matter was fractionated by density (1.85 g cm⁻³) and size (<53 μ m) into three functionally distinct fractions: light particulate organic matter, coarse heavy organic matter, and mineral-associated organic matter as described in Leuthold et al. (2024). An additional subsample of the 2-mm sieved soil was finely ground and tested for inorganic C, which was not detected in any sample. All bulk soils and fractions were then analyzed for SOC by the dry combustion method.

As the MEMS 2.34 model simulates SOC pools as POC and MAOC

(Fig. 1), we report the measured C in the light particulate organic matter as POC, and in the mineral and coarse heavy associated organic matter as MAOC. This is because the chemical characteristics of these two heavy fractions are the most similar and distinct from the light POC fraction (Leuthold et al., 2024).

2.2.3. Parameterization of perennial crop (Bahiagrass)

We parameterized bahiagrass for MEMS 2.34 using literature-based plant physiological parameters and data from three experimental sites in Alabama, Florida, and Texas (Table 1), where bahiagrass is commonly cultivated. Plant parameters were adjusted manually to minimize the overall error and bias statistics described below.

2.3. Model initialization, calibration, and validation

We aimed to validate the ability of the MEMS 2.34 model to reproduce SOC values after conversion to adaptive grazing management. To this end, we first initialized the model with our experimental site environmental conditions and brought it to equilibrium as native grassland by running the model for a 2000-year period. Then, according to verbal site management information, we simulated the onset of CG in 1974 and conversion to AMP in 2007. We adjusted the grazing management schedule from 1974 to 2007 to match the measured topsoil SOC stock (0–15 cm) at the CG sites, as the historical management information was lacking.

We used information from the NOAA database (https://www.ncdc. noaa.gov/cdo-web/datatools/findstation) and soil measurements collected at each of the study sites to prepare the weather and soil input files. Additionally, management schedule files were prepared based on information obtained from the two farmers (e.g., AU, pasture sizes, number of paddocks).

2.4. Model performance evaluation

We quantitatively assessed the MEMS 2.34 model's goodness of fit to simulate grass productivity and SOC dynamics. The fit of bahiagrass simulations was evaluated by comparing simulated to measured forage production through the coefficient of determination (R^2), BIAS, root mean square error (RMSE), and relative root mean square error (RRMSE).

The same statistical tests were applied to compare simulated and observed values of bulk SOC and its distribution in POC and MAOC for

Table 1

Summary of experiments used to parameterize bahiagrass in MEMS 2.34.

Location	Years	Treatment	Soil class	Weather data source	Citation
Auburn, AL	2006–2015	270 kg N ha ⁻¹ yr ⁻¹	Blanton loamy sand ^a	NOAA (local station: USC00010425)	Prior et al. (2019)
Ona, FL	1997–1998	0, 39, 78, 118, and 157 kg N ha ⁻¹ cutting ⁻¹	Pomona fine sand ^b	FAWN and Daymet	Johnson et al. (2001)
Eagle Lake, TX	1979–1980	0, 84, 168, 252, and 336 kg N ha ⁻¹	Crowley fine sandy loam ^b	iAIMS Climatic data	Evers (1985)

^a NCSS - National Cooperative Soil Survey Soil Characterization Database (https://ncsslabdatamart.sc.egov.usda.gov).

^b Smith et al. (2023). NOAA: National Oceanic and Atmospheric Administration (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation). iAIMS: Integrated Agricultural Information and Management System (Wilson et al., 2024). Florida Automated Weather Network [FAWN; Peeling et al. (2023)]. Daymet [Thornton et al. (2022)]. Soil data obtained from:

each soil layer across the AMP grazed sites.

2.5. Projected scenarios

Since the premise of AMP grazing is that management decisions should be tailored to site-specific conditions and responses (e.g., weather conditions, plant growth, recovery, etc.), we did not think it is appropriate or universally applicable to define a set of prescriptive practices associated with this management. Instead, focusing on fundamental grazing management levers, including timing, duration, intensity, and frequency, as characteristics of specific grazing patterns can be more representative and meaningful to ranchers. Stanley et al. (2024) recently proposed a unified conceptual framework based on ecosystem functions and soil biogeochemistry (e.g., SOC dynamics), where these grazing levers can be manipulated strategically to optimize SOC sequestration.

Following this conceptual framework, we used MEMS 2.34 to explore how manipulations to each of these grazing levers align with AMP grazing principles associated with our sites (Table 2) in affecting SOC storage and the vertical distributions of POC and MAOC (Fig. 1). The AMP sites (namely AMP-1, AMP-2, and AMP-3) were run individually in the model for each of these levers. The current AMP grazing management was the baseline scenario against which to assess SOC changes from each of the other scenarios. The grazing frequency scenarios increased the duration of the return period for each grazing event following the first event in a year. Since the last grazing events in these scenarios were scheduled to occur during the winter season after the adjustments, they were removed from all three grazing frequency scenarios (Table 2). The intensity scenarios simply reduced the AU for each grazing event and adjusted the amount of supplemental feed used in the wintertime to the new grazing intensity. The timing scenarios assumed the first two grazing events every year were delayed for a certain number of days, but the last three grazing event dates were not affected.

Weather data for the most recent five years from our data source (2018–2022) were used to represent the current climate condition. Climate change and atmospheric CO_2 concentration effects were not included in this study.

To offer a more comprehensive insight into the potential effect of these grazing levers on SOC, MAOC, and POC storage, results were presented as the average of the three study sites with a standard deviation (n = 3). For these scenarios, we report simulated SOC dynamics to a depth of 30 cm as this layer is where changes are expected to occur more intensively, while also aligning our study with the guidelines for national greenhouse inventories established by the Intergovernmental Panel on Climate Change (IPCC, 2006). However, further details about the predicted SOC dynamics at deeper soil layers are available in the supplementary material (Figures S3-S8).

3. Results and discussion

3.1. Model performance

3.1.1. Perennial grass productivity

We calibrated the perennial grass production parameters in MEMS 2.34 to represent forage production from the three experimental sites across the southern U.S. Accurate prediction of plant production is critical for modeling SOC dynamics, as plant biomass (aboveground and belowground) provides the main C and N inputs to soil (Zhang et al., 2021). In general, the model well captured the effect of N fertilization treatment and climate on forage production (Fig. 2). Statistical analyses of the calibration reveal an unbiased and relatively precise prediction of bahiagrass forage production (Fig. 2; BIAS = 9.51 g C m⁻², RMSE = 65.57 g C m⁻², RRMSE = 0.27, R² = 0.72). The absence of detailed data on soil properties (e.g., mineral nitrogen, SOC, texture, and pH) and site-specific history in the published studies likely reduced the accuracy of our simulations. To approximate the soil nutrient levels during the

Table 2

Current management information and grazing levers (frequency, intensity, timing) and associated stocking densities and return periods used to simulate the projected scenarios.

Management/	Lever	Grazing event	Stocking	Return
Lever	change	(DOY ^a)	density (AU	period (day)
			m ⁻²)	
Current	-	84	0.0080	
management		125	0.0128	40
0		186	0.0140	60
		287	0.0133	100
		320	0.0031	32
Intensity	-10%	84	0.0072	
	1070	125	0.0115	40
		186	0.0126	60
		287	0.0120	100
		320	0.0031	32
	-20%	84	0.0064	02
	-20%	125	0.0001	40
		125	0.0102	60
		287	0.0112	100
		207	0.0107	100
	2004	320 94	0.0051	32
	-30%	04 105	0.0050	40
		125	0.0090	40
		180	0.0098	60 100
		287	0.0093	100
m	. = 1	320	0.0031	32
Timing	+5 days	89	0.0080	40
		130	0.0128	40
		186	0.0140	60
		287	0.0133	100
		320	0.0031	32
	+10 days	94	0.0080	
		135	0.0128	40
		186	0.0140	60
		287	0.0133	100
		320	0.0031	32
	+15 days	99	0.0080	
		140	0.0128	40
		186	0.0140	60
		287	0.0133	100
		320	0.0031	32
Frequency	+5 days	89	0.0080	
		135	0.0128	45
		201	0.0140	65
		307	0.0133	105
	+8 days	92	0.0080	
		137	0.0128	48
		204	0.0140	68
		311	0.0133	108
	+10 days	93	0.0080	
		143	0.0128	50
		213	0.0140	70
		323	0.0133	110

^a DOY: day of year; AU: animal unit (500 kg).

^b There were four grazing events in these frequency scenarios compared with five events in the current management scenario.

experimental period, we had to simulate potential long-term historical management practices. Nevertheless, our model performance is similar to those of other models simulating perennial forages: the CROPGRO Perennial Forage model predicted harvested biomass of bahiagrass with RMSE of 72.9 g m⁻² (31 g C m⁻² assuming C content of 0.42) using six sites (Smith et al., 2023), while the DayCent model predicted productivity for a grazing system in Brazil with RRMSE of 0.37 and R² of 0.69 (Silva et al., 2022).

3.1.2. Soil organic carbon stocks and distribution across soil depths

The measured SOC stocks at the three AMP sites were similar down to 50 cm. However, below 50 cm, AMP-1 had SOC values 3.3 times higher than those observed at AMP-2 and AMP-3 (Fig. 3; Supplementary material – Table S2). The average SOC stocks across sites in 2022 were 27.9, 7.4, 5.7, 3.7, and 4.4 Mg C ha⁻¹ for 0–15, 15–30, 30–50, 50–70, and 70–100 cm, respectively, with no differences in SOC stocks observed



Fig. 2. Comparison of simulated and observed bahiagrass (*Paspalum notatum*) forage production from three sites in southern U.S. At each site, production was measured under different fertilization regimes and across multiple years.

between 2019 and 2022 at AMP-1 (Fig. 3; Supplementary material – Table S2).

We used the SOC measured in the CG treatment in 2022 as an approximation of the SOC stocks before the implementation of AMP grazing in 2007 (Fig. 3). The CG farm has been managed under conventional grazing for at least 50 years, suggesting that SOC had reached an equilibrium state (Conant et al., 2001; West and Six, 2007). According to information from the farmers, the AMP farm was also likely

maintained under CG management for a long period before transitioning to AMP practices. Given the similar soil type, climate, and management of these sites, it is reasonable to assume these sites had similar levels of SOC prior to AMP implementation. Compared to SOC stocks measured at the CG sites, AMP-2 had greater SOC stocks in the 0–15 cm layer. On the other hand, AMP-2 and AMP-3 contained slightly less SOC in deeper soil layers compared with CG, but this pattern was not observed in AMP-1 (Fig. 3). These differences in topsoil SOC stocks are similar to values observed in chronosequence data from other sites in the southeastern U. S. (Conant et al., 2004). However, it is important to note that these differences may also be partially attributable to SOC legacy effects if historical management and land-use across these sites were different.

We tested the goodness of fit of the model to predict SOC dynamics by comparing simulated against measured SOC, POC, and MAOC stocks at different depths along the soil profile (Figs. 3-5). Overall, the model well captured SOC dynamics at the study sites following the grazing management change from GC to AMP. This is indicated by the minor differences between simulated and observed values along the soil profile (Fig. 3), especially in topsoil (0-15 cm), as indicated by the low BIAS and RRMSE values across sites (Table 3). Below 15 cm, the model tended to overestimate SOC irrespective of the study site (Fig. 3D-O; Table 3). The model predictions of SOC at depths below 50 cm were almost the same across the three sites, while the SOC stock measured at AMP-1 differed from that at the other two sites (Supplementary material - Table S2). Based on our knowledge, the measured soil properties (e.g., texture), which were also used as model input, could not explain the large variations in measured SOC stocks observed at these depths across the sites. The consistent similarity between the measured values in 2019 and those in 2022 at AMP-1 suggests no evidence of bias or poor accuracy in measurements (Supplementary material - Table S2).

The overestimation in our model may be attributed to its simplistic structure, which fails to accurately represent the complex soil dynamics along the soil profile and under the given climatic conditions (Zhang et al., 2021). The grassland simulation conducted using MEMS 2.0 by



Fig. 3. Simulated and measured bulk soil organic carbon (SOC) stocks at different depths (0–15, 15–30, 30–50, 50–70, and 70–100 cm) for three sites (AMP-1, AMP-2, AMP-3) under adaptive multi-paddock (AMP) management in southern Mississippi. Mean CG represents the mean of SOC from two sites (CG-1 and CG-2) under conventional grazing (CG) which had been paired to the AMP farm (*sensu* Mosier et al., 2021). Note that values of CG were measured in 2022 but used as estimates for 2007 which was the starting point of AMP management. 2019: n = 25; 2022: n = 6.

Journal of Environmental Management 365 (2024) 121657



Fig. 4. Simulated and measured particulate organic carbon (POC) stocks at different depths (0–15, 15–30, 30–50, 50–70, and 70–100 cm) for three sites (AMP-1, AMP-2, AMP-3) under adaptive multi-paddock (AMP) management in southern Mississippi. Mean CG represents the mean of POC from two sites (CG-1 and CG-2) under conventional grazing (CG) which had been paired to the AMP farm (sensu Mosier et al., 2021). Note that values of CG were measured in 2022 but used as estimates for 2007 which was the starting point of AMP management.



Fig. 5. Simulated and measured mineral-associated organic carbon (MAOC) stocks at different depths (0–15, 15–30, 30–50, 50–70, and 70–100 cm) of three sites (AMP-1, AMP-2, AMP-3) under adaptive multi-paddock (AMP) management in southern Mississippi. Mean CG represents the mean of MAOC from two sites (CG-1 and CG-2) under conventional grazing (CG) which had been paired to the AMP farm (*sensu* Mosier et al., 2021). Note that values of CG were measured in 2022 but used as estimates for 2007 which was the starting point of AMP management.

Zhang et al. (2021) also showed substantial discrepancies between the simulated and observed values for certain soil layers at some sites. However, the overestimation by MEMS 2.34 of SOC in deep soil layers

may also be attributed to our assumption in the spin-up simulation that sites were historically CG managed. We made this assumption in lieu of a reliable land-use history at these sites. Our overestimation of SOC levels

Table 3

Statistical metrics calculated for the simulations of soil organic carbon (SOC), particulate organic matter (POC), and mineral-associated matter (MAOC) pools at distinct soil depths across the three AMP sites (AMP-1, AMP-2, and AMP-3) used for testing the MEMS model.

Soil depth (cm)	Statistical metric	SOC	POC	MAOC
		Mg C ha ⁻¹	Mg C ha ⁻¹	
0–15	BIAS	-0.23	5.32	-1.80
	RMSE	1.41	5.44	1.94
	RRMSE	0.05	1.15	0.10
15-30	BIAS	8.24	-0.48	9.89
	RMSE	8.39	0.58	9.99
	RRMSE	1.08	0.52	1.83
30-50	BIAS	10.62	-0.23	11.39
	RMSE	10.80	0.33	11.45
	RRMSE	1.71	0.50	2.24
50-70	BIAS	8.70	-0.19	8.23
	RMSE	9.09	0.20	8.31
	RRMSE	2.07	0.49	1.96
70–100	BIAS	8.19	-0.29	8.93
	RMSE	9.22	0.36	9.57
	RRMSE	1.69	0.75	2.12

in subsoil layers prior to the implementation of AMP grazing (before 2007 in Fig. 3) would be explained if these sites had been cropped in the past. In that case, their deep SOC would likely not have recovered to the level of perennial systems as estimated in our spin-up as subsoil SOC changes are slower than at the surface (DeGryze et al., 2004).

3.1.3. Particulate and mineral-associated organic matter stocks across soil depths

The measured POC stocks did not significantly vary across the AMP sites (Supplementary material – Table S3) and were higher in the topsoil (0–15 cm) than at-depth (Fig. 4). Comparable values and trends were also noted for POC stocks at CG sites. Similarly, MAOC stocks were consistent across sites, with greater and more similar values in topsoils, and lower and more variable values in subsoils below 15 cm. Similar to SOC, MAOC stocks at 70–100 cm were higher at AMP-1 compared to the AMP-2 and AMP-3 (Supplementary material – Table S3).

All simulated POC stocks fall within the standard deviation of the observed data, except in the 15-30 cm layer at the AMP-2 (Fig. 4). The simulated POC stocks were, on average, 2.1 times higher compared to the measured average values for the AMP sites in the topsoil (Fig. 4A-C). Conversely, below 15 cm, POC stocks were underestimated by approximately 43% compared to the average of observed values across sites as indicated by the negative BIAS in Table 3. Total SOC recovery after physical fractionation is often lower than 100%, especially when using density (Poeplau et al., 2018). In our measured dataset, the average C recovery rate of POC + MAOC across sites and depth varied by 93.7 \pm 16.5%, which has a higher average but also a higher standard deviation than the 90.0 \pm 5.4% C recovery observed by Leuthold et al. (2024) using the same combined size and density fractionation procedure across cropland soils. This high variability in the recovery rate of the measured SOC fractions may have played a role in the discrepancies between the observed and simulated POC stocks (Fig. 4).

Contrary to POC, the MEMS 2.34 model represented MAOC better in the topsoil (0–15 cm) than in deeper soil layers (Fig. 5). Following the same pattern observed for SOC, the model slightly underestimated MAOC stocks in the topsoil and overestimated them in deeper soil layers across the AMP sites (Fig. 5). The high agreement between predicted and observed values at 0–15 cm of depth was also supported by the statistical test results which indicated low values of BIAS and RRMSE (Fig. 5A–C; Table 3). Below 15 cm, simulated MAOC stocks remained consistent across sites but were overestimated by 9.9, 11.4, 8.2, and 8.9 Mg C ha⁻¹ at 15–30, 30–50, 50–70, and 70–100 cm, respectively, compared to observed values. Zhang et al. (2021) also observed discrepancies between measured and simulated MAOC for deeper soil layers at some simulated grassland sites using the MEMS 2.0 model. Subsoils are characterized by distinct biotic and abiotic factors governing organic matter formation and stabilization (Hicks Pries et al., 2023; Rumpel and Kögel-Knabner, 2011), yet the structure of controls of POC and MAOC dynamics at depth remain largely unknown (Cotrufo et al., 2021). This lack of mechanistic understanding and the scarcity of direct measurements of SOC inputs and decomposition processes at depth represents a significant challenge for deep SOC stocks and fraction distribution modeling (Zhang et al., 2021). Given the importance of deep SOC storage, research should focus on experimental, monitoring, and modeling studies of SOC dynamics in deep soils.

3.1.4. Predicted effects of grazing levers on SOC stocks

The long-term simulation of the current management (baseline scenario) suggests that AMP management can be a successful strategy to increase SOC in southern Mississippi pastures. Over a simulation period of 50 years, the model projected a nearly linear increase in SOC stocks by 36% at an annual sequestration rate of 0.33 Mg C ha⁻¹ yr⁻¹ under maintained AMP grazing (Fig. 6). This value fits well within the range of the SOC sequestration rates reported by Bai and Cotrufo (2022) for improved grazing practices.

The grazing levers tested in our simulations - frequency, intensity, and timing - resulted in relatively similar values of SOC stocks (ranging from 61.7 to 65.9 Mg C ha^{-1}) and SOC sequestration rates (ranging from 0.33 to 0.40 Mg C ha⁻¹ yr⁻¹) after 50 years (Fig. 6). Less frequent grazing and reduced grazing intensity were the primary contributors to increasing SOC stocks. However, the latter yielded the greatest SOC stocks (63.7-65.9 Mg C ha⁻¹) with the most substantial increase observed when stocking density was reduced by 30%. In addition to promoting greater increases in SOC stocks, reducing the stocking density led to more rapid SOC sequestration compared to the other levers in our simulation. In the first 12 years, the SOC sequestered after decreasing stocking density by 10, 20, and 30% was 7.3, 9.2, and 10.8 Mg C ha $^{-1}$, compared to a SOC sequestration of 5 Mg C ha-1 under current AMP management (Fig. 6B). Similarly, but to a lesser extent, SOC stocks increased with changes in grazing frequency (e.g., increasing the return period by 4, 8, and 10 days; Fig. 6A) compared to the current management baseline. Conversely, changes in the timing of grazing by postponing by 5, 10, or 15 days, resulted in negligible changes to SOC stocks compared to the current management baseline (Fig. 6C).

The resulting differences in SOC outcomes from changes to grazing management levers can be primarily attributed to changes in SOC inputs to soil. For instance, defoliation may increase plant quality by modifying plant composition (e.g., mobilization of carbohydrates from the reserve organ), and change allocation between roots and shoots. Additionally, removal of standing dead by defoliation may increase NPP, which may increase total SOC inputs in the long term (Supplementary material -Figure S9). In our grazing intensity scenarios, reducing grazing intensity resulted in increased NPP for the first few years (Supplementary material - Figure S9). However, in the longer term, NPP was lower in the scenario with the greatest reduction in grazing intensity. This pattern aligns with field observations suggesting that defoliation may stimulate plant production via compensatory growth mechanisms in some cases (Stanley et al., 2024). Similar explanations can be used for the frequency scenarios where SOC values were very similar among the 4, 8, and 10-day scenarios but different from the current management baseline. This suggests that the removal of the fall grazing event had a more pronounced effect on SOC dynamics than the variation in grazing frequency.

It is important to highlight that these findings are specific to the environmental conditions and management practices represented in our model simulations. The relative importance of grazing frequency, intensity, and timing may vary across different ecoregions, depending on factors such as climate, soil characteristics, plant community composition, and previous management (Stanley et al., 2024). The two scenarios that demonstrated the most significant potential SOC sequestration

Journal of Environmental Management 365 (2024) 121657



Fig. 6. Projected effects of grazing levers (frequency, intensity, and timing) on bulk soil organic carbon (SOC) stocks at 0–30 cm of depth in southern Mississippi. Shaded area represents the standard deviation of the mean (3 sites) for each scenario simulated.



Fig. 7. Projected effects of grazing levers (frequency, intensity, and timing) on particulate organic carbon (POC) stocks at 0–30 cm of depth in southern Mississippi. The shaded area represents the standard deviation of the mean (3 sites) for each scenario simulated.

(changes in grazing frequency and intensity) in our study reduced the total forage intake (fewer grazing events with the same number of animals or the same number of grazing events with fewer animals). This implies that at the whole-farm level, animal production may be reduced, presenting a trade-off that needs to be carefully considered. However, the aim of this study was to demonstrate the potential of MEMS 2.34 in informing specific grazing management decisions, rather than speculating on the broader impact that modifying grazing levers might have on SOC outcomes and trade-offs. We plan to address this broader impact in future research.

Overall, our model confirmed that AMP management has high potential to increase SOC stocks, with the rate of accrual being adjustable by tailoring grazing levers to the desired outcomes. An average SOC sequestration rate of 0.41 Mg C ha⁻¹ yr⁻¹ (0–50 cm) was reported across sites in Virginia (Conant et al., 2003), which is similar to the values obtained in our simulations. Even higher values (3.63 Mg C ha⁻¹ yr⁻¹; 0–30 cm) were reported after conversion to AMP from conventional grazing in Texas (Wang et al., 2015). This highlights that the magnitude of SOC accrual varies across regions due to differences in climate, soil, management, and previous land-use (Don et al., 2011; Soussana et al., 2004), with soils that have experienced greater losses showing higher rates of gain with improved management (Don et al., 2011).

3.2. Predicted effects of grazing levers on POC and MAOC

Under the current management baseline scenario, our simulations indicate that both POC and MAOC stocks are projected to increase in similar magnitude (POC 8.1 Mg C ha⁻¹; MAOC: 8.3 Mg C ha⁻¹) and at similar rates (POC 0.16 Mg C ha⁻¹ yr⁻¹; MAOC: 0.17 Mg C ha⁻¹ yr⁻¹; Figs. 7 and 8). However, they responded differently to simulated changes in grazing levers. Compared to the current management baseline, increases in POC and MAOC stocks were limited to changes in the frequency and intensity levers, with the latter yielding the highest SOC stocks for both fractions. On the other hand, simulated changes in the

timing of grazing events did not appear to impact POC and MAOC storage.

Although both POC and MAOC stocks increased in our simulated scenarios, POC exhibited more pronounced differences compared to MAOC, especially during the initial decade (Figs. 7 and 8). During this period, changes in the frequency and intensity levers resulted in POC stocks on average 11% and 36% higher, respectively, than those under the current management baseline (13.4 Mg C ha⁻¹) (Fig. 7A–B). Grazing intensity played a significant role in accelerating the accumulation of POC stocks in the short term, particularly when stocking density was reduced by 30%. Under this treatment, POC stocks at the end of the initial decade were similar to those under the current management baseline \sim 40 years later (19.8 Mg C ha⁻¹) (Fig. 7B).

In contrast to POC, the most noticeable differences in MAOC across grazing management manipulations were observed at the end of the simulated period (Fig. 8). However, MAOC stocks were only marginally higher compared to those in the current management baseline, irrespective of the simulated grazing management change. Overall, MAOC stocks ranged from 42.3 to 43.3 Mg C ha-1 across changes in the simulated frequency and intensity levers, which represents an increase of 0.8-3.3% in MAOC stocks compared to the current management baseline. These results contrast with the observations of higher relative increase of POC but higher absolute increase of MAOC under regenerative management in croplands (Prairie et al., 2023). There is an emerging understanding that POC and MAOC storage is controlled, in part, by different factors, with POC being controlled more by constraints on decomposition and MAOC more by constraints on productivity and mineral stabilization (Hansen et al., 2024). While our MEMS model has distinct pathways of formation for POC and MAOC, their turnover currently has similar constraints which may have reduced their possible differential response to AMP grazing levers. Given the push for multi-pool SOC management, by increasing both POC and MAOC pools (Angst et al., 2023), our model simulations indicate that AMP management may hold promise for enhancing both POC and MAOC pools in



Fig. 8. Projected effects of grazing levers (frequency, intensity, and timing) on mineral-associated organic carbon (MAOC) stocks at 0–30 cm of depth in southern Mississippi. The shaded area represents the standard deviation of the mean (3 sites) for each scenario simulated.

the long term.

3.3. Current limitations and future developments

Model calibration and validation rely heavily on field observations, which are limited by data availability. Long-term field observations of SOC changes due to grazing management are scarce, particularly regarding AMP effects on SOC fractions (Stanley et al., 2024). Besides the lack of comprehensive measurements for all required model inputs, this scarcity of information hinders understanding of how grazing influences SOC over time and space, further limiting model development.

Another limitation of our model is the lack of representation of N retention in the animal body (10–40% of total N intake for ruminants) (Calsamiglia et al., 2010). Additionally, urine is rapidly converted to ammonia under field conditions, but our model does not account for ammonia volatilization losses, which could be more than half of the excreted urine N (Haynes and Williams, 1993). The omission of these two processes could lead to an overprediction of the mineral N in the soil, consequently affecting the predictions of NPP and SOC. However, our grass biomass predictions were robust (Fig. 2), and SOC stocks were not consistently overpredicted (Fig. 3), suggesting a relatively minor impact of any potential overestimation of the mineral N addition by the grazing animals in our simulations.

In the current model implementation, we were forced to treat feces as analogous to plant material with respect to decomposition processes, due to a lack of measured data on fecal decomposition dynamics. Feces and plant residues have distinct chemical compositions and physical properties, which can influence their decomposition rates and pathways (Haynes and Williams, 1993). Feces contain a higher proportion of easily degradable organic matter, such as undigested plant materials, microbial biomass, and metabolic by-products compared to plant residues, which certainly has a downstream influence on SOC and partitioning among POC and MAOC. We invite experimental studies of manure contribution to POC and MAOC to address this knowledge gap and improve future model development.

Another major challenge is accounting for the heterogeneity of plant communities and grazing patterns. Many grazing lands exhibit a diverse mix of plant species with varying functional traits (Wang et al., 2021), which can influence soil organic matter dynamics (Bai and Cotrufo, 2022). Additionally, grazing animals can exhibit selective feeding behaviors, leading to spatially heterogeneous patterns of defoliation, nutrient redistribution, and soil compaction (Parsons and Dumont, 2003). Trampling effects on standing dead fall and soil compaction are not accounted for in this version. The effect on standing dead fall has been either simulated as a very small percentage biomass transfer to the ground per animal or omitted in many models (Chen et al., 2018; Snow et al., 2014). The soil compaction and its impact on other soil processes (e.g., soil water) are intricate and challenging to simulate accurately due to the spatial complexities involved and the lack of comprehensive data for validation (Chen et al., 2018; Snow et al., 2014; Romero-Ruiz et al., 2023).

In the present study, we did not account for the potential effects of climate change and elevated atmospheric CO₂ concentrations on future projections. These factors could significantly influence SOC dynamics and productivity in grazing lands (Briske et al., 2015; Morgan, 2005). Climate change could lead to alterations in temperature and precipitation patterns, affecting microbial activity, decomposition rates, and plant growth. Additionally, elevated atmospheric CO₂ can stimulate plant growth and enhance carbon inputs to the soil, potentially increasing SOC stocks when N is not limiting (De Graaff et al., 2006). We plan to incorporate these factors in future studies as well as the potentially different temperature sensitivity of POC and MAOC (Georgiou et al., 2024).

4. Conclusions

We have presented the first biogeochemical model capable of predicting SOC and its POC and MAOC components along the soil profile in response to AMP grazing management on pastures. The model demonstrated the capacity to properly simulate grass forage production and SOC dynamics down to 1-m depth on a grazed pasture in the southeastern U.S.A. Our future projection scenarios suggest that AMP grazing has the potential to substantially sequester SOC in these systems. Reducing grazing intensity showed the biggest effect on SOC sequestration, followed by reducing frequency; changing grazing time in our projections showed a minimal effect. However, there is a trade-off between feeding more animals and maximizing SOC sequestration.

Further work is needed to test and validate the model's performance across broader geographical regions and diverse grazing land ecosystems. Additionally, future research will focus on improving the model's representation of various processes and incorporating the potential effects of climate change. With these future developments, the MEMS model can serve as a valuable decision-making and policy-guiding tool for promoting sustainable grazing land management practices that balance productivity, SOC sequestration, and environmental conservation.

CRediT authorship contribution statement

Rafael S. Santos: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Emma K. Hamilton: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Paige L. Stanley: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. Keith Paustian: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. M. Francesca Cotrufo: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Conceptualization. Yao Zhang: Writing – review & editing, Writing – original draft, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT and Claude AI in order to improve readability and language. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

M. Francesca Cotrufo discloses to be a cofounder of Cquester Analytics LLC. 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.

Data availability

Data will be made available on request.

Acknowledgements

This research was supported by Shell International Exploration and Production Inc. (contract n.4550183252). The authors like to thank Christian Davies, Andy Robertson, and Chris Dealing from Shell International Exploration and Production Inc. for providing the field measurement data of the paired farms in Mississippi. We also thank Yezzen

Khazindar and Hao Yang from Colorado State University for relevant discussions regarding grazing management and data analysis. We extend our gratitude to Jason Rowntree, Isabella de Faria Maciel, Jim Howell, Megan Machmuller, and Erica Patterson for their contributions and inputs during the initial conceptualization phase of this work. We also thank Jocelyn M. Lavallee for her invaluable assistance with the model structure illustration.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.jenvman.2024.121657.

References

- Allen, V.G., Batello, C., Berretta, E.J., Hodgson, J., Kothmann, M., Li, X., McIvor, J., Milne, J., Morris, C., Peeters, A., Sanderson, M., 2011. An international terminology for grazing lands and grazing animals. Grass Forage Sci. 66, 2–28. https://doi.org/ 10.1111/j.1365-2494.2010.00780.x.
- Angst, G., Mueller, K.E., Castellano, M.J., Vogel, C., Wiesmeier, M., Mueller, C.W., 2023. Unlocking complex soil systems as carbon sinks: multi-pool management as the key. Nat. Commun. 14 https://doi.org/10.1038/s41467-023-38700-5.
- Apfelbaum, S.I., Thompson, R., Wang, F., Mosier, S., Teague, R., Byck, P., 2022. Vegetation, water infiltration, and soil carbon response to Adaptive Multi-Paddock and Conventional grazing in Southeastern USA ranches. J. Environ. Manag. 308, 114576 https://doi.org/10.1016/j.jenvman.2022.114576.
- Averill, C., Waring, B., 2017. Nitrogen limitation of decomposition and decay: how can it occur? Global Change Biol. 12, 3218–3221. https://doi.org/10.1111/gcb.13980.
- Bai, Y., Cotrufo, M.F., 2022. Grassland soil carbon sequestration: current understanding, challenges, and solutions. Science 377, 603–608. https://doi.org/10.1126/science. abo2380, 1979.
- Benot, M.-L., Morvan-Bertrand, A., Mony, C., Huet, J., Sulmon, C., Decau, M.-L., Prud'homme, M.-P., Bonis, A., 2019. Grazing intensity modulates carbohydrate storage pattern in five grass species from temperate grasslands. Acta Oecol. 95, 108–115. https://doi.org/10.1016/j.actao.2018.11.005.
- Brilli, L., Bechini, L., Bindi, M., Carozzi, M., Cavalli, D., Conant, R., Dorich, C.D., Doro, L., Ehrhardt, F., Farina, R., Ferrise, R., Fitton, N., Francaviglia, R., Grace, P., Iocola, I., Klumpp, K., Léonard, J., Martin, R., Massad, R.S., Recous, S., Seddaiu, G., Sharp, J., Smith, P., Smith, W.N., Soussana, J.-F., Bellocchi, G., 2017. Review and analysis of strengths and weaknesses of agro-ecosystem models for simulating C and N fluxes. Sci. Total Environ. 598, 445–470. https://doi.org/10.1016/j.scitotenv.2017.03.208.
- Briske, D.D., Joyce, L.A., Polley, H.W., Brown, J.R., Wolter, K., Morgan, J.A., McCarl, B. A., Bailey, D.W., 2015. Climate-change adaptation on rangelands: linking regional exposure with diverse adaptive capacity. Front. Ecol. Environ. 13, 249–256. https:// doi.org/10.1890/140266.
- Calsamiglia, S., Ferret, A., Reynolds, C.K., Kristensen, N.B., van Vuuren, A.M., 2010. Strategies for optimizing nitrogen use by ruminants. Animal 4, 1184–1196. https:// doi.org/10.1017/S1751731110000911.
- Chen, Y., Tao, Y., Cheng, Y., Ju, W., Ye, J., Hickler, T., Liao, C., Feng, L., Ruan, H., 2018. Great uncertainties in modeling grazing impact on carbon sequestration: a multimodel inter-comparison in temperate Eurasian Steppe. Environ. Res. Lett. 13, 075005 https://doi.org/10.1088/1748-9326/aacc75.
- Conant, RichardT., Six, J., Paustian, K., 2004. Land use effects on soil carbon fractions in the southeastern United States. II. changes in soil carbon fractions along a forest to pasture chronosequence. Biol. Fertil. Soils 40, 194–200. https://doi.org/10.1007/ s00374-004-0754-2.
- Conant, R.T., Cerri, C.E.P., Osborne, B.B., Paustian, K., 2017. Grassland management impacts on soil carbon stocks: a new synthesis. Ecol. Appl. 27, 662–668. https://doi org/10.1002/eap.1473.
- Conant, R.T., Paustian, K., Elliott, E.T., 2001. Grassland management and conversion into grassland: effects on soil carbon. Ecol. Appl. 11, 343–355. https://doi.org/ 10.1890/1051-0761(2001)011[0343:GMACIG]2.0.CO;2.
- Conant, R.T., Six, J., Paustian, K., 2003. Land use effects on soil carbon fractions in the southeastern United States. I. Management-intensive versus extensive grazing. Biol. Fertil. Soils 38, 386–392. https://doi.org/10.1007/s00374-003-0652-z.
- Cotrufo, M.F., Lavallee, J.M., 2022. Soil organic matter formation, persistence, and functioning: A synthesis of current understanding to inform its conservation and regeneration. In: Advances in Agronomy. Academic Press Inc, pp. 1–66. https://doi. org/10.1016/bs.agron.2021.11.002.
- Cotruto, M.F., Lavallee, J.M., Zhang, Y., Hansen, P.M., Paustian, K.H., Schipanski, M., Wallenstein, M.D., 2021. In-N-Out: a hierarchical framework to understand and predict soil carbon storage and nitrogen recycling. In: Global Change Biology, vol. 27. John Wiley and Sons Inc, pp. 4465–4468. https://doi.org/10.1111/gcb.15782. Issue 19.
- Cotrufo, M.F., Ranalli, M.G., Haddix, M.L., Six, J., Lugato, E., 2019. Soil carbon storage informed by particulate and mineral-associated organic matter. Nat. Geosci. 12, 989–994. https://doi.org/10.1038/s41561-019-0484-6.
- 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. Nat. Geosci. 8, 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 Biol. 19, 988–995. https://doi.org/ 10.1111/gcb.12113.
- Damian, J.M., Matos, E.S., Pedreira, B.C., Carvalho, P.C.F., Premazzi, L.M., Williams, S., Paustian, K., Cerri, C.E.P., 2021. Predicting soil C changes after pasture intensification and diversification in Brazil. Catena 202. https://doi.org/10.1016/j. catena 2021 105238
- De Graaff, M., Van Groenigen, K., Six, J., Hungate, B., Van Kessel, C., 2006. Interactions between plant growth and soil nutrient cycling under elevated CO2 : a meta-analysis. Global Change Biol. 12, 2077–2091. https://doi.org/10.1111/j.1365-2486.2006.01240.x.
- DeGryze, S., Six, J., Paustian, K., Morris, S.J., Paul, E.A., Merckx, R., 2004. Soil organic carbon pool changes following land-use conversions. Global Change Biol. 10, 1120–1132. https://doi.org/10.1111/j.1529-8817.2003.00786.x.
- Don, A., Schumacher, J., Freibauer, A., 2011. Impact of tropical land-use change on soil organic carbon stocks - a meta-analysis. Global Change Biol. 17, 1658–1670. https:// doi.org/10.1111/j.1365-2486.2010.02336.x.
- Dondini, M., Martin, M., De Camillis, C., Uwizeye, A., Soussana, J.-F., Robinson, T., Steinfeld, H., 2023. Global assessment of soil carbon in grasslands – from current stock estimates to sequestration potential. In: FAO Animal Production and Health Paper No. 187. FAO, Rom. https://doi.org/10.4060/cc3981en.Ehrhardt, F., Soussana, J., Bellocchi, G., Grace, P., McAuliffe, R., Recous, S., Sándor, R.,
- Ehrhardt, F., Soussana, J., Bellocchi, G., Grace, P., McAuliffe, R., Recous, S., Sándor, R., Smith, P., Snow, V., de Antoni Migliorati, M., Basso, B., Bhatia, A., Brilli, L., Doltra, J., Dorich, C.D., Doro, L., Fitton, N., Giacomini, S.J., Grant, B., Harrison, M. T., Jones, S.K., Kirschbaum, M.U.F., Klumpp, K., Laville, P., Léonard, J., Liebig, M., Lieffering, M., Martin, R., Massad, R.S., Meier, E., Merbold, L., Moore, A.D., Myrgiotis, V., Newton, P., Pattey, E., Rolinski, S., Sharp, J., Smith, W.N., Wu, L., Zhang, Q., 2018. Assessing uncertainties in crop and pasture ensemble model simulations of productivity and N 2 O emissions. Global Change Biol. 24, e603–e616. https://doi.org/10.1111/gcb.13965.
- Evers, G.W., 1985. Forage and nitrogen contributions of arrowleaf and subterranean clovers overseeded on bermudagrass and bahiagrass 1. Agron. J. 77, 960–963. https://doi.org/10.2134/agronj1985.00021962007700060030x.
- Georgiou, K., Koven, C.D., Wieder, W.R., Hartman, M.D., Riley, W.J., Pett-Ridge, J., Bouskill, N.J., Abramoff, R.Z., Slessarev, E.W., Ahlström, A., Parton, W.J., Pellegrini, A.F.A., Pierson, D., Sulman, B.N., Zhu, Q., Jackson, R.B., 2024. Emergent temperature sensitivity of soil organic carbon driven by mineral associations. Nat. Geosci. 17, 205–212. https://doi.org/10.1038/s41561-024-01384-7.
- Gong, X.Y., Fanselow, N., Dittert, K., Taube, F., Lin, S., 2015. Response of primary production and biomass allocation to nitrogen and water supplementation along a grazing intensity gradient in semiarid grassland. Eur. J. Agron. 63, 27–35. https:// doi.org/10.1016/j.eja.2014.11.004.
- Hansen, P.M., Even, R., King, A.E., Lavallee, J., Schipanski, M., Cotrufo, M.F., 2024. Distinct, direct and climate-mediated environmental controls on global particulate and mineral-associated organic carbon storage. Global Change Biol. 30, e17080 https://doi.org/10.1111/gcb.17080.
 Hartman, M., Parton, W., Del Grosso, S., Easter, M., Hendryx, J., Hilinski, T.,
- Hartman, M., Parton, W., Del Grosso, S., Easter, M., Hendryx, J., Hilinski, T., Williams, S., 2018. The daily century ecosystem, soil organic matter, nutrient cycling, nitrogen trace gas, and methane model: user manual, scientific basis, and technical documentation. Natural Resource Ecology Laboratory. Colorado State University, Fort Collins, CO.
- Haynes, R.J., Williams, P.H., 1993. Nutrient cycling and soil fertility in the grazed pasture ecosystem 119–199. https://doi.org/10.1016/S0065-2113(08)60794-4.
- Heinke, J., Rolinski, S., Müller, C., 2023. Modelling the role of livestock grazing in C and N cycling in grasslands with LPJmL5.0-grazing. Geosci. Model Dev. (GMD) 16, 2455–2475. https://doi.org/10.5194/gmd-16-2455-2023.
- Herrmann, A., Schachtel, G.A., 2001. OSYAQ, an organ-specific growth model for forage grasses. Grass Forage Sci. 56, 268–284. https://doi.org/10.1046/j.1365-2494.2001.00274.x.
- Hicks Pries, C.E., Ryals, R., Zhu, B., Min, K., Cooper, A., Goldsmith, S., Pett-Ridge, J., Torn, M., Berhe, A.A., 2023. The deep soil organic carbon response to global change. Annu. Rev. Ecol. Evol. Syst. 54, 375–401. https://doi.org/10.1146/annurev-ecolsys-102320-085332.
- IPCC, 2006. In: Eggleston, H.S., Buendia, L., Miwa, K., Ngara, T., Tanabe, K. (Eds.), IPCC Guidelines for National Greenhouse Gas Inventories, Prepared by the National Greenhouse Gas Inventories Programme. Published: IGES, Japan. https://www. ipcc-nggip.iges.or.jp/public/2006gl/vol4.html.
- Jing, Q., Bélanger, G., Baron, V., Bonesmo, H., Virkajärvi, P., Young, D., 2012. Regrowth simulation of the perennial grass timothy. Ecol. Model. 232, 64–77. https://doi.org/ 10.1016/j.ecolmodel.2012.02.016.
- Johnson, C.R., Reiling, B.A., Mislevy, P., Hall, M.B., 2001. Effects of nitrogen fertilization and harvest date on yield, digestibility, fiber, and protein fractions of tropical grasses. J. Anim. Sci. 79, 2439–2448. https://doi.org/10.2527/2001.7992439x.
- Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., Nico, P.S., 2015. Mineral-organic associations: formation, properties, and relevance in soil environments. Adv. Agron. 130, 1–140. https://doi.org/10.1016/bs. agron.2014.10.005.
- Knapp, A.K., 1984. Post-Burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. Am. J. Bot. 71, 220. https://doi.org/10.2307/2443749.
- 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 Biol. 26, 261–273. https://doi.org/10.1111/gcb.14859.

- Leuthold, S., Lavallee, J.M., Haddix, M.L., Cotrufo, M.F., 2024. Contrasting properties of soil organic matter fractions isolated by different physical separation methodologies. Geoderma 445, 116870. https://doi.org/10.1016/j.geoderma.2024.116870.
- Ma, L., Derner, J.D., Harmel, R.D., Tatarko, J., Moore, A.D., Rotz, C.A., Augustine, D.J., Boone, R.B., Coughenour, M.B., Beukes, P.C., van Wijk, M.T., Bellocchi, G., Cullen, B. R., Wilmer, H., 2019. Application of grazing land models in ecosystem management: current status and next frontiers. In: Advances in Agronomy. Academic Press Inc, pp. 173–215. https://doi.org/10.1016/bs.agron.2019.07.003.
- Monsi, M., Saeki, T., 2005. On the factor light in plant communities and its importance for matter production. Ann. Bot. 95, 549–567. https://doi.org/10.1093/aob/ mci052.
- Morgan, J.A., 2005. Rising atmospheric CO2 and global climate change: responses and management implications for grazing lands. In: Grasslands. CRC Press.
- Mosier, S., Apfelbaum, S., Byck, P., Calderon, F., Teague, R., Thompson, R., Cotrufo, M. F., 2021. Adaptive multi-paddock grazing enhances soil carbon and nitrogen stocks and stabilization through mineral association in southeastern U.S. grazing lands. J. Environ. Manag. 288, 112409 https://doi.org/10.1016/j.jenvman.2021.112409.
- National Research Council, 2001. Nutrient Requirements of Dairy Cattle, Seventh Revised Edition, 2001. The National Academies Press. National Academies Press, Washington, DC. https://doi.org/10.17226/9825. Washington, D.C.
- Oesterheld, M., Semmartin, M., 2011. Impact of grazing on species composition: adding complexity to a generalized model. Austral Ecol. 36, 881–890. https://doi.org/ 10.1111/j.1442-9993.2010.02235.x.
- Parsons, A.J., Dumont, B., 2003. Spatial heterogeneity and grazing processes. Anim. Res. 52, 161–179. https://doi.org/10.1051/animres:2003013.
- Peeling, J.A., Judge, J., Misra, V., Jayasankar, C.B., Lusher, W.R., 2023. Gap-free 16-year (2005–2020) sub-diurnal surface meteorological observations across Florida. Sci. Data 10, 907. https://doi.org/10.1038/s41597-023-02826-4.
- Piao, S., Friedlingstein, P., Ciais, P., Viovy, N., Demarty, J., 2007. Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. Global Biogeochem. Cycles 21. https://doi.org/10.1029/ 2006GB002888.
- Poeplau, C., Don, A., Six, J., Kaiser, M., Benbi, D., Chenu, C., Cotrufo, M.F., Derrien, D., Gioacchini, P., Grand, S., Gregorich, E., Griepentrog, M., Gunina, A., Haddix, M., Kuzyakov, Y., Kühnel, A., Macdonald, L.M., Soong, J., Trigalet, S., et al., 2018. Isolating organic carbon fractions with varying turnover rates in temperate agricultural soils – a comprehensive method comparison. Soil Biol. Biochem. 125 (April), 10–26. https://doi.org/10.1016/j.soilbio.2018.06.025.Prairie, A.M., King, A.E., Cotrufo, M.F., 2023. Restoring particulate and mineral-
- Prairie, A.M., King, A.E., Cotruto, M.F., 2023. Restoring particulate and mineralassociated organic carbon through regenerative agriculture. Proc. Natl. Acad. Sci. USA 120. https://doi.org/10.1073/pnas.2217481120.
- Prior, S.A., Runion, G.B., Torbert, H.A., 2019. Long-term response of a bahiagrass pasture to elevated CO2 and soil fertility management. Soil Tillage Res. 194 https://doi.org/ 10.1016/j.still.2019.104326.
- Robertson, A.D., Paustian, K., Ogle, S., Wallenstein, M.D., Lugato, E., Francesca Cotrufo, M., 2019. Unifying soil organic matter formation and persistence frameworks: the MEMS model. Biogeosciences 16, 1225–1248. https://doi.org/ 10.5194/bg-16-1225-2019.
- Rocci, K.S., Cotrufo, M.F., Ernakovich, J., Foster, E., Frey, S., Georgiou, K., Grandy, A.S., Malhotra, A., Reich, P.B., Schlerman, E.P., Wieder, W.R., 2024. Bridging 20 Years of Soil Organic Matter Frameworks: Empirical Support, Model Representation, and Next Steps. J Geophys Res Biogeosci 129. https://doi.org/10.1029/2023JG007964.
- Rocci, K.S., Lavallee, J.M., Stewart, C.E., Cotrufo, M.F., 2021. Soil organic carbon response to global environmental change depends on its distribution between mineral-associated and particulate organic matter: a meta-analysis. Sci. Total Environ. 793, 148569 https://doi.org/10.1016/j.scitotenv.2021.148569.
- Romero-Ruiz, A., Rivero, M.J., Milne, A., Morgan, S., Meo Filho, P., Pulley, S., Segura, C., Harris, P., Lee, M.R.F., Coleman, K., Cardenas, L., Whitmore, A.P., 2023. Grazing livestock move by Lévy walks: implications for soil health and environment. J. Environ. Manag. 345, 118835 https://doi.org/10.1016/j.jenvman.2023.118835.
- Rowland, A.P., Roberts, J.D., 1994. Ligan and cellulose fractionation in decomposition studies using acid-detergent fibre methods. Commun. Soil Sci. Plant Anal. 25 (3–4), 269–277. https://doi.org/10.1080/00103629409369035.
- Ruelle, E., Hennessy, D., Delaby, L., 2018. Development of the Moorepark St Gilles grass growth model (MoSt GG model): a predictive model for grass growth for pasture based systems. Eur. J. Agron. 99, 80–91. https://doi.org/10.1016/j.eja.2018.06.010.
- Rumpel, C., Kögel-Knabner, I., 2011. Deep soil organic matter-a key but poorly understood component of terrestrial C cycle. Plant Soil 338, 143–158. https://doi. org/10.1007/s11104-010-0391-5.
- Rymph, S.J., 2004. Modeling Growth and Composition of Perennial Tropical Forage Grasses. University of Florida.
- Saggar, S., Andrew, R.M., Tate, K.R., Hedley, C.B., Rodda, N.J., Townsend, J.A., 2004. Modelling nitrous oxide emissions from dairy-grazed pastures. Nutrient Cycl. Agroecosyst. 68 (3), 243–255. https://doi.org/10.1023/B:FRES.0000019463.92440. a3.
- Sanderman, J., Hengl, T., Fiske, G.J., 2017. Soil carbon debt of 12,000 years of human land use. In: Proceedings of the National Academy of Sciences, vol. 114, pp. 9575–9580. https://doi.org/10.1073/pnas.1706103114.
- Schrumpf, M., Kaiser, K., Mayer, A., Hempel, G., Trumbore, S., 2021. Age distribution, extractability, and stability of mineral-bound organic carbon in central European soils. Biogeosciences 18, 1241–1257. https://doi.org/10.5194/bg-18-1241-2021.
- soils. Biogeosciences 18, 1241–1257. https://doi.org/10.5194/bg-18-1241-2021.
 Silva, Y.F., Valadares, R.V., Dias, H.B., Cuadra, S.V., Campbell, E.E., Lamparelli, R.A.C., Moro, E., Battisti, R., Alves, M.R., Magalhães, P.S.G., Figueiredo, G.K.D.A., 2022.

Intense pasture management in Brazil in an integrated crop-livestock system simulated by the DayCent model. Sustainability 14. https://doi.org/10.3390/ su14063517.

- Smith, H.D., Wilson, C.H., Rymph, S.J., Santos, E.R.S., Boote, K.J., 2023. Adapting the CROPGRO perennial forage model to predict growth and development of Pensacola bahiagrass. Field Crops Res. 302 https://doi.org/10.1016/j.fcr.2023.109095.
- Snow, V.O., Rotz, C.A., Moore, A.D., Martin-Clouaire, R., Johnson, I.R., Hutchings, N.J., Eckard, R.J., 2014. The challenges – and some solutions – to process-based modelling of grazed agricultural systems. Environ. Model. Software 62, 420–436. https://doi.org/10.1016/i.envsoft.2014.03.009.
- Sokol, N.W., Sanderman, J., Bradford, M.A., 2019. Pathways of mineral-associated soil organic matter formation: integrating the role of plant carbon source, chemistry, and point of entry. Global Change Biol. 25, 12–24. https://doi.org/10.1111/gcb.14482.
- Soltani, A., Sinclair, T.R., 2012. Modeling Physiology of Crop Development, Growth and Yield. CABI, Wallingford. https://doi.org/10.1079/9781845939700.0000.
- Soong, J.L., Parton, W.J., Calderon, F., Campbell, E.E., Cotrufo, M.F., 2015. A new conceptual model on the fate and controls of fresh and pyrolized plant litter decomposition. Biogeochemistry 124, 27–44. https://doi.org/10.1007/s10533-015-0079-2.
- Soussana, J.-F., Soussana, J.-F., Loiseau, P., Vuichard, N., Ceschia, E., Balesdent, J., Chevallier, T., Arrouays, D., 2004. Carbon cycling and sequestration opportunities in temperate grasslands. Soil Use Manag. 20, 219–230. https://doi.org/10.1079/ sum2003234.
- Spitters, C.J.T., Aerts, R., 1983. Simulation of competition for light and water in cropweed associations. Aspect Appl. Biol. 4, 467–483.
- Stanley, P., Spertus, J., Chiartas, J., Stark, P.B., Bowles, T., 2023. Valid inferences about soil carbon in heterogeneous landscapes. Geoderma 430, 116323. https://doi.org/ 10.1016/j.geoderma.2022.116323.
- Stanley, P.L., Wilson, C., Patterson, E., Machmuller, M.B., Cotrufo, M.F., 2024. Ruminating on soil carbon: applying current understanding to inform grazing management. Global Change Biol. 30 https://doi.org/10.1111/gcb.17223.
- Thornton, M.M., Shrestha, R., Wei, Y., Thornton, P.E., Kao, S.-C., Wilson, B.E., 2022. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 4 R1. ORNL DAAC, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ ORNLDAAC/2129.
- Turner, C.L., Seastedt, T.R., Dyer, M.I., 1993. Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. Ecol. Appl. 3, 175–186. https://doi.org/10.2307/1941800.Van Soest, P.J., Robertson, J.B., Lewis, B.A., 1991. Methods for dietary fiber, neutral
- Van Soest, P.J., Robertson, J.B., Lewis, B.A., 1991. Methods for dietary fiber, neutral detergent fiber, and non starch polysaccharides in relation to animal nutrition. J. Dairy Sci. 74 (10), 3583–3597. https://doi.org/10.3168/jds.S0022-0302(91) 78551-2.
- Wang, F., Apfelbaum, S.I., Thompson, R.L., Teague, R., Byck, P., 2021. Effects of adaptive multiple paddock and continuous grazing on fine-scale spatial patterns of vegetation species and biomass in commercial ranches. Landsc. Ecol. 36, 2725–2741. https:// doi.org/10.1007/s10980-021-01273-z.
- Wang, J., Li, Y., Bork, E.W., Richter, G.M., Eum, H.-I., Chen, C., Shah, S.H.H., Mezbahuddin, S., 2020. Modelling spatio-temporal patterns of soil carbon and greenhouse gas emissions in grazing lands: current status and prospects. Sci. Total Environ. 739, 139092 https://doi.org/10.1016/j.scitotenv.2020.139092.
- Wang, T., Teague, W., Park, S., Bevers, S., 2015. GHG mitigation potential of different grazing strategies in the United States Southern Great Plains. Sustainability 7, 13500–13521. https://doi.org/10.3390/su71013500.
- Wardeh, M.F., 1981. Models for estimating energy and protein utilization for feeds. All Graduate Theses and Dissertations. 4556. Utah State University, Utah. https://doi. org/10.26076/9026-5aad.
- Weiss, W.P., Conrad, H.R., St Pierre, N.R., 1992. A theoretically-based model for predicting total digestible nutrient values of forages and concentrates. Anim. Feed Sci. Technol. 39, 95–110. https://doi.org/10.1016/0377-8401(92)90034-4.
- West, T.O., Six, J., 2007. Considering the influence of sequestration duration and carbon saturation on estimates of soil carbon capacity. Clim. Change 80, 25–41. https://doi. org/10.1007/s10584-006-9173-8.
- White, L.J., Yeater, K.M., Lehman, R.M., 2023. Soil microorganisms respond distinctively to adaptive multi-paddock and conventional grazing in the southeastern United States. Soil Sci. Soc. Am. J. 87, 1096–1108. https://doi.org/10.1002/saj2.20573.
- White, L.M., 1973. Carbohydrate reserves of grasses: a review. J. Range Manag. 26, 13. https://doi.org/10.2307/3896873.
- Wilson, L.T., Yang, Y., Wang, J., 2024. Integrated Agricultural Information and Management System (iAIMS): World Climatic Data. January 2024. https://beaum ont.tanu.edu/(ClimaticData/)
- Xin, Q., Broich, M., Zhu, P., Gong, P., 2015. Modeling grassland spring onset across the Western United States using climate variables and MODIS-derived phenology metrics. Remote Sens. Environ. 161, 63–77. https://doi.org/10.1016/j. rse.2015.02.003.
- Yin, X., 2000. A generic equation for nitrogen-limited leaf area index and its application in crop growth models for predicting leaf senescence. Ann. Bot. 85, 579–585. https://doi.org/10.1006/anbo.1999.1104.
- Yin, X., Laar, H.H. van, 2005. Crop Systems Dynamics: an Ecophysiological Simulation Model for Genotype-By-Environment Interactions. Wageningen Academic Pub.
- Zhang, Y., Lavallee, J.M., Robertson, A.D., Even, R., Ogle, S.M., Paustian, K., Cotrufo, M. F., 2021. Simulating measurable ecosystem carbon and nitrogen dynamics with the mechanistically defined MEMS 2.0 model. Biogeosciences 18, 3147–3171. https:// doi.org/10.5194/bg-18-3147-2021.