

JGR Biogeosciences

RESEARCH ARTICLE

10.1029/2022JG006807

Key Points:

- We use a dynamic model of wetland soil processes to understand the fate of soil carbon upon land loss by submergence
- The key parameters controlling the changing patterns of soil carbon are related to how humification and mineralization vary with depth
- Fitting the model to a Louisiana coastal salt marsh suggests that the timescale of changes after submergence is long, about 200 years

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:

Schoolmaster, D. R. Jr., Stagg, C. L., Creamer, C., Laurenzano, C., Ward, E. J., Waldrop, M. P., et al. (2022). A model of the spatiotemporal dynamics of soil carbon following coastal wetland loss applied to a Louisiana salt marsh in the Mississippi River Deltaic Plain. Journal of Geophysical Research: Biogeosciences, 127, e2022JG006807. https://doi. org/10.1029/2022JG006807

Received 18 JAN 2022 Accepted 31 MAY 2022

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A Model of the Spatiotemporal Dynamics of Soil Carbon Following Coastal Wetland Loss Applied to a Louisiana Salt Marsh in the Mississippi River Deltaic Plain

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Abstract The potential for carbon sequestration in coastal wetlands is high due to protection of carbon (C) in flooded soils. However, excessive flooding can result in the conversion of the vegetated wetland to open water. This transition results in the loss of wetland habitat in addition to the potential loss of soil carbon. Thus, in areas experiencing rapid wetland submergence, such as the Mississippi River Delta, coastal wetlands could become a significant source of carbon emissions if land loss is not mitigated. To accurately assess the capacity of wetlands to store (or emit) carbon in dynamic environments, it is critical to understand the fate of soil carbon following the transition from vegetated wetland to open water. We developed a simple soil carbon model representing soil depths to 1 m using the data collected from a Louisiana coastal salt marsh in the Mississippi River Deltaic Plain to predict soil carbon density and stock following the transition from a vegetated salt marsh to an open water pond. While immediate effects of ponding on the distribution of carbon stocks 14 years, following wetland submergence. Rather, the model predicts that soil carbon losses in the first meter will be realized over long periods of time (~200 years) due to changes in the source of carbon (biomass vs. mineral sediment) with minimal losses through mineralization.

Plain Language Summary In nature, many processes, while dynamic, are thought to settle to a stable state. For example, coastal wetlands are dynamic systems, continually changing in response to environmental conditions, such as sea-level rise, including submergence of the wetland. We use the model to ask what happens to the steady state of soil carbon if the wetland is lost to submergence. We use parameters that specify environmental conditions to assess how the steady state changes, how long the system takes to reach the new steady state, and the fate of the carbon as it changes, how much is buried, and how much lost to the atmosphere. The answer to these questions has important implications for understanding the contribution of coastal wetlands to the global carbon cycle as wetlands are lost to rising sea levels.

1. Introduction

Over the last decade, a growing body of research has highlighted the significant contribution of coastal wetlands to the global carbon budget (Chmura et al., 2003; Duarte, 2017; Mcleod et al., 2011; Page & Baird, 2016; USGCRP, 2018), revealing coastal wetlands as ideal ecosystems for accumulating and storing carbon as well as making them key components of nature-based climate mitigation plans (Drever et al., 2021; Larson et al., 2020; United States Environmental Protection Agency, 2021).

However, in many regions of the world, coastal wetlands are threatened by climate and land use change impacts, such as relative sea-level rise and extreme climate events (Babcock et al., 2019; IPCC, 2021; Schuerch et al., 2018; Stagg et al., 2021) and barriers to inland migration (Borchert et al., 2018), putting decades and even centuries of stored carbon at risk (Baustian et al., 2021). For example, while carbon sequestration in U.S. coastal wetlands provides an overall net sink of 8.5–8.7 Mt $CO_2 e y^{-1}$, high rates of coastal wetland land loss in the Mississippi River Delta Plain, through processes like submergence, have resulted in significant emissions,



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Writing – review & editing: Donald R. Schoolmaster, Camille L. Stagg, Courtney Creamer, Claudia Laurenzano, Eric J. Ward, Mark P. Waldrop, Melissa M. Baustian, Tiong Aw, Sergio Merino, Rachel Villani weakening the coastal wetland sink (Crooks et al., 2018) and potentially exacerbating climate impacts. Yet, the fate of soil carbon following wetland submergence remains a critical source of uncertainty that can significantly affect assumptions about wetland conversion to open water in assessments of carbon sequestration capacity and sustainability (Holmquist et al., 2018). Thus, it is critical to improve our understanding of the mechanisms that control soil carbon density and stocks in dynamic wetland environments to predict the fate of soil carbon following wetlands ubmergence and to assess the impact of future climate and land use change on carbon sequestration in coastal wetlands.

In general, there are two main sources of soil organic carbon (SOC) in coastal wetlands: (a) allochthonous carbon and (b) autochthonous carbon (Neubauer, 2008; Nyman et al., 2006). Since submergence results in large reductions in above and below ground biomass production or autochthonous carbon production (Nyman et al., 1993; Stagg et al., 2020), it follows that the transition from vegetated state to open water state could result in a loss of SOC (DeLaune & White, 2012; Lane et al., 2016; Sapkota & White, 2021). However, because there are multiple processes contributing to carbon import (sedimentation and primary production) as well as carbon export (mineralization, burial, and erosion) from a given stratum of wetland soils, the pattern and timescale of soil carbon loss over time are difficult to predict. Thus, numerous potential trajectories of carbon loss are possible, depending upon the relationship of these processes and how it changes through space and time (Figure 1). These scenarios for transient dynamics represent potentially different implications for assessment and management. For example, given scenarios I and II, where carbon loss is initially very slow and increases significantly over time, short-term assessments are likely to underestimate the final impact of wetland submergence. On the other hand, because of the slow initiation of carbon loss dynamics following conversion of the vegetated wetland to open water, these scenarios provide the greatest opportunity for mitigation before full impact of carbon loss is realized. Given scenarios III and IV, where carbon stocks rapidly decline following submergence, short-term assessments could reveal a more accurate estimate of the rates of future carbon loss, but provide less time for mitigation.

The overarching objective of this study is not to build a model that predicts the likelihood or mechanism of wetland loss, but rather to determine the fate of SOC density and stock after wetland submergence. This is a multifaceted problem since the outcomes for an individual wetland will likely depend on the complex interaction of the traits of the vegetation community, the decomposer community, geomorphology, environmental conditions, and site history. The goal of this paper is to synthesize what is known about the processes controlling the fate of SOC in coastal wetlands in the form of a simple dynamic model. The model will be used as a complex multivariate hypothesis to predict possible trajectories and timescales of the post-submergence soil carbon dynamics as well as to identify the concepts, represented as model parameters, that are crucial for different outcomes. Finally, relating parameters to biological and environmental factors and processes will allow us to use the model as a foundation for organizing and interpreting future empirical investigations of this system.

The specific goals of this paper are to (a) develop a simple, general model of coastal wetland soil carbon dynamics; (b) apply the model to determine which factors control SOC density and stock under vegetated conditions, ponded conditions, and the dynamic features of the transition between them; and (c) predict the fate of soil carbon density and stock following the transition from vegetated marsh to open water pond.

2. Model

Our strategy was to introduce a simple, single-stratum, model of soil carbon dynamics derived from agricultural models and adapt it for coastal wetlands. The single-stratum model focuses on the deterministic, incremental processes associated with carbon dynamics and does not include the temporal variation in processes, such as accretion and erosion. We analyzed equilibria and stability of the single-stratum model to develop the understanding of the model's behavior and how it depends on the parameters. We then used the single-stratum model as a sub-model to be coupled with others to create 1-m soil profiles. We used the resulting system of coupled equations to simulate the effects of wetland submergence on the fate of the soil carbon density in the profile to represent the stock (1 m). Finally, we compared the model output to data from Louisiana coastal wetlands to identify hypotheses that will guide future research on the processes that control carbon densities in transitioning ecosystems. The goal of the comparison with data is to act as a feasibility check and to demonstrate the types of insights that are possible, not to present a definitive full analysis of the particular system.





Figure 1. (a) Graphical representation of hypothesized scenarios of soil carbon stock change over time during the transition from a vegetated to ponded state. Roman numerals denote different scenarios: (I) transient increase followed by rapid decline, (II) concave decrease, (III) linear decline, and (IV) convex decline. (b) Healthy, vegetated salt marsh plot. (c) Ponded salt marsh plot.

2.1. Single-Stratum Model

We start with a model of SOC introduced originally by Hénin and Dupuis (1945) and adapted by many others (e.g., Andriulo et al., 1999; Huggins et al., 1998; Kemanian & Stöckle, 2010). This model conceives the breakdown of plant residues as resulting in a fraction of stable, humified carbon (residence times of decades–centuries) (Andriulo et al., 1999; Unger et al., 2016). This pool represented by the symbol, C, is followed as the main state variable of the model. In addition, we assume the existence of a highly resistant fraction, often called the passive pool (millennial residence times), which remains constant at the timescales considered here. In this model, the passive pool can be effectively considered a constant offset when calculating total organic carbon. We will refer to the carbon in plant residues as "residue carbon"; carbon in the stable pool, represented by the variable C, as "humified carbon"; and sum of residue, humified, and passive carbon as "total carbon" and measure each in units of g/cm^3 . For simplicity, during model development, unless otherwise stated, we will assume that the passive pool is zero.

In the model of Hénin and Dupuis (1945), the labile portion of plant residues is decomposed to result in the emission of CO₂ or CH4 (depending on oxygen availability and salinity) and an increase in the amount of carbon in the humified fraction at rate k_0 . The humified carbon is lost through mineralization at the per unit rate f_0 (Figure 2). Combining these gives,



 $\frac{dC}{dt} = k_0 \gamma_0 B - f_0 C, \qquad (1)$

where *B* is the density of plant residues in the soil volume and γ_0 is a conversion constant describing how much carbon is in each unit of plant residue. We adapted this model to make it more appropriate for coastal wetlands in two ways. First, we included the effect of accretion, which occurs at rate *r* and adds sediment with a carbon density of C_{in} . To ensure that the volume of soil that we are modeling remains constant, we account for the change in carbon from the bottom of the soil volume as the elevation is shifted by accretion (i.e., burial) (Figure 3). Thus, note that this model does not account for changes in bulk density; those are accounted for in the data-fitting process (described below). This results in the equation,

Figure 2. Graphical representation of the soil carbon and residue models shown in Equations 2 and 3, where the humified fraction (*C*) increases through accretion at rate *r* and at the per unit *B* humification rate *k*. Humified carbon (*C*) decreases at the per unit *C* mineralization rate *f* and burial rate *r*. Plant residues (*B*) increase at maximum per-unit *B* production rate α and are lost to burial at rate *r*.

$$\frac{dC}{dt} = rC_{in} + k_0 \gamma_0 B - f_0 C - rC.$$
⁽²⁾





Figure 3. The cylinder on the left represents the core of soil being modeled at time t = 0. The length of the core is always a distance *h* from the soil surface. The cylinder on the right shows that after some passage of time δt , additional soil has been added to the top via accretion at rate r_0 . To conserve the total volume being modeled, we shift the frame of reference by $r_0 \delta t$ to include this new soil (the light gray area), leaving behind the same volume of soil from the bottom of the core (the dark gray area).

Next, we included the dynamics of the plant residues explicitly,

$$\frac{dB}{dt} = \alpha_0 B \left(1 - B/B_{\text{max}} \right) - k_0 B - rB, \tag{3}$$

where α_0 is the rate of plant residue production (i.e., biomass production) and B_{max} is the maximum capacity of plant residues. To summarize Equations 2 and 3 in words, Equation 2 indicates that within the 1-m strata soil carbon increases through accretion and the humification of plant residues and decreases through mineralization and burial. Equation 3 indicates that plant residues are produced at a decreasing rate of plant residue concentration and are lost through humification and burial. We do not explicitly include erosion in this model, but the accretion rate can represent a net rate, which could include losses from erosion. In the current analysis, we only consider cases in which accretion rate is positive. The units for each of the variables and parameters of this model are shown in Table 1.

To generalize this model and simplify the analysis, we nondimensionalize Equations 2 and 3 by introducing dimensionless concepts of humified carbon c, plant residues b, and time τ , such that,

$$c = C/C_{in} \tag{4}$$

$$= B/B_{\rm max}$$
 (5)

$$\tau = t r. \tag{6}$$

Substituting Equations 4-6 into Equations 2 and 3 and rearranging gives,

$$\frac{dc}{d\tau} = 1 + \frac{k_0}{r} \gamma_0 \frac{B_{\text{max}}}{C_{in}} b - \frac{f_0}{r} c - c, \qquad (7)$$

$$\frac{db}{d\tau} = \frac{\alpha_0}{r}b(1-b) - \frac{k_0}{r}b - b.$$
(8)

Defining the scaled parameters $k = \frac{k_0}{r}$, $f = \frac{f_0}{r}$, $\alpha = \frac{\alpha_0}{r}$, and $\gamma = \gamma_0 \frac{B_{\text{max}}}{C_{in}}$ gives the final form,

b

$$\frac{dc}{d\tau} = 1 + k\gamma b - fc - c, \tag{9}$$

Table 1

Published System Estimates for Model Parameters

Parameter	Meaning	Value range	Source
C _{in}	Accreted Carbon Density	0.03 g/cm ³	Baustian et al., 2021
B _{max}	Maximum Biomass Residue Density	0.01-0.1 g/cm ²	Stagg et al., 2017
r	Scaled Accretion Rate	0.25 1/yr	Baustian et al., 2021
k_0	Humification Rate	2%-4% 1/day	Stagg et al., 2018
f_0	Mineralization Rate	0.4%-0.8% 1/day	Stagg et al., 2018
γ_0	Carbon Content Per Unit Residue	0.4	
$lpha_0$	Per-unit Residue Production Rate	101/yr	-
$\lambda_{B\max}$	Rate Residue Density Decreases with Depth	0.11/cm	Stagg et al., 2017
λ_k	Rate Humification Slows with Depth	0.025-0.05 1/cm	Stagg et al., 2018
λ_f	Rate Mineralization Slows with Depth	0.025-0.05 1/cm	Stagg et al., 2018
ϕ_k	Reduction of Surface Humification Rate with Ponding	0.25-0.5	Stagg et al., 2018
$\phi_{_f}$	Reduction in Surface Mineralization Rate with Ponding	0.25-0.5	Stagg et al., 2018

Note. These ranges were used to select constant values and initial estimates for model fitting and in simulations.



$$\frac{db}{d\tau} = \alpha b(1-b) - kb - b. \tag{10}$$

The scaled rate parameters are interpreted as the rates relative to accretion rate, for example, k = 2 indicates that the humification rate is twice the rate of accretion. Dimensionless carbon, c, is the density of carbon relative to that coming from accretion and dimensionless plant residue, b, is the density relative to the maximum, thus $0 \le b \le 1$.

Solving the system $(\frac{dc}{d\tau} = 0, \frac{db}{d\tau} = 0)$ for equilibria expressions, $\{c^*, b^*\}$ gives two possible steady state conditions. A ponded state, represented by

$$b^* = 0 \tag{11}$$

$$c^* = \frac{1}{1+f}.$$
 (12)

This equilibrium is stable for $\alpha < 1 + k$, which can be interpreted as where the low-density per-unit production rate of plant residues is less than the per-unit loss rate. The other, vegetated, steady-state condition is

$$b^* = 1 - \frac{1+k}{\alpha} \tag{13}$$

$$c^* = \frac{1+k\gamma}{1+f} - \frac{k\gamma(1+k)}{\alpha(1+f)},$$
(14)

which is stable when the low-density per-unit production rate of plant residues is greater than the per-unit loss rate, $\alpha > 1 + k$. Examples of visualizations of these solutions for different parameter values are presented in the Supporting Information S1.

This model can be solved explicitly to give the time course of plant residues and humified soil carbon for the transition from vegetated to ponded conditions. This is done by setting $\alpha = 0$ and solving for $c(\tau)$ and $b(\tau)$ with initial conditions given by the equilibrium values of the vegetated state (Equations 13 and 14). Doing so gives,

$$c(\tau) = \frac{\gamma k(k+1)(-\alpha'+k+1)}{\alpha'^{(f+1)(f-k)}} e^{-(f+1)\tau} + \frac{\gamma k(-\alpha'+k+1)}{\alpha'^{(k-f)}} e^{-(k+1)\tau} + \frac{1}{f+1}$$
(15)

$$b(\tau) = \frac{(\alpha' - k - 1)}{\alpha'} e^{-(k+1)\tau},$$
(16)

where α' is the low-density per-unit plant residue production rate of the vegetated state. The dynamics given by Equation 15 is the sum of two negative exponential functions of time. Curves defined in Equation 15 all have similar form; they describe a state where soil carbon initially decreases slowly but at a rate that increases with time until slowing as the zero-residue steady state at $\frac{1}{f+1}$ is neared. The dynamics given for $b(\tau)$ in Equation 16 is a simple negative exponential, which decreases fastest initially and slows as it nears zero. Note that the accretion rate, r, is relative to the depth of the soil core being modeled. For example, if the measured accretion rate is $r_0 = 0.5$ cm/y and the volume of soil being modeled is based on 2-cm sections, then $r = \frac{0.5 \text{cm/y}}{2\text{cm}} = 0.25 \text{ l/yr}$ and $t = \tau/r = \tau \times 4 \text{ yr}$.

2.2. Soil Profile Model

In this section, we modify the model to allow for variation in parameters with depth. We do this by treating the volume of soil as a series of, n + 1, stacked strata, denoted by $i = \{0, 1, ..., n\}$, such that i = 0 is nearest the surface and i = n is the deepest. We assume homogeneity within strata. We also treat parameter constants k, f, and B_{max} as functions that vary with depth. We assume that each follows a negative exponential relationship with depth stratum, i, of the form

$$g(i) = g_0 e^{-\lambda i}, \ \lambda \ge 0. \tag{17}$$



Table 2	
Constant and Estimated Parameter	Values

Parameter	Fitted value
Passive pool C (ψ)	10.24 (0.34)%
C _{in}	0.03 g/cm ³
r	0.25 1/yr
k ₀	1.78% 1/day
f_0	0.35% 1/day
α_0	5.35 1/yr
$\gamma_0 \frac{B_{\max}}{C_{in}}$	0,07 (0.001)
$\lambda_{B_{\max}}$	0.11/cm
λ_k	0.03 (0.001)1/cm
λ_f	0.76 (0.15) 1/cm
ϕ_k	0.5
ϕ_{f}	0.5

Note. Estimated values shown with standard errors in parentheses.

The rate constant $\lambda_{B\max}$ is a species-specific parameter related to how plant residue distribution varies with depth and λ_k , λ_f are functions of environmental conditions and decomposer community. Later in the analysis, we assume that the humification and mineralization rates are slower under ponded than vegetated conditions due to decreased oxygen availability. To achieve this, we allow $g_0(1 - \phi s)$, where $0 \le \phi \le 1$ is the proportional decrease in the rate caused by submergence and *s* is an indicator variable such that s = 0 indicates the vegetated state and s = 1 indicates the ponded state. For simplicity, unless otherwise stated, we set $\phi_k = 0$ and $\phi_f = 0$ for the analytical treatment and $\phi_k = \phi_f = 0.5$ for the data fitting (Table 2).

The modified model is, for i = 0,

$$\frac{dC_i}{dt} = rC_{in} + g_k(0)\gamma_0 B_i - g_f(0)C_i - rC_i$$
(18)

$$\frac{dB_i}{dt} = \alpha_0 B_i \left(1 - B_i / g_{B_{\text{max}}}(0) \right) - g_k(0) B_i - r B_i,$$
(19)

and for i > 0,

$$\frac{lC_i}{dt} = rC_{i-1} + g_k(i)\gamma_0 B_i - g_f(i)C_i - rC_i$$
(20)

$$\frac{dB_i}{dt} = rB_{i-1} + \alpha_0 B_i \left(1 - B_i / g_{B_{\max}}(i) \right) - g_k(i) B_i - rB_i,$$
(21)

Notice that strata are coupled so that the losses due to the burial at stratum i are inputs at stratum i + 1.

a

For completeness we define

$$g_{B_{\max}}(i) = B_{\max} e^{-\lambda_{B_{\max}}i}$$
(22)

$$g_k(i) = k_0 e^{-\lambda_k i} \tag{23}$$

$$g_f(i) = f_0 e^{-\lambda_f i}.$$
(24)

The nondimensionalization and reparameterization from the last section can be applied to this model without modification.

As with the homogenous system, this system has two possible equilibrium solutions. The ponded equilibrium is given by

$$b_i^* = 0$$
 (25)

$$c_i^* = \frac{1}{\prod_{i=0}^n 1 + g_k(i)},\tag{26}$$

and is locally stable for $\alpha < 1 + g_k(0)$. Notice that since each element of the product of the denominator of Equation 26, $1 + g_k(i)$, is greater than one, the equilibrium depth profile for carbon in the ponded state will be a decreasing function of depth. The expressions for the vegetated equilibrium are the same as Equations 13 and 14 for i = 0, but increasingly complex and harder to interpret symbolically for i > 0. This equilibrium is stable for $\alpha > 1 + g_k(0)$.

2.3. Simulations

We used simulation to inspect the vertical profiles and dynamics of transition between vegetated and ponded equilibria predicted by the heterogenous depth model. These simulations assume that the transition from vegetated to ponded equilibria occurs due to the death of vegetation and the subsidence of the soil profile resulting in a ponded condition (i.e., peat collapse, *sensu* Chambers et al., 2019). For each of the simulations, we imagine a 1-m





Figure 4. Location of data collection. (a) Site location in southeast Louisiana; (b) site location along the northern Gulf of Mexico; and (c) detailed geographical relationship of data collection sites; color indicates site state (vegetated and ponded) and pond age.

core divided into 50 equal 2-cm sections labeled as stratum $i = \{0, 1, ..., 49\}$. Because the potential full parameter space of the model is very large, we restrict simulations to a range similar to what has been observed in Louisiana coastal wetlands of the Northern Gulf of Mexico (Table 1 $\phi_k = \phi_f = 0$), and once with a ponding-induced decrease in humification and mineralization rates ($\phi_k = \phi_f > 0$). The results of the simulations are helpful for understanding how the various parameters affect both the predicted depth profiles for plant residue and humified carbon density and for the dynamics of total carbon stocks (labile, humified, and passive pools) after ponding. The simulation results are presented in Supporting Information S1.

3. Data Collection and Analysis

Empirical data were collected from a tidal salt marsh site (CRMS0224, https://lacoast.gov/crms/) located along the northern Gulf of Mexico, in the Mississippi River Deltaic Plain of Louisiana, USA (Figure 4). The salt marsh composition was a classic mosaic of vegetated patches interspersed with tidal creeks and small open water ponds (<10 m²). The vegetated patches were dominated by *Spartina alternifora* and *Juncus roemerianus*. The ponds varied in age from less than 1 year to greater than 20 years as determined from the land cover change analysis during 1998–2018 (Cadigan et al., in review). Empirical data were collected from both vegetated sites and ponded sites, providing a chronosequence of pond formation.

During the end of the season peak biomass (October 2019), soil cores were collected to a 1-m depth from the soil surface using a McCauley corer, which collect the soil with minimal disturbance or compaction in a half-barrel chamber (2.5-cm radius of half-volume core) (Baustian et al., 2017). Soil cores were visually characterized in the field (United States Department of Agriculture, Natural Resources Conservation Service, 2018), halved into two ~50-cm sections, and transferred into 50-cm-long PVC half-pipes for storage. Soil core length within



the half-pipe was recorded to 0.5-cm resolution, pore spaces were filled with plastic wrap, and the entire unit (half-pipe + soil core) was secured in plastic wrap and placed flat on dry ice while in the field. Upon returning from the field, soil cores were stored in a freezer (-20° C) until they were shipped on dry ice to the USGS Soil Ecology Lab (Menlo Park, CA) for analysis.

3.1. Chemical Analyses

Prior to the analysis, frozen soil cores were cut into 2-cm segments using a bandsaw, measured to the nearest 0.01 mm, air dried for 7 days at room temperature, oven-dried to a constant weight for 24 hr at 60°C, and all material was ground to <144 μ m. Total carbon and nitrogen concentrations were quantified for every ground 2-cm segment after mixing using a high-temperature combustion CN analyzer (Carlo-Erba; Thermo Scientific). The samples did not contain carbonates (negative test for the presence of inorganic carbon indicated by an absence of effervescence within 5 min after the addition of 4 M hydrochloric acid to moist soils; Nelson & Sommers, 1996); therefore, measured total carbon is equivalent to total organic carbon.

We calculated bulk density (g cm⁻³, mass of dry soil/half-core volume of soil) for each 2-cm section, where soil core diameter = 5.1 cm as the half-core volume times the length of the section. For any sections where exact lengths could not be measured, the length was assumed to be 2 cm. This calculation assumes that any sediment gaps in the cores were due to hydric zones, not to loss of material during coring. Carbon density (g C cm⁻³, bulk density x carbon concentration) was calculated for each 2-cm segment, and carbon stocks (g C cm⁻², carbon density/core length) were calculated for the entire core (1-m depth).

3.2. Quantitative Analyses

For comparisons between model output and data, we grouped sites by time since ponding had occurred. For this analysis, we used the two groups on either end of the spectrum; currently vegetated sites (0 Year) and sites that have been ponded for 14 or more years (14+ Year). The period of the post-ponding group was chosen to give multiple observations of oldest set of sites possible to allow for the greatest potential difference from the vegetated site. There were 4 sites in the 0 Year group and 3 sites in the 14+ Year group. The total number of parameters of the model is large and varied in the amount of information available in the literature. We decided which parameters to fit versus which parameters to set as a constant based on the results of simulations and a literature review. We chose parameters to set as constants that were well known for the system or seemed to have little effect on the shape of the soil carbon profile based on simulations. We fit parameters that had strong potential to affect the shape of the soil profile and were less well specified in the literature.

To fit model output (carbon density) to the observed data (percent carbon), we divided the carbon density output by the model by the observed value of bulk density at the given stratum and included a parameter, ψ , to account for the percent carbon in the passive pool. We fit the numerically simulated model results of the equilibrium value of the vegetated state and t = 18 for the ponded state to the respective observed percent carbon data by setting most of the model parameter values within observed ranges and minimizing the total negative log likelihood at each depth interval, given the data and assuming residuals follow a Normal distribution, $N(0,\sigma)$. Values of $\{\lambda_k, \lambda_p \psi, \gamma\}$ and σ were fit recursively. First, σ was estimated given initial estimates of $\{\psi, \lambda_k, \lambda_p \gamma\}$. Then, $\{\psi, \lambda_k, \lambda_p \gamma\}$ were estimated, given the resulting estimate of σ . This was repeated until the estimated parameter values stabilized. Standard errors of fitted parameters were estimated using likelihood profiles (Venzon & Moolgavkar, 1988). The values of all model parameters are shown in Table 2. Constant values were chosen from the specified ranges based on expert opinon, and the results of alternatives values within those ranges were not explored. Those that were fit are shown with the estimate of standard error. It should be noted that the parameters estimates, standard errors, and total model fit are likely to change, given different choices of parameters to fit versus set as a constant. Alternative choices may give equivalent or better overall fits.

We quantified the uncertainty of model predictions of the data by resampling. We generated 1,000 samples of each of the fitted parameters assuming that they were independent and followed a Normal distribution defined by the ML estimates and standard errors. For each set of sampled parameters, we generated a new set of model predictions. The standard deviations of the resulting prediction were used to define the uncertainty envelopes shown in Figures 5–9.





Figure 5. Percent carbon over depth profile for (a) vegetated (0 Year) and (b) pond (14–21 Years) sites. In both figures, the points are observations. Observations from the same core are connected by a thin line and common plot marker (black, white, and dark gray, or light gray). The thick lines in panel (a) present the model prediction (a solid line) plus and minus 1.96 standard deviations (the gray envelope). The thick lines in panel (b) present the model prediction (solid) plus and minus 1.96 standard deviations (the gray envelope). The thick lines in panel (b) present the model prediction (solid) plus and minus 1.96 standard deviations (the gray envelope) that result from setting model parameters to values fitted to vegetated (0 Year) sites and simulating model dynamics for 18 years.

Given the fitted parameters, the dynamics of the post-submergence (i.e., t > 0) total carbon stock (g/cm²) of the core was calculated for each time, *t*, as

$$C_{\text{core}}(t) = \sum_{i=0}^{n} 2\left(\rho_i C_p + C_i(t) + \gamma_0 B_i(t)\right)$$
(27)

We used the parameterized model to estimate the fate of the soil carbon after submergence by calculating stock of carbon in (g/cm²) lost to burial (i.e., sequestered) and mineralization (conversion to carbon gases) at each time *t* after ponding. The stock of carbon (g/cm²) lost to burial over each increment Δt at each time, *t*, after submergence was calculated as

$$C_b(t) = 2r\Delta t \left(\rho_n C_p + C_n(t) + \gamma_0 B_n(t)\right).$$
(28)

The stock of carbon (g/cm²) lost to mineralization over each increment Δt at each time, *t*, after submergence was calculated as

$$C_m(t) = 2\Delta t \sum_{i=0}^{n} g_f(i) C_i(t).$$
 (29)

The proportion of lost carbon that was mineralized over increment Δt at each time, *t*, was calculated as $C_m/(C_m + C_b)$.

4. Results

The depth profiles for percent total carbon for the vegetated (0 Year) group and submerged (ponded) (14+ Year) group are shown in Figures 5a and 5b. Percent carbon in the soil cores from both groups varied with depth. Following steep initial losses at the surface, sharp increases and decreases resulted in a soil carbon peak between ~20 and 40 cm and a final more gradual increase between ~60 and 100 cm (Figures 5a and 5b). The model fit depth profiles of percent total carbon for both the vegetated (0 Year, RMSE = 5.85%) and pond (14+ Year, RMSE = 6.47%) groups well. The values of the constant



Figure 6. The depth-integrated total carbon stock of the cores from vegetated (0 Year) and 14+ Year pond sites. Observed carbon stocks represented by white dots, and modeled carbon stocks represented by black dots. The confidence intervals for model predictions $(2.35 \pm 0.0170481 \text{ and } 2.31 \pm 0.0169132$, respectively) are smaller than plot markers.





Figure 7. Model-predicted change over years in (a) humified carbon stock, (b) residue carbon stock, and (c) total carbon stock after submergence at estimated parameter values. Total stock is the sum of the humified, residue and passive pools of depth-integrated values to 1 m. The light gray uncertainty envelopes show the resampling-based confidence interval.

and fitted parameters are shown in Table 2, and the resulting fit to the vegetated sites (0 Year group) is shown in Figure 5a. Figure 5b shows the model-predicted depth profile of carbon content for a randomly selected year within the relevant time period, 18 years after submergence, overlaid on the observed profile for the sites in the 14+ Year ponded group. Model predictions illustrate an abrupt decline in C at the surface with a subsequent increase beginning at 20 cm and peaking at ~60 cm deep in the pond sites 18 years after submergence.

The depth-integrated total carbon stock (g/cm²) of the cores from vegetated and pond sites along with the model-predicted stocks are shown in Figure 6. Some observations of soil carbon stocks were lower in the vegetated state (0 Year, m = 2.02 g/cm², sd = 0.377 g/cm²) than the pond state (14+ Year, m = 2.29 g/cm², sd = 0.019 g/cm²); however, soil carbon stocks in the vegetated state were highly variable, and no difference was detected between the two states (t(3.02) and p = 0.26).

The model-predicted long-term trajectory of carbon stock (integrated over 1 m) is shown in Figure 7. At the estimated parameter values, the humified carbon stock decreases slowly until nearing the pond equilibrium at approximately t = 200 yrs (Figure 7a). The stock of carbon in plant residues decreases very quickly, reaching the pond equilibrium at approximately t = 4 yrs (Figure 7b). The trajectory of total carbon stock, which includes the passive pools, follows dynamics similar to that of the humified carbon stock before settling at the pond equilibrium (Figure 7c), which results in an overall net decline in carbon stocks of 404%.

The projected dynamics of carbon content after submergence varies greatly by depth. Figure 8 shows the longer-term trajectory of percent total carbon over time at three depths, 0–2 cm, 20–22 cm, and 40–42 cm. For the parameter values shown in Table 2, carbon loss occurs most quickly at the 20–22 cm stratum, following a negative exponential shape similar to scenario IV shown in Figure 1a (the dashed line in Figure 8). The deeper stratum (the dotted line in Figure 8) follows a double exponential decay trajectory, similar to scenario II of Figure 1a, which decreases slowly at first, but with an increasing rate. The total percent carbon increases in the surface stratum (top 2 cm, the solid line in Figure 8) reflect the decrease in the humification and mineralization rates due to submersion and are reflected in the parameters ϕ_k and ϕ_h respectively.

Figure 9a shows the loss in carbon stock from the 1-m core over time at a 1-year time step. Carbon stocks are lost by mineralization (i.e., as gases or lateral movement of DOC/DIC) or exported by burial (i.e., sequestration by shifting below the 1-m depth of our core). Figure 9b shows the proportion of this loss that is mineralized as opposed to sequestered by burial (shifting below the 1-m depth of our core). Initially, under this parameterization, the model predicts that about 4% of the carbon stock lost from the 1-m core annu-

ally is attributable to mineralization (95% carbon stock sequestered by burial). This proportion fluctuates slightly to 7.5% as it reaches the ponded equilibrium.

5. Discussion

This simple model of the processes involved in soil carbon dynamics in coastal wetlands fits observational data and allows for complex behavior. This model predicts that the decline in soil carbon density to the pond equilibrium will be on the order of hundreds of years but varies greatly at different depths. At the broadest scale, this model predicts that submergence will result in loss of soil carbon density, reflecting the change in carbon source





Figure 8. The predicted trajectory of change in total carbon after submergence follows different paths at different depths, reaching the pond equilibrium fastest at the surface (the solid line) and most slowly at depth (the dotted line). The light gray uncertainty envelopes show the resampling-based confidence interval.



Figure 9. (a) Carbon stock change per year from 1-m core to mineralization and burial (shifting below the 1-m depth of our core) over transition from vegetated (t = 0) to pond equilibria (~200 years), showing the rate of carbon loss increases quickly, then slows as the pond equilibrium is reached. (b) Proportion of carbon stock in panel (a) that was mineralized as opposed to buried (sequestered).

from carbon-rich vegetation residues to the relatively carbon-poor substrate brought in by mineral sediment deposition (accretion). Under the parameterization used, the model predicts that carbon losses in the top 1 m of soil will occur primarily through burial, such that the majority of carbon lost from the top 1-m of soil over time will be sequestered. Yet, the net decline in carbon density in the top 1-m of soil represents a reduction in the capacity of these ecosystems to remove carbon from the atmosphere.

In addition to accretion of less carbon-rich material, mineralization contributes to carbon losses, but to a lesser extent than burial. Following plant mortality and the conversion to open water pond, mineralization rates increase without the offset of primary production, resulting in a net loss of carbon (Wilson et al., 2018). Mineralization rates in wetland soils are generally limited by oxygen availability; however, microbial activity may also be limited by labile carbon subrates and nutrients (Rejmánková & Houdková, 2006). Plant exudates, such as nutrients and labile carbon, known to stimulate microbial activity (Mueller et al., 2016), could be released by dying plants to increase mineralization rates (Kuzyakov, 2010). The small post-submergence increase in mineralization products could be fluxed to the atmosphere or the aquatic pool or likely a combination of both (Ganju et al., 2019; Najjar et al., 2018). Although atmospheric versus aquatic emissions are not explicitly quantified by this model, this model improves estimates of overall carbon loss in interior ponds and supports a better understanding of the mechanisms controlling that loss.

These data can inform existing assumptions and uncertainty about emissions following wetland loss that have implications for greenhouse gas assessments and subsequent climate policy (Holmquist et al., 2018). For example, these data project that the 1-m soil carbon stock of the submerged wetland at equilibrium (pond site ~200 years post-submergence) will be reduced by 40%, approximately 7.5% of which is attributable to mineralization. Indeed, in the near term (<14 years), both observations and model projections show minimal change in soil carbon stocks, following conversion from the vegetated

state to the pond state, and greater than 90% of the 1-m stock reduction is sequestered in the soil. In contrast, the U.S. national Greenhouse Gas Inventory approach assumes that conversion of all vegetated coastal wetlands to open water results in emission of 100% of the soil carbon in the top 1 m (United States Environmental Protection Agency, 2021).

These differences highlight the importance of accounting for different mechanisms of wetland loss and soil displacement when estimating carbon emissions. Our model projections assume that the conversion of vegetated wetlands to small interior ponds occurred through vertical subsidence, associated with vegetation death and loss of soil structure, resulting in minimal soil displacement (Day et al., 2011; DeLaune et al., 1994), also called "peat collapse" (sensu Chambers et al., 2019). Importantly, the U.S. Greenhouse Gas Inventory does not distinguish between interior marsh subsidence and open edge erosion and assumes that the top 1 m of soil is eroded in all wetlands that undergo conversion to open water (United States Environmental Protection Agency, 2021). Thus, our results indicate that not stratifying for interior subsidence could result in an overestimation in the estimation of soil displacement and carbon emissions. This spatially stratified approach is currently implemented in the Verified Carbon Standards methodology for tidal wetland and seagrass restoration, which estimates the impacts of sea-level rise differently across geomorphic setting, where interior wetlands not exposed to wave energy will have little soil carbon displacement compared to edge habitats with high wave energy and higher soil carbon removal (Emmer et al., 2015). Furthermore, over the modeled time period (200 years), most of the surrounding wetlands in this region are expected to convert to open water (Kirwan et al., 2010; Moon et al., 2021), which will affect local hydrogeomorphic feedbacks that control mechanisms of organic matter production, decomposition, and net organic matter accumulation or loss (Kirwan & Guntenspergen, 2012). Thus, it is important to realize that our model projections at equilibrium do not account for potential changes in hydrogeomorphic forcing on production and decomposition of organic matter that may occur in the future.

Nonetheless, this model provides a framework for future investigations that could resolve even more uncertainty in the processes that control mineralization rates and losses and ultimately the fate of the carbon emissions. In addition to the dynamic predictions, the model produces a set of testable hypotheses based upon the parameter estimates required to fit the patterns observed in the data. For example, the proportion of carbon lost through burial versus mineralization depends strongly on how quickly mineralization rate changes with depth (λ_f). Our model predicted that mineralization rates decline more rapidly with depth than do humification rates (i.e., $\lambda_f > \lambda_k$, Table 2). In the absence of empirical data, defining these parameter estimates to achieve the best model fit provides a set of testable hypotheses about the relationship between mineralization, humification, and depth. The prediction that mineralization rates decline faster with depth than humification rates accords well with our understanding of the system. In general, mineralization increases with microbial activity. Humification is a function of both the molecular structure of wetland carbon and the environmental conditions that reduce microbial activity or carbon use efficiency or both and lead to its persistence (e.g., limiting nutrients or O₂, Schmidt et al., 2011). Thus, steeper relative declines in microbial mineralization could occur if oxygen, sulfate, or nitrate becomes limiting due to the higher energetic demands needed to mineralize reduced forms of carbon (Boye et al., 2017). This phenomenon could be directly tested in the lab (*sensu* Steinmuller et al., 2019).

The model also suggests the existence of a passive pool of carbon of about 10% for vegetated plots and about 14% after submergence. The size of these pools is relevant because as shown in Figure 7 at the pond equilibrium most of the carbon stock is composed of the passive pool. To test hypotheses about the mechanisms controlling the passive pool, one could measure changes in microbial community composition with submergence and depth or mineral composition with depth (Spivak et al., 2019). For example, a larger passive pool may result from a shift in the microbial community to one more efficient at converting carbon from the humified pool to the passive pool or it could occur from proportionately more carbon held in stable (i.e., mineral-associated) pools (Luk et al., 2020).

Each of the parameters of this model is the net result of complex ecological processes. For example, the parameters associated with residue dynamics will depend greatly on the marsh community type (Schoolmaster & Stagg, 2018; Stagg et al., 2017). For example, mineralization of plant residues will depend upon litter quality, which varies among wetland communities (Stagg et al., 2018), and thus carbon loss following submergence will also likely vary across these communities. Similarly, the humification and mineralization rates will likely depend on environmental conditions and the traits of the microbial decomposer community (Reddy & DeLaune, 2008). As such, we hope that this model can provide a central touchstone for integrating information across subfields of ecology to help synthesize understanding of how environmental and spatial variation in these processes and

communities drive both the characteristics of soil carbon depth profiles under vegetated conditions and how these change with wetland submergence. In addition, this model can be used as a tool for testing how intervention (via manipulating the model's parameters) may be used to slow or mitigate the effect of soil carbon loss after submergence.

For the data fitting we presented here, some parameters were set to values derived from previous studies (Table 1), while others were treated as free, and fit statistically (Table 2). As a result, it is unclear whether the set of estimates provides a unique fit to the data, or whether other combinations might provide a fit just as good or better. Examination of these, through the sensitivity analysis, for example, would provide a measure in the robustness of the predictions. Ecological models are, by necessity, greatly simplified representations of the processes and phenomena they are used to understand. Most can be placed on a trade-off spectrum between generalizability and accuracy. For this model, we made the choice to keep the representation of processes very simple. For example, both humification and mineralization rates are modeled as linearly dependent on substrate density. This reflects the strong control that microbial accessibility to organic substrates has on decomposition rates (Dungait et al., 2012). Other models of soil carbon use more complex functions to model microbial processes and carbon sorption to make precise predictions (Ahrens et al., 2015; Kemanian & Stöckle, 2010; Sulman et al., 2014; Wieder et al., 2014). In addition, the relationship between vegetation dynamics and residue production was left purposely vague. Our goal in using a simple model was to both keep the number of parameters as low and directly measurable as possible and have a model that could be used to provide analytical results.

Finally, it is important to acknowledge that these simplified processes represent one of many potential mechanisms of wetland loss that are variable across space and time. We assume that submergence results from subsidence of the wetland platform, whereby the marsh surface elevation declines over time in relation to the water level, ultimately surpassing the threshold for wetland vegetation survival and leading to pond formation via peat collapse (Chambers et al., 2019; DeLaune et al., 1994; Nyman et al., 1993; Stagg et al., 2020). Our model performs well within the context of subsidence and gives robust estimates of the carbon that remains after pond formation. Although subsidence has been identified as a primary contributor to coastal wetland loss in Louisiana (Morton et al., 2010), it is highly unlikely that all wetland loss in coastal Louisiana is caused by a single mechanism, and currently we do not have an estimate of the relative contribution of these other mechanisms, such as shoreline erosion, to historic and current wetland loss rates. Nonetheless, future updates to this soil carbon model to include other primary processes, such as direct erosion and lateral transport of material, would resolve even more uncertainty in our estimates of the vulnerability of soil carbon to wetland loss and ultimately our assessment of the coastal wetland blue carbon sink.

Data Availability Statement

The data and code used for this work are publicly available at: Schoolmaster et al., 2022, https://doi.org/10.5066/P916JH3L.

Acknowledgments

The authors would like to thank Apache Minerals, LLC, and the Louisiana Coastwide Reference Monitoring System for providing access to the study sites. This work was supported by the U.S. Geological Survey, Ecosystems Program and South Central Climate Adaptation Science Center. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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