CHAPTER 6

Physical and Biological Regulation of Carbon Sequestration in Tidal Marshes

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CONTENTS

HIGHLIGHTS

1. The rate of carbon sequestration in tidal marshes is regulated by complex feedbacks among biological and physical factors including the rate of sea level rise (SLR), biomass production, tidal amplitude, and the concentration of suspended sediment. We used the Marsh Equilibrium Model (MEM) to explore the effects on C-sequestration across a wide range of permutations of these variables.
2. C-sequestration increased with the rate of SLR to a maximum, then decreased down to a vanishing point at higher SLR when marshes convert to mudflats. An acceleration in SLR will increase C-sequestration in marshes that can keep pace, but at high rates of SLR, this is only possible with high biomass and suspended sediment concentrations. We found there were no feasible solutions at SLR >13 mm $year^{-1}$ for permutations of variables that characterize the great majority of tidal marshes, i.e., the equilibrium elevation exists below the lower vertical limit for survival of marsh vegetation.

3. The rate of SLR resulting in maximum C-sequestration varies with biomass production. C-sequestration rates at SLR = 1 mm $year^{-1}$ averaged only 36 g C m^{-2} $year^{-1}$, but at the highest maximum biomass tested (5,000 g m^{-2}) the mean C-sequestration reached 399 g C m^{-2} $year^{-1}$ at SLR = 14 mm $year^{-1}$.
4. The empirical estimate of C-sequestration in a core dated 50-years overestimates the theoretical long-term rate by 34% for realistic values of decomposition rate and belowground production. The overestimate of the empirical method arises from the live and decaying biomass contained within the carbon inventory above the marker horizon, and overestimates were even greater for shorter surface cores.

6.1 INTRODUCTION

Tidal marshes are one of the blue carbon ecosystems—marine ecosystems that sequester carbon over centuries to millennia. Conservatively, blue carbon ecosystems (marshes, mangroves, other tidal wetlands including forests and seagrasses) store roughly 45 Tg C $year^{-1}$ (Chmura et al. 2003), which is globally significant because of the millennial time scale on which they operate. As long as sea level rises, carbon storage in coastal sediments will continue unabated as marshes either keep pace with SLR or transgress inland. In addition to conservation of extant C pools, continued C accretion creates opportunities for management of greenhouse gas (GHG) offset programs, which have been established by multiple state, regional, and national programs across the world (see Chapters 15–20).

While there is a growing collection of data on tidal marsh carbon dynamics (e.g., see recent papers by Ouyang and Lee 2014; DeLaune et al. 2016; Nahlik and Fennessy 2016; Van de Broek et al. 2016), measured rates have been calculated using a wide range of different approaches; from short-term sediment markers to dated cores using time scales from decades to millennia (see Chapter 7 in this volume for review of methods and related definitions). Most recent estimates have used either ^{137}Cs or ^{210}Pb, along with measurements of soil carbon density, usually by converting estimates of organic matter from loss on ignition (Chmura et al. 2003; Ouyang and Lee 2014). Estimates of sequestration using dated horizons incorporate a variety of carbon pools, including living roots and rhizomes and labile organic matter in modern surface soils; however, the only pool that contributes to long-term carbon sequestration is the refractory one. With dated cores or horizons, it is impossible to separate out these various pools, and better estimates of carbon sequestration can be made by use of models that account for the important, interacting factors that govern the processes contributing to sequestration.

The rate of carbon sequestration in tidal marshes is regulated by complex feedbacks among biological and physical factors. The physical factors include 1) the rate of SLR, 2) the tidal amplitude, and 3) the concentration of suspended sediments in tidal floodwater. Important biological factors include 4) the growth response of vegetation to relative site elevation, 5) the maximum productivity, 6) belowground productivity, and 7) the refractory carbon content of these tissues. In this chapter, we use the MEM to explore interactions of these factors with the goal of generalizing about how feedbacks regulate carbon sequestration. We also use the model to evaluate the contribution of different forms of carbon (labile versus refractory) to measured rates of carbon sequestration using dated sediment cores.

An equilibrium marsh is one that is in balance with sea level, meaning that the elevation of the marsh surface *relative to sea level* is constant through time. The elevation of an equilibrium marsh surface will track the long-term rate of SLR (Redfield and Rubin 1962; Redfield 1972), and by long-term we mean decades to a century. Marshes do not adjust quickly to changes in sea level. Anomalies in annual mean sea level (MSL) change the hydroperiod and productivity of a marsh (Morris and Haskin 1990; Morris et al. 1990; Morris et al. 2002). So, the relative elevation of a marsh in equilibrium is not necessarily constant on annual or shorter time scales, but it is stable over longer time scales. As such, it is a dynamic equilibrium. In equilibrium, the long-term annual productivity of the marsh also should be constant through time, but can and will vary on annual time scales with changes in hydroperiod, climate, and weather. Plant community composition will likely be constant

over time and, if not, changes in composition in an equilibrium state will not alter the feedback among tides, plant response, hydroperiod, or the rate of vertical accretion. Additionally, sediment supply and hydrodynamic variables such as tidal amplitude are also assumed to be constant over long-time scales.

Disequilibrium states can arise when there is a step change in one of the forcing variables, like sediment supply, including episodic deposition of sand or sediment from overwash, storms, or thin layer placement of sediment (e.g., Orson et al. 1998). A marsh restoration site can also be in a state of disequilibrium for decades (Craft et al. 1999, 2002; Callaway 2005). MEM simulates marsh responses to multiple environmental factors. The model has been shown to accurately simulate marsh development at multiple sites (e.g. San Francisco Bay, CA and North Inlet, SC) and to synthesize knowledge of key environmental factors driving marsh accretion and sustainability, both abiotic and biotic. It also has been used to predict sustainability of marshes under different climate change scenarios (Kirwan et al. 2010; Schile et al. 2014; Byrd et al. 2016; Alizad et al. 2016a,b). MEM is able to numerically simulate disequilibrium states, but results reported in this chapter apply to equilibrium states calculated for permutations of key parameters.

6.2 MODEL DESCRIPTION

The MEM describes important feedbacks that regulate vertical accretion rate, soil organic matter concentration, and primary production as a function of SLR, tidal range, and suspended sediment concentrations. We report here results of an experiment in which important input variables (maximum biomass, SLR, tidal range, and suspended sediment concentration) were systematically varied to evaluate their effects on marsh resilience and carbon sequestration for virtual marshes in equilibrium with SLR. The current model is the successor to a model published earlier (Morris et al. 2002). We use MEM in an exploratory mode, not calibrated for a single site/location but comparing responses across widely ranging conditions in order to evaluate the determinants of soil organic matter concentration and carbon sequestration rates. We are not using the model here to evaluate marsh dynamics under future scenarios of accelerating SLR. Rather SLR is a constant within an individual model run but is varied among simulations to evaluate the effects of different rates on equilibrium elevation and carbon dynamics.

A feature of MEM is a description of the response of aboveground biomass to the relative elevation of a site and tide range (Morris et al. 2002). For an intertidal species such as *Spartina alterniflora*, the vertical range of growth lies approximately between MSL and mean higher high water (MHHW) (McKee and Patrick 1988). At both the upper and lower extremes of its vertical range, biomass and primary production approach zero (Figure 6.1a). At the lower limit, hypoxia is most important, while osmotic stress sets the upper limit (Mendelssohn and Morris 2000). There is an optimum relative elevation for growth that lies near the middle of the range (Morris et al. 2002, 2013). In other words, the growth response to relative elevation, or alternately depth (D) of the marsh surface below relative MHW, is approximately parabolic:

$$B_s = aD + bD^2 + c : \text{seasonal maximum standing biomass } (\text{g m}^{-2})$$

The coefficients a, b, and c are calculated after specifying the upper and lower limits of growth, the optimum depth, and biomass at the optimum depth. Biomass at the optimum depth is subsequently referred to as B_{max}. For all simulations reported here we put the lower limit at 10 cm below MSL (positive D) and the upper limit at 20 cm above MHW (negative D), and optimum depth in the middle of the range.

6.2.1 Mass Inputs: Mineral Sediment

The model describes net accretion only; erosion is not explicitly accounted for. Consequently, MEM is not appropriate for marsh edges where erosion is likely to be an important factor. MEM

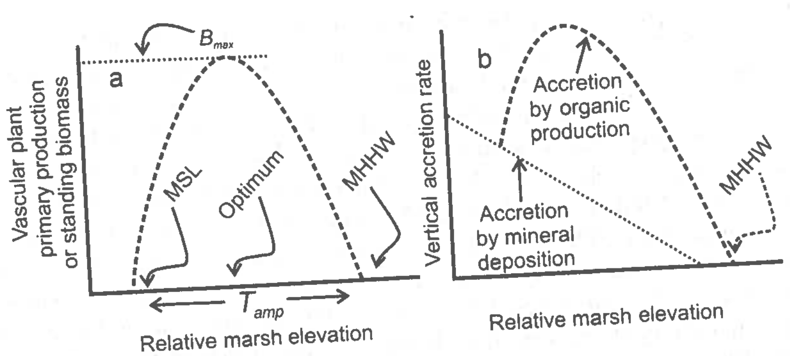

Figure 6.1 Conceptual relationship between marsh productivity (a) and vertical accretion (b) as functions of relative elevation. Marsh production (a) adds organic matter to soil, generating biovolume proportionally and marsh accretion (b). Mineral deposition is proportional to the depth of floodwater and suspended sediment concentration, and decreases as relative elevation increases (b).

decomposes sedimentation dynamics into several contributing processes, reflecting the importance of both mineral and organic matter inputs to sediment accretion (Nyman et al. 1990, 1993; Turner et al. 2000; Morris et al. 2016). Mineral sedimentation resulting from the settling of suspended particles is proportional to the concentration of suspended solids and the amount of time that the surface is flooded. Inorganic sediment load (S_{max}) is calculated as the product of the average depth of water over 1 cm² of marsh surface during a flood tide, (MHW–Z)/2, the number of tides in a year (704), and the concentration of suspended mineral sediment m (g cm^{-3}), hereafter denoted SSC. Marsh elevation is Z (cm relative to MSL); MHW is mean high water level.

$$S_{max} = m \times 704 \times 0.5 \times (\mathrm{MHW} - Z) : \text{sediment load}\,(\mathrm{g\,cm^{-2}\,year^{-1}})$$

Similar to Krone's settling velocity w_s (Krone 1962), MEM multiplies the sediment load S_{max} by a capture coefficient q, scaled by inundation time (w) to calculate the surface sedimentation rate. Inundation time is calculated as $w = (\mathrm{MHW} - Z)/(\mathrm{MHW} - \mathrm{MLW})$ for $\mathrm{MLW} \le Z \le \mathrm{MHW}$. Scaling q by the fractional inundation time accounts for effects of tidal amplitude on sedimentation. For example, the inundation time of 5 cm of water over a marsh in a macrotidal estuary with a 150 cm tidal amplitude is (150–145)/300 = 0.017, which is just a fraction of the inundation time of 5 cm of water over the surface in a microtidal estuary with a 20 cm tidal amplitude, (20–15)/40 = 0.125. The capture coefficient q was set to 2.8 based on work at North Inlet and assumed constant for simulations reported here. Vegetation enhances the deposition of mineral sediment by sorbing suspended sediment directly onto leaf and stem surfaces (Mudd et al. 2010), but this detail is omitted here because of its autocorrelation with the growth of root and rhizome biovolume. With the multi-decadal dataset we have from North Inlet we cannot separate these processes statistically (sediment trapping by vegetation versus biovolume) (Morris, pers. obs.).

6.2.2 Mass Inputs: Organic Matter

Belowground organic matter accumulation has been shown to be a critical component of overall marsh accretion across a wide range of tidal marshes (Nyman et al. 1993, 2006; Turner et al. 2004). Accretion by virtue of primary production is possible because inputs of stable or refractory organic matter ($k_r \varphi \tau B_s$, g dry wt cm^{-2} year^{-1}) add increments of volume to sediment. Coefficient k_r (g g^{-1}) is the fraction of belowground production incorporated into the stable fraction of soil carbon, φ is the ratio of belowground production to aboveground standing biomass, and τ is the turnover rate of belowground biomass (year^{-1}). Based on the lignin content of *Spartina* (Hodson et al. 1984; Wilson

Table 6.1 Permutations of Parameters That Gave Rise to the Model Results Reported Here

Parameter	Permutations
Tidal amplitude (T_{amp})	20–180 cm in steps of 5 cm
Susp. mineral sediment concentration (SSC)	10–160 mg L^{-1} in steps of 5 mg L^{-1}
Standing biomass at the optimum elevation (B_{max})	1,000–5,000 g m^{-2} in steps of 1,000
Constant rate of SLR	1–40 mm year^{-1} in steps of 1 mm year^{-1}

et al. 1986; Buth and Voesenek 1987), we assumed in all simulations here $k_r = 0.1$ and that the ratio of belowground to aboveground standing biomass was 2:1 (Schubauer and Hopkinson 1984). The turnover rate of belowground biomass was assumed to be 1.0 per year. Keep in mind that about half of the belowground biomass is rhizome tissue which is perennial and long-lived. The rhizome fraction of belowground biomass probably turns over much less than 1.0 per year, while the root fraction could turnover several times a year. Because net organic matter inputs are a function of all four parameters above, there is a trade-off in how these parameters affect organic matter inputs. One of the permutations of the simulations reported here includes a range of values of (1,000–5,000 g m^{-2}) for aboveground biomass (Table 6.1), and these can be viewed alternatively as changes in the allocation and turnover of belowground production, i.e., an aboveground production of 1,000 g m^{-2} with root:shoot ratio of 2.0 is equivalent to 2,000 g m^{-2} aboveground production with root:shoot ratio of 1.0, assuming equal turnover rates.

6.2.3 Vertical Accretion, Bulk Density, and Soil Organic Matter

Vertical accretion rate (dz/dt, cm year^{-1}) resulting from the settling of particles and biovolume growth is defined by the summation of the inorganic and organic mass inputs divided by their respective self-packing densities:

$$\frac{dz}{dt} = \left[\frac{S_{max} q \omega}{k_2} + \frac{k_r \varphi \tau B_s}{k_1}\right] =$$

$$\left[\frac{qm \times 704 \times \dfrac{0.5D^2}{\mathrm{MHW} - \mathrm{MLW}}}{k_2} + \frac{k_r \varphi \tau (aD + bD^2 + c)}{k_1}\right] : \text{vertical accretion rate (cm year}^{-1}\text{)}$$

Coefficients k_1 = 0.085 g cm^{-3} and k_2 = 1.99 g cm^{-3} are the self-packing densities of organic and mineral sediment respectively (Morris et al. 2016).

In the model, LOI (loss on ignition) is calculated as the concentration of soil organic matter below the root zone at a depth characterized by the stable fraction of organic matter inputs.

$$\mathrm{LOI} = k_r \varphi \tau B_s / \left[k_r \varphi \tau B_s + S_{max} q \omega\right] : \text{soil organic matter concentration or LOI}\,(\mathrm{g\,g^{-1}})$$

6.2.4 Equilibrum and Dimensionless Elevation

In equilibrium dz/dt is equal to the rate of SLR. After specifying the values of the constants and variables in the model, dz/dt is determined only by the depth D of the surface below MHW. Finding the equlibrium is a matter of setting a constant rate of SLR and iterating across the range of all possible depths D to identify the depth that results in a vertical accretion rate dz/dt equivalent to

SLR: $f(D) = dz/dt = \text{SLR}$. Relative marsh elevation (Z) at equilibrium was then calculated as tidal amplitude (T_{amp}) minus the equlibrium depth. As a means of standardizing across tidal ranges we computed a dimensionless relative elevation (DimE) at equlibrium as $(Z-E_{min})/(E_{max}-E_{min})$, where E_{max} and E_{min} are the maximum and minimum limits of the vegetation relative to MSL, respectively, and $0 \leq \text{DimE} \leq 1$ irrespective of tide range for a vegetated marsh surface.

6.2.5 Carbon Sequestration

When the marsh is in equilibrium with SLR, the annual rate of carbon sequestration (refractory carbon input) in any year is $0.42 \times k_r \varphi\tau B_s$ where $\varphi\tau B_s$ is the annual production of belowground dry weight, as discussed above. This is the theoretical, long-term rate of carbon sequestration for a marsh in equilibrium with SLR. The constant 0.42 is taken as the elemental carbon fraction of dry *Spartina* tissue based on reports that place it between 0.4 and 0.44 (Osgood and Zieman 1993; Cartaxana and Catarino 1997; Tobias et al. 2014; Byrd et al. in review).

In addition to the theoretical long-term rate of sequestration, we simulated typical field-based measures of carbon sequestration (e.g., Craft et al. 1993; Callaway et al. 2012 and citations in Chmura et al. 2003). Carbon sequestration is often measured empirically by locating a marker horizon or dated soil layer, such as the ^{137}Cs peak corresponding to the peak in fallout from atmospheric nuclear testing in 1963 (DeLaune et al. 1978; Ritchie and McHenry 1990 and see Chapter 7 in this volume). In a typical scenario, one would estimate the total inventory of carbon in the section of core above a dated horizon and divide by time in years. For simplicity we simulated a horizon-derived C-sequestration rate assuming dated horizon of 50 years below the surface, as this is a time frame similar to many measurements made with ^{137}Cs. In dry weight units (g m^{-2}), the total inventory of organic matter would include the total live root biomass (φB_s), 50 years of refractory inputs ($50k_r\varphi\tau B_s$), and the decaying, labile fraction of root inputs given by $\int_1^{50}(1-k_r)\varphi\tau B_s e^{rt} = \frac{(1-k_r)\varphi\tau B_s}{r}\left(e^{r50}-e^{r}\right)$ where r is the annual decay rate (the fractional loss, $r<0$), and t is time in years. Since e^{50r} approaches zero, the solution of this equation simplifies to $(1-k_r)\varphi\tau B_s\left(e^r/-r\right)$. Thus, the total dry weight inventory of organic matter O_i is:

$$O_i = \varphi B_s + 50k_r\varphi\tau B_s - (1-k_r)\varphi\tau B_s(e^r/r):$$

soil organic matter inventory in 50 year old sediment column (g dry wt m^{-2})

The estimated annual rate of carbon sequestration (g C m^{-2} year^{-1}) from such a measure of the organic inventory over a 50-year-old marker horizon is $0.42\ O_i\ /\ 50$.

6.3 MODEL EXPERIMENTS

In order to evaluate constraints on carbon sequestration rates, we exercised the model using a range of permutations encompassing combinations of four key variables: tidal amplitude (1/2 of the tidal range), suspended sediment concentration (m), biomass at the optimum depth (B_{max}), and the rate of SLR (Table 6.1). As above, for each permutation, the model was run iteratively with adjustments to the depth until $dZ/dt = \text{SLR}$, resulting in 838,860 equilibrium solutions. This range of variables (Table 6.1) should define the conditions that describe virtually all tidal marshes. Other model parameters which were held constant across all permutations included the ratio of live belowground biomass to standing biomass ($\varphi = 2$ g g^{-1}), the turnover rate of belowground material ($\tau = 1$/year), the decay rate of labile organic matter (−0.4/year, Blum 1993; Blum and Christian 2004), the refractory fraction of organic production ($k_r = 0.1$), and the capture coefficient of suspended minerals ($q = 2.8$), as discussed above.

6.4 STATISTICAL ANALYSIS

Outputs from all permutations were grouped first into feasible and non-feasible solutions. A feasible solution is one in which the dimensionless elevation (DimE) at equilibrium ($dz/dt = \text{SLR}$) was greater than zero, i.e., vegetation remained in place within its growth range. Solutions in which the equilibrium elevation was below the lower limit for the vegetation were deemed to be non-feasible since the marsh would be converted to mudflat and no carbon sequestration would be possible. The group of feasible solutions was subsequently analyzed by cross-correlation analysis, grouped by SLR, and by computing the means of select dependent variables (DimE, C-sequestration rate, soil organic matter concentration, mineral accretion rate, and equilibrium biomass).

6.5 RESULTS

Most virtual marshes equilibrated at elevations feasible for vegetation across the range of variables evaluated when SLR ≤ 13 mm year^{-1} (Figure 6.2, Table 6.2). For each level of SLR there were 41,943 possible permutations of T_{amp}, SSC, and B_{max}. There was 100% survival at the lowest rates of SLR, 1 and 2 mm year^{-1} (Figure 6.2, Table 6.2). Among all possible permutations, the proportion of feasible combinations started to decline significantly by SLR = 10 mm year^{-1}, and by 23 mm year^{-1} the proportion surviving had dropped to 47% (Figure 6.2 and see Table 6.2). However, marshes first started to drop out at SLR = 3 mm year^{-1} and B_{max} = 1,000 g m^{-2}. When we restricted the permutations to values of B_{max} (≤3,000 g m^{-2}), SSC (≤50 mg L^{-1}), and T_{amp} (≤100 cm)—parameter values that we think characterize the great majority of U.S. tidal marshes, with exceptions found in the Mississippi River and Sacramento–San Joaquin Deltas and other unusual locations—we found no feasible solutions at SLR ≥ 13 mm year^{-1}. By SLR = 7 mm year^{-1}, only 43% of the permutations were feasible among this restricted group (Figure 6.2).

The complex feedbacks that characterize the sediment dynamics of an intertidal marsh are illustrated by the correlations among dependent and independent variables, with effects of some factors changing substantially with SLR (Table 6.2). For example, tidal amplitude was negatively correlated with soil organic matter concentration (LOI) and C-sequestration at SLR = 2 mm year^{-1} (r = −0.08 and −0.23 respectively), but positively correlated with these variables (r = 0.49 and 0.55) at SLR = 20 mm year^{-1}. This can be explained by the fact that elevation capital, which becomes more important as the rate of SLR increases, is affected by tidal amplitude. Suspended sediment

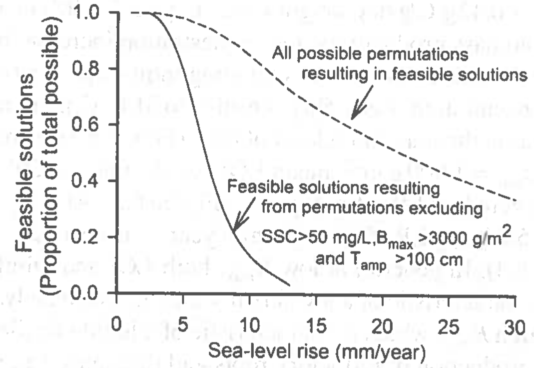

Figure 6.2 The proportion of feasible (DimE > 0) solutions found among 41943 possible permutations of B_{max}, SSC, and T_{amp} as a function of the rate of SLR. Also shown is the proportion of feasible solutions for a restricted group of permutations representing the majority of the universe of existing tidal U.S. saltmarshes (B_{max} ≤ 3,000 g m^{-2}, SSC ≤ 50 mg L^{-1}, and T_{amp} ≤ 100 cm).

Table 6.2 Pearson Correlation Coefficients among Dependent and Independent Variables from the Universe of Simulations Resulting in Feasible (DimE > 0) Virtual Marshes, Each Equilibrated (dz/dt = SLR) with Constant Rates of SLR (2, 10, and 20 mm year^{-1})

	SLR = 2 mm year^{-1}		SLR = 10 mm year^{-1}		SLR = 20 mm year^{-1}	
	LOI	Carbon Sequestration Rate	LOI	Carbon Sequestration Rate	LOI	Carbon Sequestration Rate
Tidal amplitude (T_{amp})	−0.08	−0.23	−0.07	0.32	0.49	0.55
Suspended Inorg. Sed. Conc. (SSC)	ns	ns	−0.05	0.15	0.40	0.45
Maximum biomass (B_{max})	0.09	0.27	0.78	0.75	0.42	0.37
Means ± 1 SD	87.9 ± 1.8	71.1 ± 0.1	22.4 ± 32.1	189.1 ± 135.7	0.7 ± 1.1	88.4 ± 115.8
	n = 41,943		n = 36,907		n = 30,545	

Also shown are the means ± 1 SD of dependent variables LOI and C-Sequestration and the number of feasible solutions found for each level of SLR. Every correlation is significant at $p < 0.0001$ except where noted.

concentration was not correlated with LOI or C-sequestration at 2 mm year^{-1} SLR, but positively correlated with LOI and C-sequestration (r = 0.49 and 0.55) at SLR = 20 mm year^{-1}. At low rates of SLR, marshes equilibrate high in the tidal frame where mineral sediment input is unimportant, but its importance increases at higher SLR because it supports overall accretion and helps to maintain elevation. Consequently, the low input of mineral matter at low SLR results in a high mean LOI (87.9% ± 1.8), while the increasing importance of minerals at high SLR results in a low LOI (0.7% ± 1.1) (Table 6.2).

The most striking example of the importance of these feedbacks is shown by the changes in C-sequestration rates across the range of SLR (Table 6.2). As a consequence of the vertical distribution of biomass productivity and its dependence on equilibrium elevation (Figure 6.1a), C-sequestration shows non-linear behavior with change in SLR. Essentially, it mimics the biomass profile (Figure 6.1), because equilibrium elevation declines with increasing SLR (Morris et al. 2002). Average C-sequestration for marshes in equilibrium ranged from 71 at SLR = 2 mm year^{-1} to 189.1 ± 135.7 g C m^{-2} year^{-1} at SLR = 10 mm year^{-1}, and then dropped to 88.4 ± 115.8 at SLR = 20 mm year^{-1} (Table 6.2). Average C-sequestration at 2 mm year^{-1} is essentially the theoretical maximum of 71.4 g C m^{-2} year^{-1}, calculated as the product of the self-packing density of pure organic matter (Morris et al. 2016), the carbon faction of organic matter, and the rate of SLR (= 0.085 g dry weight cm^{-3} × 0.42 g C/g dry weight × 0.2 cm year^{-1} × 10^4 cm^2 m^{-2}). As SLR increases, elevation decreases, and biomass productivity and sequestration increase, but at even greater SLR, the elevation decreases to the point where excess flooding inhibits productivity.

Soil organic matter concentration was highly sensitive to SLR, depending on B_{max}. At the lowest SLR, LOI in every case was at the maximum level of 88% (Figure 6.3) corresponding to DimE at or near 1.0 (Figure 6.4). At B_{max} = 1,000 g m^{-2}, mean LOI had declined to 50% at SLR < 3 mm year^{-1}. The LOI was approaching zero by SLR = 5 mm year^{-1} (Figure 6.3). At B_{max} = 3,000 and 5,000 g m^{-2}, LOI declined to less than 50% by SLR <7 and <13 mm year^{-1}, respectively, roughly in line with the decline in DimE (Figure 6.4). In general, at low B_{max}, both LOI and DimE declined rapidly with increasing SLR, which is characteristic of a low fertility marsh. Conversely, LOI and DimE decline less rapidly with SLR at high B_{max}, which is characteristic of a highly fertile marsh or, alternatively, a marsh with a very high production of refractory roots and rhizomes, i.e., very high $k_r \varphi \tau$.

Dimensionless elevation (DimE) is a measure of where the equilibrium elevation occurs within the vertical range of the vegetation. A DimE of 1.0 denotes equilibrium at the highest possible relative elevation for tidal marsh vegetation, assumed here to be MHW + 30 cm, while a DimE of 0 equals the lowest vertical limit of the vegetation, 10 cm below MSL. A DimE of 0.5 is the elevation

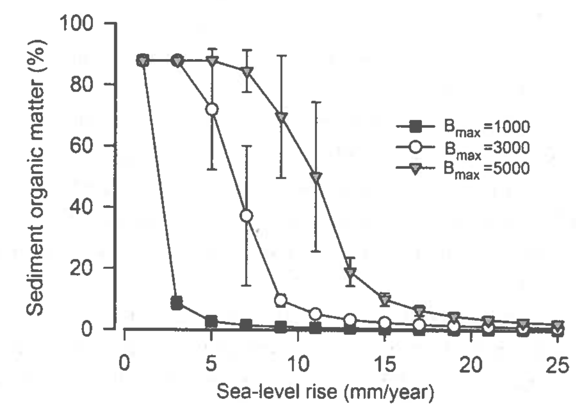

Figure 6.3 Mean dimensionless elevation ± 1 STD for each level of SLR and three levels of maximum biomass (B_{max}). Only feasible solutions (DimE>0) were included. Dimensionless elevation was averaged over all possible SSC and T_{amp} for each combination of SLR and B_{max}.

of maximum biomass along the parabolic response of biomass to elevation. DimE was highly sensitive to SLR and dependent upon the maximum biomass (B_{max}) (Figure 6.4). At the lowest B_{max} (1,000 g m^{-2}), mean DimE (averaged over all feasible solutions by SLR) dropped to 0.48 by 5 mm year^{-1} SLR, indicating that the average marsh in this class was at an elevation below the optimum for the vegetation. For B_{max} = 3,000 g m^{-2} the mean DimE dropped just below 0.5 between 9 and 11 mm year^{-1} SLR, but at B_{max} = 5,000 g m^{-2}, the mean DimE did not drop below 0.5 until SLR exceeded 17 mm year^{-1}. Again, this was for all feasible solutions, including the full range of SSC and T_{amp}.

High rates of mineral sediment input dilute sediment organic matter and reduce sediment LOI. The relative elevation at which a marsh equilibrates, which is inversely related to SLR (Figure 6.4) and SSC determine the input of mineral sediment and biomass production, and consequently, LOI. At low SLR, the high elevations at which these marshes equilibrated (Figure 6.4) resulted in the accretion of soils composed of peat (i.e., very high LOI) (Figure 6.3). Similar peat buildup occurred at 4 mm year^{-1}, but only at higher biomass levels. By 15 mm year^{-1} SLR, all surviving marshes were below the optimum elevation for biomass production and approaching the lower limit of elevation for survival (Figure 6.4) and with mineral inputs dominating sediment accretion (Figure 6.3).

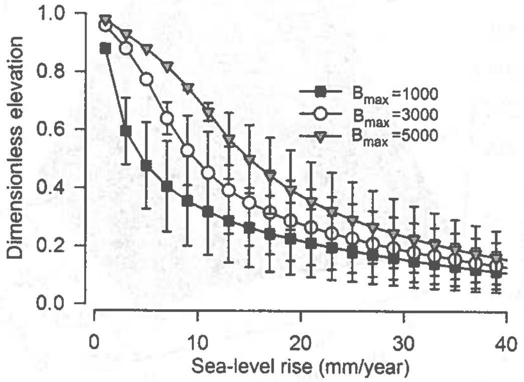

Figure 6.4 Mean sediment organic matter concentration (LOI) ± 1 STD for each level of SLR and three levels of maximum possible B_{max}. Only feasible (DimE>0) solutions were included. LOI at equilibrium was averaged over all possible SSC and T_{amp} for each combination of SLR and B_{max}.

Across all variables, C-sequestration was least at the lowest rate of SLR, and greatest at a combined high SLR and B_{max} (Figure 6.5). Increasing B_{max} led to greater average C-sequestration rates except at the lowest rate of SLR (1 mm year^{-1}). At SLR = 0, marsh elevation will equilibrate at E_{max} where equilibrium biomass and C-sequestration are zero. For every level of B_{max} there is an optimum SLR with respect to C-sequestration, and the optimum SLR increases with increasing B_{max}. At B_{max} = 5,000 g m^{-2}, the maximum, mean C-sequestration reached 399 g C m^{-2} year^{-1} at SLR = 14 mm year^{-1}. At B_{max} = 1,000 g m^{-2}, the mean C-sequestration was maximized at SLR = 4 mm year^{-1}, but only at 77 g C m^{-2} year^{-1}. Across all B_{max}, C-sequestration was uniformly 36 g C m^{-2} year^{-1} when SLR was 1 mm year^{-1} (Figure 6.5).

Dated cores of both the virtual and real varieties include a mix of both labile and refractory carbon. From the derivation above, the ratio of the theoretical, long-term rate of C-sequestration to the simulated horizon-derived rate in a 50-year-core (similar to ^{137}Cs dating methods) is:

$$\frac{0.42 k_r \varphi \tau B_s}{\left\{0.42\left[\varphi B_s + 50 k_r \varphi \tau B_s + (1-k_r)\varphi \tau B_s\left(\frac{e^r}{-r}\right)\right]\Big/50\right\}}$$

This simplifies to $\left\{50 r k_r \tau \big/ \left[r + \tau e^r (k_r - 1) + 50 r k_r \tau\right]\right\}$ for $r < 0$. Interestingly, the biomass variable and root:shoot ratio (φB_s) drop out, and the quotient depends only on the refractory fraction k_r, the decay rate r, and the turnover rate of belowground biomass τ. Substituting for our assumptions ($k_r = 0.1$, $r = -0.4$, and $\tau = 1$), we found that the theoretical rate of C-sequestration was always 66% of the simulated, horizon-derived rate integrated over 50 years. The difference between the two rates decreases as the decay rate r increases (becomes more negative), due to the fact that there is less labile organic matter remaining in the deeper soil layers, but even when $r = -0.9$, the theoretical rate was still 78% of the horizon-dated rate. The decay rate r does not affect the theoretical, long-term rate of refractory C-sequestration, even though it does affect the measured rate of carbon in dated cores. If the age of the core decreases, as it may in shallower cores, the difference between the theoretical and empirical rates will increase. For a core of length 25 years, the theoretical rate of C-sequestration decreases to 50% of the empirically derived rate using our original assumptions ($k_r = 0.1$, $r = -0.4$, and $\tau = 1$).

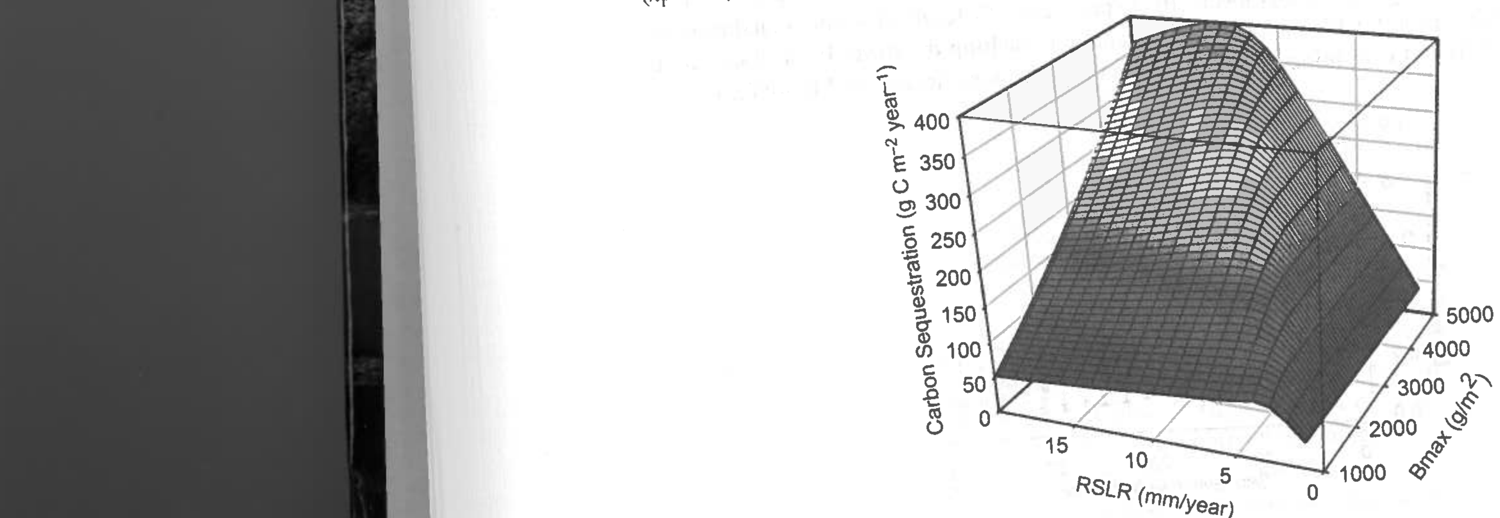

Figure 6.5 **(See color insert following page 266.)** Mean carbon sequestration rate as a function of the relative rate of SLR and maximum biomass (B_{max}). Only feasible (DimE > 0) solutions were included.

6.6 DISCUSSION

6.6.1 Elevation and Resilience

At the lower rates of SLR, virtual marshes equilibrated at an elevation within the vegetated zone of the marsh (Figure 6.1), although the equilibrium elevation tended to decline at increasing rates of SLR. In both natural and modeled conditions, marshes maintain this equilibrium with a mix of mineral and organic matter sediment inputs, and as they gain elevation in the tidal frame there is a shift toward greater domination by organic matter accumulation. Ultimately, for a marsh at the highest elevation, in equilibrium with SLR, it is the input and preservation of refractory organic matter that creates new volume and contributes to vertical accretion. Marshes low in the tidal frame (Figure 6.4) are more dependent on mineral inputs to maintain their equilibrium (Figure 6.3 and Table 6.2). This pattern of peat buildup in high elevation locations within tidal marshes is reflected in the consistent pattern of increasing soil organic matter content from low to high elevation marshes across many different locations (e.g., French et al. 1995; Callaway et al. 2012; Roner et al. 2016). It also is implied in the longstanding concept of marshes tracking SLR through peat accumulation (e.g., Redfield 1972). In cases of high SLR, low SSC, small T_{amp}, or low B_{max}, the equilibrium elevation fell below the lower vertical limit of vegetation (E_{min}), indicating a conversion of vegetated marsh to unvegetated mudflat.

In discussions about marshes, the equilibrium question arises often: how do we know if a marsh is in equilibrium with SLR? We would argue that relative to the low rates of eustatic SLR in the recent past, almost all tidal marshes globally must be in equilibrium, or at least in a dynamic equilibrium. If they were not, they would either grow out of the water and transition to a terrestrial ecosystem outside the tidal frame, or they would lose elevation so rapidly that they would be converted to mudflat ecosystems. There is no evidence of the former occurring, and the latter has occurred only in locations with very high rates of local subsidence. In theory, tidal marshes will always be chasing the equilibrium, and in a perfectly stable climate with constant SLR, they will find it. In a variable world, they will always be in a dynamic equilibrium. However, we know of tidal marshes today that are not in equilibrium. Disequilibrium will occur in modern times when conditions change rapidly, such as a change in sediment supply or a rapid acceleration in subsidence, and hence local SLR. From our sensitivity analysis of the virtual marshes generated by MEM we can project that the first marshes to fail with an acceleration of SLR (those with the least resilience) will be those with low primary productivity, i.e., low fertility, low SSC (e.g., DeLaune et al. 1978; Butzeck et al. 2015), and in microtidal estuaries (e.g., Kearney and Turner 2016). Those that are more resilient and more likely to survive will have the opposite characteristics, namely high productivity, high SSC (e.g., Patrick and DeLaune 1990; DeLaune et al. 1987; 2016), and tides of large amplitude (Cahoon and Guntenspergen 2010).

We have not addressed here how quickly marshes will fail; however, this is a function of the same variables—productivity, SSC, and tidal amplitude, and as well as the acceleration rate of SLR. Much has been written about elevation capital, and how it affects the vulnerability of a marsh to SLR (Reed 2002; Cahoon et al. 2011); in general, marshes at higher elevations, i.e., greater elevation capital, are less vulnerable to SLR because they have more elevation to lose before they reach the threshold elevation for conversion from marsh to mudflat (Cahoon and Guntenspergen 2010). However, it is important to note that elevation capital is limited by tidal amplitude. By definition, tidal marshes in a microtidal estuary will have very little elevation capital to lose before they are converted to mudflats, and hence are highly vulnerable. Whereas, marshes at the same dimensionless elevation in a macrotidal estuary (same relative elevation capital but much greater absolute elevation capital) are much less vulnerable to SLR. A tidal marsh with a meter of elevation capital will survive a 1 m rise in sea level, though it will lose relative elevation over the course of a century and still maintain vegetated.

Marshes can also be in disequilibrium in the opposite direction, i.e., building elevation rapidly. This situation is most likely to relate to newly constructed marshes that are established at relatively low elevations in sediment-rich environments or naturally occurring deltaic marshes. Under these conditions, the new marshes build elevation rapidly through the rapid accumulation of both mineral matter and belowground organic matter (living, decaying, and refractory material that builds soil volume). Prior to vegetation colonization, restoration sites build elevation solely through mineral sediment accumulation (and hence are reliant on relatively high SSC). This evolution has been observed in San Francisco Bay tidal marsh restoration projects (Williams and Orr 2002; Brand et al. 2012), but is likely to occur in any sediment-rich system. While the early development of these marshes is affected by mineral accumulation, over time the gains in elevation are more strongly affected by organic matter accumulation (Figure 6.2), with a gradual gain in relative elevation ($dZ/dt > SLR$) until the marsh reaches an equilibrium point.

6.6.2 Carbon Sequestration

Although there were complex feedbacks across variables, the modeled rates of carbon sequestration were affected most directly by two variables: B_{max} and SLR. This is not surprising as B_{max} along with elevation determines overall productivity, as well as belowground biomass, which is the primary source of carbon for sequestration, and SLR creates the opportunity for the ongoing accumulation of material. The direct relationship between SLR and carbon sequestration rates over moderate rates of SLR indicates that up to a point, increases in SLR will lead to greater rates of carbon sequestration.

There is an interaction between SLR and B_{max} that determines C-sequestration. B_{max} is really a proxy for maximum potential production of belowground biomass. For any given level of B_{max} there is a SLR that results in maximum C-sequestration, and the SLR that gives maximum sequestration rises as B_{max} increases (Figure 6.5). As you would expect, higher C-sequestration rates are found in productive ecosystems/locations, and many of the high rates from previous compilations of carbon sequestration rates come from locations like Louisiana, with high rates of local SLR (e.g., see data in Chmura et al. 2003; Ouyang and Lee 2014).

At low rates of SLR, marshes tend to maintain an elevation close to MHW (Figure 6.4), and at this high elevation, they build virtual carbon-rich, peat soils, in large part because of the irregular tidal flooding and reduced input of mineral sediment. This has been observed in many natural marshes, from the Everglades (Craft and Richardson 1993) to New England marshes (Bricker-Urso 1980) and high elevation San Francisco Bay marshes (Callaway et al. 2012). In these cases, carbon sequestration is equal to SLR×carbon density. With recent rates of SLR equal to 2–3 mm $year^{-1}$, and typical carbon density values of 25–35 mg C cm^{-3}, (Gosselink et al. 1984), this would result in carbon sequestration rates ranging from 50 to 105 g C m^{-2} $year^{-1}$. This pattern also reflects the peat buildup for high elevation marshes discussed above. Stable, low-elevation marshes are more likely to be associated with higher rates of SLR, and they will be maintained by a mix of both mineral and organic matter inputs, resulting in soils with lower organic concentration (Figure 6.3) in low-elevation (Figure 6.4), equilibrium marshes.

At some point, the virtual marsh cannot keep pace with accelerating SLR and begins to lose elevation when $dZ/dt < SLR$ (disequilibrium). Under model conditions with constant inputs, the marsh will continue to lose relative elevation; however, in natural marshes, there could be storm inputs or other shifts that push the marsh back towards equilibrium. As the virtual marsh loses elevation, sequestration will decline due to declining productivity at lower elevations (the declining arm of the elevation-biomass parabola) (Figure 6.1). When equilibrium DimE declines to a level below 0.5, the optimum for biomass production, further increases in the rate of SLR will lead to more rapid loss of relative elevation, and lower biomass production, and eventually to loss of C-sequestration potential as the equilibrium elevation drops below the threshold for plant survival. The virtual system eventually reaches an equilibrium elevation, but this will be below the threshold for plant survival.

Our definition of carbon sequestration focuses on refractory carbon that will be retained in the soil over the long term; however, most field-based measurements of tidal marsh carbon sequestration are based on dated sediment cores with a time frame of ~50 years for ^{137}Cs and ~100 years for ^{210}Pb. Some estimates have also been made using short-term methods, such as marker horizons, as well as longer term methods, e.g., ^{14}C. As indicated above and discussed in the chapter on accretion methods (Chapter 7 in this volume), all of these methods integrate surface soil layers, which inherently include a mix of labile and refractory carbon, and will result in inflated estimates of carbon sequestration. Surface layers have the greatest ratio of labile carbon:refractory carbon, and this ratio is likely to decline consistently with depth. As a result, short-term methods that incorporate more surface layers relative to deep soil layers will result in the largest overestimates of carbon sequestration. This issue can be seen in previous compilations of carbon data using a mix of measurement methods (e.g., Chmura et al. 2003).

Finally, it is important to note that historical rates of carbon sequestration from individual sites are informative, but these rates alone are not necessarily a good predictor of future potential for carbon sequestration. Future rates will be affected by changes in SLR, shifts in marsh elevation that could lead to changes in productivity, as well as changes in suspended sediment inputs (affected by both changes in overall sediment loads and marsh elevation). Given these potential shifts, future carbon sequestration could be higher than historical rates (e.g., if there is a slight increase in SLR, allowing the marsh to keep pace; refer to Figure 6.5) or lower than historical rates (e.g., if the marsh loses substantial elevation, plants become stressed and productivity is reduced). These shifts not only highlight the benefit of using a model that is calibrated with historical accretion and sequestration rates, but also the ability of the model processes to respond to future conditions in order to predict future rates of sequestration. Similarly, a model could be used to predict conditions in a newly developing, restored marsh based on historical conditions in a reference marsh, with shifts in elevation and other critical parameters.

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