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Mangrove Trees Outperform Saltmarsh Grasses in Building Elevation but Collapse Rapidly Under High Rates of Sea-Level Rise

James T. Morris¹ , J. Adam Langley², William C. Vervaeke³, Nicole Dix⁴, Ilka C. Feller⁵, Pam Marcum⁴, and Samantha K. Chapman²

Key Points:

- Mangrove trees are invading saltmarshes at subtropical ecotones, limited by dispersal which can be managed
- Mangroves are more resilient to rising sea levels because they build elevation more rapidly than saltmarshes
- When mangroves drown, we predict that their soils will abruptly lose elevation due to the large volume of quickly decomposing necromass

Supporting Information:

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

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Abstract Mangrove trees are invading saltmarshes at subtropical ecotones globally, but the consequences of this vegetation shift for ecosystem sustainability remain unknown. Using the Coastal Wetland Equilibrium Model (CWEM) to simulate vegetation survival and sediment accretion, we predict that black mangroves, *Avicennia germinans*, can build soil elevation by 8 mm yr⁻¹, four times greater than saltmarshes at the same site, a finding that is broadly consistent with field measurements of elevation change. Mangroves build elevation more rapidly than saltmarshes by producing much greater live and labile belowground biomass, but when mangroves drown, they abruptly lose elevation due to the large volume of quickly decomposing necromass following flood-induced mortality. Under certain conditions, young mangroves can accumulate root mass faster than mature trees and, therefore, gain elevation more rapidly, but neither saltmarshes nor mangroves of any age survived a centenary sea-level increase of 100 cm. The acceleration of sea-level rise that coastal marshes are encountering raises the question of how coastal wetlands should be optimally managed and these results provide managers with predictive information on wetland building capacity of mangroves versus marshes.

Plain Language Summary The conversion of coastal wetlands from non-woody marsh grasses to mangrove forests is proceeding now in subtropical transition zones due to a warming climate. Conversion of salt marsh habitats to mangrove forests will enhance coastal protection and carbon storage.

1. Introduction

Mangroves and marshes protect humans from coastal storms and maintain a vertical position relative to rising seas by building elevation (Cahoon et al., 2020; Doughty et al., 2017; Krauss et al., 2014; Morris et al., 2002). Owing to low soil oxygen levels and limited decomposition, organic matter accumulates in coastal wetland soils over time, contributing to high rates of vertical elevation gain, hereafter referred to as vertical accretion, and carbon accumulation (Cahoon et al., 2020; Reddy & Patrick, 1975; Redfield, 1965). Mangroves and marshes have kept pace with historical rates of sea-level rise (SLR) for thousands of years through organic matter accumulation and plant-assisted sediment trapping (Kirwan et al., 2016; McKee et al., 2007; Saintilan et al., 2020). However, large areas of coastal wetlands have converted to mudflats or open water, and models predict more will be lost as SLR accelerates (Chambers et al., 2013; Li et al., 2018; Lovelock et al., 2017; Thorne et al., 2018). The capacity of coastal wetlands to continue building elevation remains highly uncertain (Lovelock et al., 2015; Saintilan et al., 2022; Ward et al., 2016), especially as other anthropogenic forces such as land use change alter the structure of these ecosystems (Friess et al., 2019).

Mangroves are tropical woody wetland plants that disperse via water-borne propagules into new habitats, episodically traveling great distances (Kennedy et al., 2020; Van der Stocken et al., 2019; Yando et al., 2021). The latitudinal range throughout which mangroves can establish is limited by freezing temperatures where saltmarshes predominate. The mangroves that have colonized ecotonal environments at the limits of their range can exhibit precocious reproduction, in which young mangroves reproduce much earlier than expected, accelerating expansion into saltmarshes (Dangremond & Feller, 2016). Reduced frequency of freeze events, increasing sediment loads, drought, and nutrient pollution have spurred the encroachment of low-stature, shrubby mangroves,

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into higher latitude saltmarshes, which are comprised of herbaceous, succulent plants or grasses (Cavanaugh et al., 2014; Dangremond et al., 2020; D'Odorico et al., 2013; Lovelock et al., 2017; Osland et al., 2013, 2018; Rogers et al., 2006).

This transformation of coastal wetland ecosystems from grasslands to mangrove shrublands is occurring around the world and altering coastal ecosystem services, habitats, and biodiversity (Guo et al., 2017; Kelleway et al., 2017; Saintilan & Rogers, 2015). Some parts of Florida USA, the U.S. Gulf Coast, and Australia have experienced especially rapid increases in mangrove abundance and spread (Cavanaugh et al., 2019; Doughty et al., 2016; Rogers & Krauss, 2019; Saintilan et al., 2014). As of 2021, the most cold-tolerant mangrove in North America, *Avicennia germinans* (black mangrove) has expanded its range into northeast (NE) Florida USA (FL). It is within 20 km of the Florida-Georgia border and the vast saltmarshes to the north into which mangroves could encroach (Cavanaugh et al., 2019) as the climate warms. As elsewhere, stronger hurricanes and storm surges have been occurring in NE FL and can drive dispersal events and influence sediment delivery, likely contributing to the current and future northward migration of mangroves if severe freezes do not prevent this biome shift in the United States (Cavanaugh et al., 2019; Kennedy et al., 2020).

Mangroves and marsh plants build elevation by a combination of organic matter production and sediment trapping. Root zone processes can dominate control of wetland elevation in ecosystems without large sediment loads. Experimental manipulations such as CO₂ additions and warming have shown that differences in wetland elevation gain correlate with changes in root growth (Cherry et al., 2009; Coldren et al., 2019; Langley et al., 2009). However, past studies yield conflicting results on whether the capacity to build elevation differs between mangroves and marshes (Chen et al., 2021; Coldren et al., 2019; Comeaux et al., 2012; Howard et al., 2020; McKee & Vervaeke, 2018; Perry & Mendelsohn, 2009; Rogers et al., 2013), partly because the two plant types are often compared at different sites with confounding physical variables. Mangrove roots may be more resistant to decomposition than the organic matter of herbaceous marsh plants (Benner et al., 1991; Ola & Lovelock, 2021) which may result in more recalcitrant soil organic matter in mangrove soils (Bianchi et al., 2013). Resistance to decay and ability to build elevation, however, varies among mangrove species (Krauss et al., 2003, 2014; McKee et al., 2007). Models such as the Marsh Equilibrium Model (MEM) can resolve these differences in organic matter quality and, in combination with other biogenic, geomorphic, and hydrological parameters forecast wetland elevation (Morris et al., 2002). We use a modified MEM here, the Coastal Wetland Equilibrium Model (CWEM), to simulate the growth of woody, perennial wetland plants like mangroves that can produce over time much greater biomass than saltmarsh grasses.

To determine how wetland resilience to SLR will change if *A. germinans* continues to move northward into saltmarsh habitats along the southeastern U.S. coast, we parameterized the model with data from ecotonal mangrove and saltmarsh plots in NE FL at the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR; www.wetfeetproject.com). The encroachment of mangroves at these ecotonal sites, which are similar to the vast areas of saltmarsh in coastal Georgia and South Carolina, provides an opportunity to examine elevation controls in coexisting mangrove and marsh plots with similar hydrology, geomorphology, and climate (Dix et al., 2021). We obtained data on *A. germinans* root productivity, root mass, decomposition, elevation, and other key parameters from marsh-dominated and mangrove-dominated plots at three sites in NE FL. Specifically, we modified the existing MEM model to accommodate perennial mangrove growth and used the new CWEM to simulate vertical accretion and calculate survival times resulting from permutations of three vegetation types × three SLR scenarios. The permutations included simulations of growing young and mature (defined as 30-yr old trees) *A. germinans* trees and *S. alterniflora* grasses, each subjected to centenary SLR (CSLR) scenarios of 40, 60, and 100 cm. To test the model, we examined relative elevation change from monitoring sites in the GTMNERR and compared sites with encroaching *A. germinans* to those still dominated by *S. alterniflora* (Dix et al., 2021).

2. Materials and Methods

2.1. Coastal Wetland Equilibrium Model (CWEM)

To explore how mangroves and marshes compare in their ability to build elevation in response to rising sea levels, numerical experiments were performed using this latest version of the Coastal Wetland Equilibrium Model (CWEM v9.01), which was developed originally as the Marsh Equilibrium Model (MEM) for saltmarshes

(Morris et al., 2002) and modified for the growth of *A. germinans* in the transition zone in NE Florida. The CWEM simulates the growth and survival of mangroves and marshes and predicts the response of wetland elevation to rising sea levels. The term equilibrium is used to connote that an intertidal wetland is always moving toward equilibrium with sea level, not that it is necessarily in equilibrium or that it succeeds in achieving equilibrium. MEM and CWEM compute vertical accretion as a mass balance of mineral sediment and organic inputs, converted to volume from their respective self-packing densities, which are based on an extensive sampling across many diverse wetland sites, including mangroves (Morris et al., 2016). The models incorporate feedback among vegetation, sediments, and tides that enable a wetland to track sea level, within limits (Morris et al., 2002). Feedback between primary production and vertical accretion can be positive or negative, depending on the relative elevation of the wetland surface, and this is a function of the rate of SLR. The original model has evolved and now incorporates additional variables that explicitly define processes that contribute to soil volume, such as below-ground biomass accretion and increasing accommodation space. For young mangrove trees, we had to account for growth and the change in the feasible vertical distribution that accompanies growth.

Relative surface elevation and productivity are the proximate determinants of vertical accretion rate. The vertical accretion rate (dz/dt , cm/yr) at a given point on the surface of the wetland is a function of both organic and mineral inputs:

$$\frac{dz}{dt} = \frac{dz_{org}}{dt} + \frac{dz_{min}}{dt} \quad (1)$$

where the organic and mineral contributions are $\frac{dz_{org}}{dt}$ and $\frac{dz_{min}}{dt}$. Both terms are functions of the depth of the surface below the mean high water (MHW) level of the tide, but surface deposition is solely responsible for $\frac{dz_{min}}{dt}$ whereas $\frac{dz_{org}}{dt}$ is accounted for largely by belowground production. For a given suspended sediment concentration in floodwater, mineral deposition increases with the depth of floodwater and time of submergence. For example, if the wetland surface is above MHW, the delivery of sediment to the surface approaches zero. The governing equations are documented elsewhere (Morris & Callaway, 2018; Morris et al., 2021).

Key to the contribution of organic matter or biovolume is belowground biomass production, with is allometrically proportional to aboveground standing biomass (B_s). For *S. alterniflora*, the proportionality of maximum below:above-ground biomass is approximately 2:1 (Darby & Turner, 2008; Morris, 1982), and we assume *Spartina* root biomass turns over annually based on bioassay experiments. Only a fraction of the organic production is preserved, related to the lignin concentration in plant tissue, which for *Spartina* is about 10% of dry weight (Buth & Voeselek, 1987; Hodson et al., 1984; Wilson et al., 1986).

Peak aboveground biomass B_s is dependent on the duration of flooding, which is a function of the average depth (D) of water that floods the wetland surface:

$$B_s = aD + bD^2 + c \quad (2)$$

The empirical coefficients, a , b , and c , describe the shape of a growth curve that spans a vertical range, limited at one extreme by hypoxia (the soil is too wet) and the other by osmotic stress (the soil is too dry and salty). That curve is known for *S. alterniflora* from bioassay experiments (Morris et al., 2013) and field measurements (Miller et al., 2019). The model solves for the empirical constants by specifying the maximum and minimum depths of the growth curve—these define the vertical growth range, and the optimum depths and biomass:

$$a = -\{(-D_{min} B_{max} - D_{max} B_{max}) / [(D_{min} - D_{opt})(D_{opt} - D_{max})]\} \quad (3)$$

$$b = -\{B_{max} / [(D_{min} - D_{opt})(D_{opt} - D_{max})]\} \quad (4)$$

$$c = \{(D_{min} B_{max} D_{max}) / [(D_{min} - D_{opt})(D_{opt} - D_{max})]\} \quad (5)$$

where D_{min} , D_{opt} , and D_{max} are the minimum, optimum, and maximum depths below MHW, and B_{max} is the biomass at the optimum depth. The depth below MHW is positive. For *Spartina*, this curve can vary from year to year depending on rainfall and other factors, and for colonizing mangroves this curve changes significantly as the trees mature (Figure 2c). Consequently, it is necessary to describe how the vertical growth range, optimum depth, and maximum biomass vary with the age of mangrove tree. We assume for simplicity that growth is linear to the point of maturity. Hence, for mangroves the growth factors are defined, for example, as

$$GF_{B_{\max}} = (B_{\max(\text{mat})} - B_{\max(0)})/T_{\text{mat}} \quad (6)$$

where $B_{\max(0)}$ and $B_{\max(\text{mat})}$ are the maximum standing biomass of juveniles and mature trees, respectively, and T_{mat} is the time to maturity (years). These growth factors are computed for maximum standing biomass, minimum, maximum, and optimum depths, maximum root depth, and root turnover rate. For mangroves, Equations 3–5 are updated annually using the growth factors to compute the updated variables B_{\max} and so on until time T_{mat} .

2.2. Numerical Experiments

The model was solved for each of three centenary sea-level rise (CSLR) scenarios: 40, 60, and 100 cm of SLR, where the mean sea level (MSL) was allowed to increase to a final specified value ($MSL_{(100)}$) using a formula adopted by the NRC (NRC, 1987):

$$MSL_{(t)} = MSL_{(0)} + c_2t + c_3t^2 \quad (7)$$

where t is time ($0 < t < 100$ years) and the c_i are constants that determine the acceleration of sea level. The 40 cm scenario is essentially the current, approximate rate of SLR, while the 100 cm scenario is the forecasted intermediate level (Sweet et al., 2017) and is within the likely range of RCP8.5. The 60 cm CSLR, at the high end of the RCP2.6 likely range (Oppenheimer et al., 2019), was found by trial and error to be the rate at which mature trees drown, while juveniles do not. For each SLR scenario, communities of *S. alterniflora*, pioneer (first-years), and mature (>30 years of age) *A. germinans* were simulated with starting elevations at the median at GTM for each type.

To determine the survival time of pioneer and mature mangroves in NE Florida at different rates of SLR, a fourth group of experiments was run in which the rate of SLR was assumed to be constant. A range of constant rates was tested from 10 to 20 mm yr⁻¹. Simulations were run for starting relative elevations of 45 and 55 cm (NAVD 88), which are within the range of elevations observed for pioneer and mature *A. germinans* in the study site (Table S3 in Supporting Information S1).

2.3. Validation

A comparison was made of simulated and observed rates of vertical accretion on GTM sites dominated by monotypic stands of *S. alterniflora* and a site experiencing a transition from *S. alterniflora* to *A. germinans*. From established Surface Elevation Tables (Lynch et al., 2015) (SET), we calculated the slopes of elevation versus time at each SET station for each of the four cardinal directions and tested for statistical significance between plant community types by analysis of covariance. The CWEM was run for each plant community, starting at each of the measured (by real-time kinematic positioning) elevations around the SET stations. A constant SLR of 0.35 cm yr⁻¹ was assumed. All other model parameters were as reported (Table S2 in Supporting Information S1).

3. Data

A summary of the data is available from <https://nerssciencecollaborative.org/resource/national-synthesis-nerf-surface-elevation-table-data>. At each site there are five Surface Elevation Tables (Lynch et al., 2015) (SET) stations. Creekbank stations experiencing edge erosion were excluded.

4. Results

4.1. *S. alterniflora* Marshes and *A. germinans* Wetlands at Different Sea-Level Accelerations

Marsh equilibrium theory predicts that the vertical accretion rate and elevation of a tidal wetland surface will equilibrate to the rate of sea-level rise (RSLR) or collapse (Morris et al., 2002, 2021). The elevation of the wetland surface elevation relative to MSL will remain constant so long as the RSLR is constant. However, RSLR is accelerating (Nerem et al., 2018). Consequently, wetland surface elevations and vertical accretion rates will change as the biomass of the plant community and relative site elevation respond to the acceleration in RSLR, and our model demonstrates that these changes in accretion rates and elevation depend on species and assumptions about the ultimate rise in sea level (Figure 1).

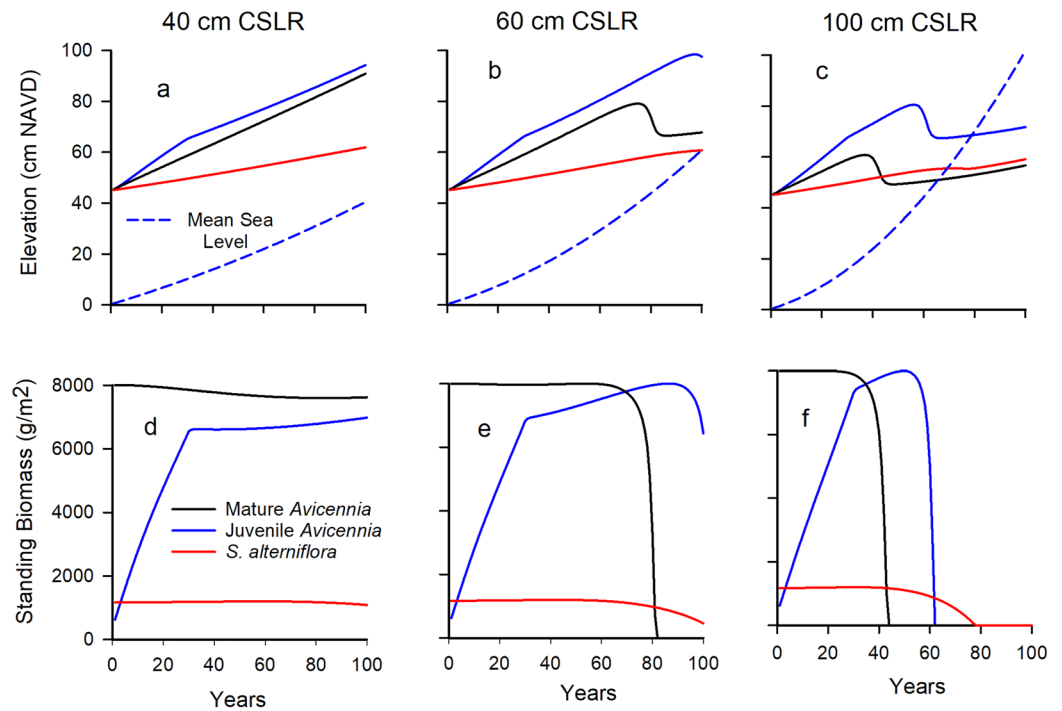


Figure 1. Simulations Responses. Time series of simulation results for three centenary sea-level rise scenarios (40, 60, and 100 cm) are shown for communities of *S. alterniflora* grasses (—), mature (—), and juvenile (—) *A. germinans* trees. Outputs include sediment surface elevations and MSL (cm NAVD) (a–c) and standing biomass (d–f) versus elapsed time.

Starting from an initial RSLR of 2 mm yr^{-1} , the RSLR obtained by fitting a quadratic to a 40 cm CSLR rise of MSL resulted in RSLR rising to 6 mm yr^{-1} by the end of a century (EOC), which outpaced the maximum accretion rate of the saltmarsh (Figure 1a). A CSLR to 60 and 100 cm resulted in RSLR of 10 and 18 mm yr^{-1} by the EOC (Table S1 in Supporting Information S1). Our saltmarsh simulations indicated that at no time did gains in marsh elevation keep pace with the rise in sea level (Figure 1a–1c). In the first 25 yr, vertical accretion of *S. alterniflora* marsh averaged about 1.6 mm yr^{-1} irrespective of the assumed CSLR, up to 100 cm (Table 1). At the lowest and highest CSLR scenarios (40 and 100 cm), absolute EOC gains in elevation in the saltmarsh ranged from 17 to 14 cm, respectively, and by the end of the simulations, elevation had decreased to 21 cm relative (to MSL) in the low and -43 cm in the high CSLR scenario from a starting relative elevation of 45 cm.

Organic matter accretion dominated vertical accretion in all simulations of marshes and mangroves irrespective of CSLR as shown by the predicted volume percent of mineral matter (Table 1). Mineral sediment inputs in the marsh were predicted to comprise 19% of total accretion in the first 25 yr, irrespective of the sea-level scenario, rising to 25%–34% of volume after 100 yr in the 60 and 100 cm CSLR scenarios (Table 1) as the depth of flooding increased. Mineral inputs were more important in the marsh than in the mangroves in most simulations.

Time-series plots from the biomass simulations showed that survival times of the marshes at all CSLRs were predicted to exceed those of the mangroves (Figure 1d–1f) owing to differences in flood tolerance. *S. alterniflora* will survive at lower relative elevations than *A. germinans*. The standing biomass of *S. alterniflora* in the low CSLR scenario was almost stable throughout the entire simulation, while biomass in the high CSLR scenario dropped precipitously to zero beginning at the mid-point in the simulation (Figures 1d and 1f). Although the *Spartina* biomass was nearly stable in the 40 cm scenario, the predicted relative elevation had decreased by about 50% by the end of the simulation (Figure 1a).

Contrasting sharply with the *S. alterniflora* simulations, predicted gains in elevation were much greater and mineral sediment inputs comprised less of total vertical accretion in mangrove simulations (Table 1). The pioneer *A. germinans* wetlands gained 168–182 mm in the first 25 yr or 4.5 to 4.8 times as much as the *S. alterniflora* marshes depending on the CSLR. By the end of the simulation, pioneers had gained from 1.9 to 3.6 times more elevation than the saltmarshes and 1.1 to 2.3 times the accretion in the mature mangroves, depending on the

Table 1
Dependence of Accretion Rate and Sediment Composition on Centenary SLR (CSLR) and Plant Community

Site	Years	40 cm CSLR			60 cm CSLR			100 cm CSLR		
		Total gain (mm)	Min. Vol. %	Accr. Rate (mm/yr)	Total gain (mm)	Min. Vol. %	Ann. Accr. (mm/yr)	Total gain (mm)	Min. Vol. %	Accr. Rate (mm/yr)
<i>S. alterniflora</i> Salt Marsh	25	37	19	1.6	38	19	1.6	38	19	1.7
	50	78	19	1.7	80	19	1.8	82	20	1.7
	75	122	19	1.8	125	21	1.7	103	26	-0.5
	100	168	20	1.8	156	25	0.6	140	34	2.1
Pioneer <i>A. germinans</i> Mangrove	25	168	15	6.7	173	15	7.3	182	14	8.2
	50	278	12	3.9	302	11	4.9	332	11	5.1
	75	380	11	4.2	432	9	5.4	228	17	1.1
	100	490	9	4.6	523	9	-6.7	265	22	1.8
Mature <i>A. germinans</i> Mangrove	25	110	15	4.5	112	15	4.7	113	15	4.7
	50	222	12	4.5	234	12	5.0	39	20	0.6
	75	337	10	4.6	337	11	0.5	68	26	1.5
	100	455	9	4.8	223	17	1.1	113	34	2.1

Note. Shown here for different forecasted rates of CSLR and different plant communities are the total gains to date in vertical accretion (mm) at quarter-century intervals, accretion attributable to mineral deposition (volume %), and annual accretion rate (mm/yr) at points in time.

CSLR (Table 1). Simulations of pioneer *A. germinans* returned the highest annual vertical accretion rates—ranging from 6.7 to 8.2 mm yr⁻¹ at the 25-yr point in the lowest and highest CSLR scenarios, respectively. In all simulations of pioneer *A. germinans*, vertical accretion rates were greatest in the first quarter. At the end of the simulations, the annual accretion rate had declined to 4.6, -6.7, and 1.8 mm yr⁻¹ in the 40, 60, and 100 cm CSLR scenarios (Table 1).

The advantage of pioneer *A. germinans* during the first quarter can be attributed to the production of organic matter arising from belowground production. Organic contributions maintained elevation near the top of the tidal frame where the depth of flooding and the opportunity for mineral sedimentation are greatly reduced. Consequently, mineral sediment accounted for 17% or less of sediment volume in all but the last quarter of the 100 cm CSLR scenario (Table 1). At the end of the simulations, mineral sediment made up 22% of pioneer mangrove soil volume at the highest and 9% at the lowest CSLR scenario.

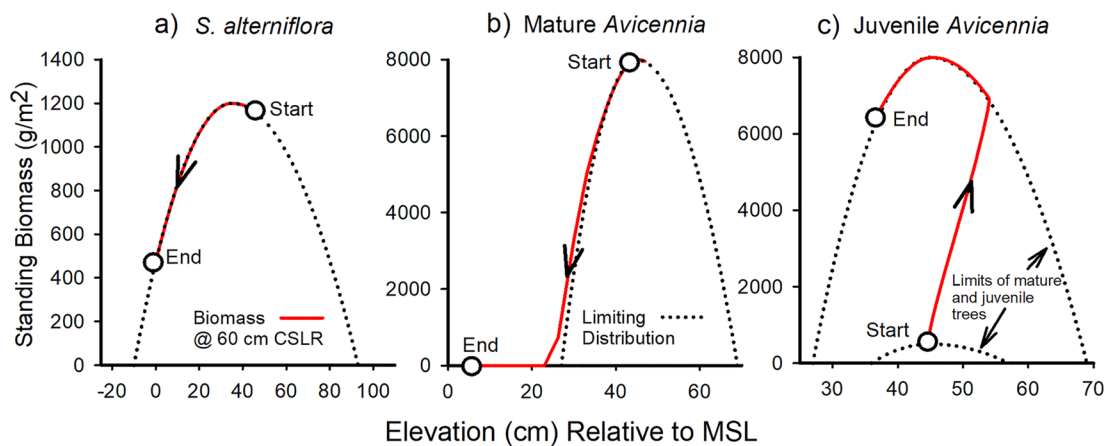


Figure 2. Phase plane plots of the biomass versus relative elevation. Biomass and relative (to MSL) elevations from the 60 cm CSLR simulations shown in Figure 1 are plotted for (a) *S. alterniflora*, (b) mature *Avicennia*, and (c) juvenile *Avicennia*. The theoretical vertical biomass distributions are shown as dotted parabolas. The beginning elevations and biomass are indicated as starting points. Simulations ended after 100 years at the endpoints. Their relative elevations change as sea level and surface elevations change with time as shown in Figure 1.

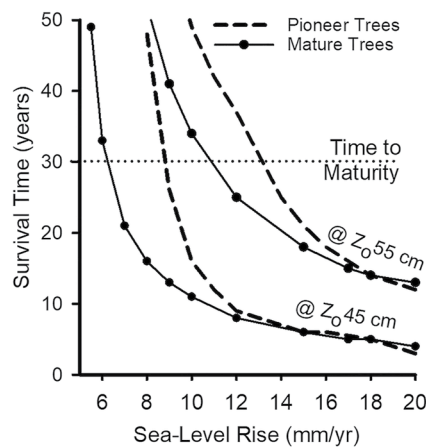


Figure 3. Survival times of pioneer and mature trees at constant SLR. From simulations started at 45 or 55 cm elevation (relative to MSL) the survival times of juvenile and mature *Avicennia* trees are shown at different, constant rates of SLR. Pioneer trees had lower and upper vertical limits of 36 and 57 cm relative to MSL.

The growth of *A. germinans* is bounded by the pattern of biomass accumulation relative to sea level of first-year pioneers and mature trees (Figure 2c). Field-based surveys at the GTM NERR showed that the vertical distribution of mature *A. germinans* is broader than that of first-year (pioneer) trees. The minimum relative elevations of pioneer and mature trees were 36 and 34 cm, indicating similar tolerances to flooding stress, but the upper elevation limit of mature trees was greater (Table S2 in Supporting Information S1).

Time-series plots from the pioneer *A. germinans* simulations demonstrated the importance of biomass growth that occurred over the first 30-yr of development. A post-maturation expansion of biomass occurred as the relative elevation of the black mangrove stand decreased, moving toward the optimum. Biomass continued to rise after the trees matured in all CSLR scenarios (Figure 1d–1f), but the decrease in relative elevation after 30 yr at CSLR 60 and 100 cm (Figures 1b and 1c) eventually reduced the relative elevation of those sites to the suboptimal side of the growth curve (Figure 2c), and biomass subsequently declined. The acceleration in RSLR at CSLR 100 to 1 cm yr⁻¹ and higher (Table S1 in Supporting Information S1) greatly exceeded the rate of accretion (Table 1) and the mangroves, which by this time were mature, drowned by about year 60 (Figure 1f).

Vertical accretion rates in simulations of mature *A. germinans* were similar to those of the pioneers in terms of the dominance of sediment organic matter contributions to soil volume and elevation gain. Otherwise, the dynamics differed during the early years of the simulations when pioneer trees were growing roots rapidly. Accretion rates in the mature trees at the end of the first quarter ranged from 4.5 to 4.7 mm yr⁻¹ (Table 1), which was 2.2–3.5 mm yr⁻¹ less than pioneer trees due to the growth advantage of younger trees. The annual accretion rate in the mature trees at the highest CSLR forecast dropped from 4.7 mm yr⁻¹ at the end of the first quarter to 2.1 mm yr⁻¹ after the final quarter of the simulation due to the loss of biomass (Figure 1f), and soil mineral content increased from 15% to 34% (Table 1).

Mature *A. germinans* had the lowest survival times of the three vegetation types (Figures 1e and 1f) and, compared to pioneers in the 60 and 100 cm CSLR scenarios, had lower final elevation gains and higher sediment mineral contents (Table 1). Elevation gains in mature *A. germinans* were 110–113 mm after the first 25 yr, and after 100 years the relative elevation of mature mangrove communities was 455 mm at the lowest CSLR forecast and 233 mm in the intermediate CSLR scenario. At the highest CSLR, the elevation gain in mature mangroves had decreased from 113 to 39 mm from the first to the second quarter before rising again to 133 mm after 100 yrs. A loss of relative elevation increased the importance of mineral sedimentation (Table 1).

4.2. *Avicennia germinans* at Constant Sea-Level Rise

The survival time of pioneer *A. germinans* decreased with an increasing and constant rate of SLR and decreased with starting elevation (Figure 3). Starting at a super-optimal elevation for *A. germinans* growth, 55 cm, survival time approached 30 yr, the maturation time, when RSLR was a constant 14 mm yr⁻¹ (Figure 3). However, at a starting elevation of 45 cm, the optimum for pioneer *A. germinans*, the survival time of pioneers was less than their time to maturity when RSLR was greater than 10 mm yr⁻¹. At the highest CSLR scenario, 100 cm, an RSLR of 10 mm yr⁻¹ will be realized by mid-century. At a CSLR of 60 cm, an RSLR of 10 mm yr⁻¹ will be realized in 100 years.

4.3. Model Validation

To support model results, we compared observed vertical accretion rates at GTM in plant communities supporting monotypic stands of *S. alterniflora* (2.9 ± 3.3 mm yr⁻¹) with those in a mixed plant community of *S. alterniflora* and invading *A. germinans* (Table 2). The elevation measurements in these plots show that accretion rates were higher in the mixed community (4.7 ± 2.3 mm yr⁻¹) as predicted and that no observed loss of elevation occurred as the mangroves became more dominant. The predicted accretion rate in the mixed community of pioneer mangroves was 4.5 ± 1.7 mm yr⁻¹. An example of the acceleration in elevation gain following

Table 2
Comparison of Model Predictions With Field Observations

Community	Mean elevation veg. Plots (cm rel. MTL)_	Accretion rate (mm/yr)	
		Observed ^a	Predicted ^b
<i>Spartina</i>	55 ± 13	2.9 ± 3.3	1.4 ± 0.2
Young <i>Avicennia</i>	44 ± 21	4.7 ± 2.3	4.5 ± 1.7
Mature <i>Avicennia</i>	na	na	3.1 ± 0.6

Note. Observed elevation, observed and predicted mean (±1 STD), and accretion rates in plant communities at GTM sites dominated by *Spartina* and transitioning from *Spartina* to *Avicennia*.

^aObserved mean elevation change is derived from Sedimentation-Erosion Tables (SETs) established in 2013 and measured biannually through 2021 at three sites: Moses Creek, Pine Island, and Hat Island. There were 3 SETs at each site. Observed accretion rates in the *Avicennia* transition and *Spartina* sites differed significantly ($F_{1, 5819} = 109.6, p < 0.0001$). ^bPredictions for the site (East Creek) originally dominated by *Spartina* and now supporting a young *Avicennia* community were generated using a CSLR = 35 cm and current SLR = 3.5 mm/yr. Reported are means of each simulation by community type, each starting at elevations in GTM *Spartina* and *Avicennia* sites where RTK elevations have been measured ($N = 35$ and 12, respectively).

the invasion of *A. germinans* trees into a saltmarsh is shown in Figure 4. Here, vertical accretion of a pioneer community of *A. germinans* in a later stage was as great as 20 mm/yr during a 4-yr period, followed by a rate of about 5 mm/yr. The latter is comparable to the 6.7 mm/yr rate predicted for pioneers after 25-yr in the 40 CLSR scenario (Table 1). The total gain in observed elevation across the entire transition has been about 160 mm (Figure 4), which matches the 168 mm gain predicted for pioneers in the first 25 yr (Table 1). The model-calculated accretion rate in the *S. alterniflora* community was 1.4 ± 0.2 mm yr⁻¹, lower than the observed rate of 2.9 ± 3.3 mm yr⁻¹ (Table 2). The mean elevation of the mixed mangrove community, 44 ± 21 cm, is near the presumed optimum elevation for *A. germinans*, 45 cm, whereas the elevation in the *S. alterniflora* community, 55 ± 13 cm, is higher than its presumed optimum of 35 cm.

5. Discussion

We compared three vegetation scenarios to determine the survival or collapse of coastal wetlands in the face of three SLR scenarios. Using environmental conditions representative of sites in NE Florida, USA, but similar to other coastal wetlands in the southeast, we found that, while *S. alterniflora* marshes have greater flood tolerance than *A. germinans* by virtue of the lower limit of the saltmarsh vertical range, both pioneer and mature *A. germinans* support

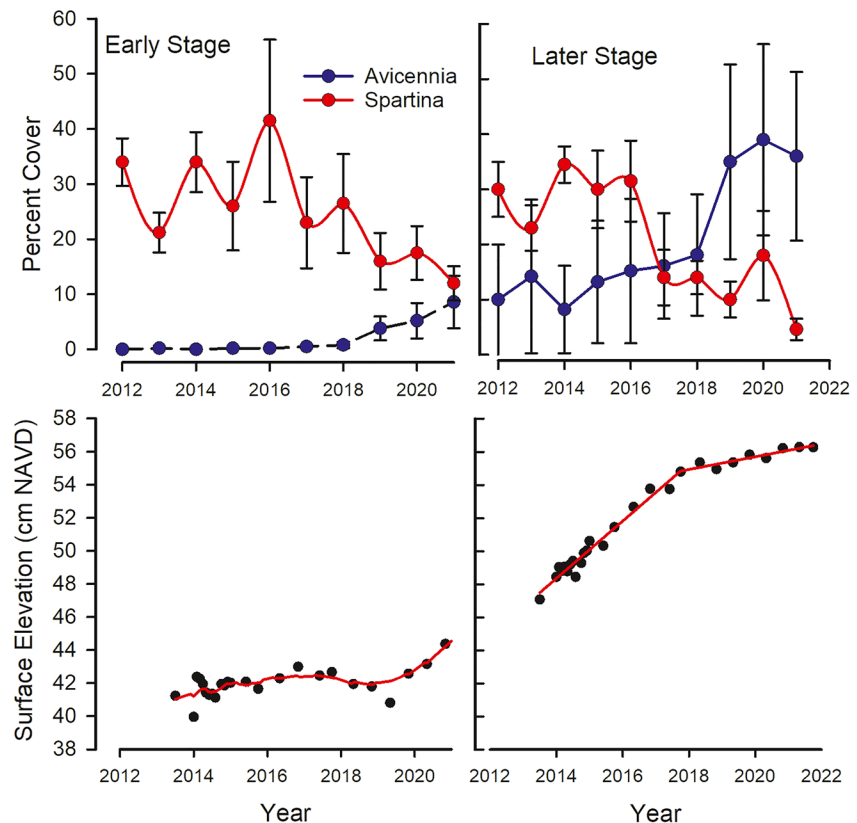


Figure 4. An example of mean vegetation cover (±1 SE, top panels) and elevation (bottom panels). Data are from the East Creek monitoring site (GTM-NERR) where adjacent SETs have captured the full transition from nearly pure *S. alterniflora* to dominance by *A. germinans*. The total plant cover does not add up to 100% because the remaining area is composed mostly of bare ground. Surface elevation in the later stage increased by about 20 mm/yr between 2014 and 2018 and 5 mm/yr between 2018 and 2022.

greater vertical accretion rates (Figures 1 and 3, Table 1). The mangroves were predicted to accrete more organic sediment and have higher vertical accretion rates than the marshes due to the higher biomass production of *A. germinans* over the century, but also due to the greater preservation of mangrove organic matter. The higher modeled rates of sediment organic matter accretion for mangroves are consistent with observations from wetland sediments in the region (Bianchi et al., 2013).

Observed accretion rates in the GTMNERR qualitatively support the model predictions (Table 2). The model-predicted rates of vertical accretion for *S. alterniflora* are lower than observed rates but observed and predicted rates for the mangrove community are equivalent (4.7 vs. 4.5 mm yr⁻¹) and greater than those in the saltmarsh grasses. It is notable that these field data show no observed loss of elevation as *A. germinans* become more dominant (higher percent cover) and outcompete the existing *S. alterniflora* (Figure 4). The rates of observed accretion in the saltmarsh grasses are lower than the current RSLR but should rise as the relative elevation decreases toward the optimum and as productivity increases. The observed accretion rate of the young mangrove community is greater than the current RSLR. Consequently, elevations should rise until the mangroves are mature and elevation has risen toward the upper vertical range limit of *A. germinans*.

With the ongoing conversion from marshes to mangroves both regionally and globally (Guo et al., 2017; Kelleway et al., 2017; Saintilan & Rogers, 2015), the most relevant output for predicting the near future of these dynamically changing sites is the fate of pioneer trees. When pioneer *A. germinans* colonize, the ultimate fate of the wetland depends on the conditions under which they grow. The growth premium of the pioneers is clear (Figure 1, Table 1). At CSLR 100 and when started at 45 cm relative elevation, they accumulated 35 cm of sediment before collapsing (Figure 1c). They reached that elevation by virtue of the 30 years of growth that occurred just before the collapse. Mature trees in comparison, starting at the same relative elevation accumulated 15 cm of sediment before they collapsed. The mature trees in these virtual wetlands already carried the maximum root biomass, and they accumulated much less soil volume before their collapse than the pioneers. Consequently, the model predicts that the collapse of mature trees happens more quickly than pioneer trees.

The CWEM predicts that both *S. alterniflora* and *A. germinans* primarily build elevation due to organic processes rather than mineral sediment trapping (Table 1). *A. germinans*' capacity for vertical accretion and biomass gain increased with and exceeded RSLR in all but the final half of the 60 and 100-cm CSLR scenarios. However, CWEM also predicted young pioneer *A. germinans* that establish in the future when RSLR is greater will not survive to reach a mature size (Figure 3). The limiting RSLR was predicted to be about 9 mm yr⁻¹ for seedlings establishing at the optimum elevation of 45 cm (Figure 3). Based on soil core reconstructions since the Holocene, a threshold SLR of 5.2–7.1 mm yr⁻¹ was reported for mangrove survival (Saintilan et al., 2020). The higher of these rates of SLR will be reached in 75 yr at 60 cm CSLR, and by 50 yr in the 100 cm CSLR scenario. The corresponding accretion rates are predicted to be only 0.5–0.6 mm yr⁻¹ in mature black mangroves or 5.4 to 1.8 mm yr⁻¹ in matured juveniles (Table 1) which supports the Holocene threshold. Empirical estimates of mangrove tolerance for SLR can be sensitive to site-specific environmental conditions, climate, assumptions about peat preservation in the reconstructions, and estimates of RSLR by the glacio-isostatic adjustment (GIA) model. The CWEM estimate of tolerance is sensitive to assumptions of mangrove organic matter recalcitrance, root turnover (From et al., 2021), the CLSR, and boundary conditions (vertical range).

Our ability to parameterize this model for *S. alterniflora* marshes and *A. germinans* wetlands at the same geographic location allows us to isolate biological from confounding physical effects on surface elevation. Whereas previous analyses have compared past rates of elevation gain across marshes and mangroves in the same habitats (Coldren et al., 2019; Comeaux et al., 2012; McKee & Vervaeke, 2018), we use an established biogeomorphic accretion model to project into the future and isolate the influences of marsh plants and mangroves on wetland sustainability along this currently shifting ecotone. We parameterized the model using both our field and literature-based values (Table S2 in Supporting Information S1) and found that the CWEM outputs are sensitive to root turnover, vertical boundary conditions, and by extension, parameters that control the production of refractory soil organic matter. Decreasing *A. germinans*' time-to-maturity had little or no effect on cumulative accretion (Table S3 in Supporting Information S1) because, by reaching maturity at an earlier age, the trees grew to a higher elevation more quickly.

Root turnover and other parameters that dictate the production and preservation of soil organic matter most strongly determined the rate of biogenic accretion. The sensitivity of accretion to root turnover was a driver of our result that *A. germinans* wetlands displayed significantly higher accretion rates than *S. alterniflora*

saltmarshes (Table 1 and Table S3 in Supporting Information S1). Root productivity in mangrove-dominated plots is higher than in saltmarsh-dominated plots, which has correlated positively with elevation gain, yielding a more organically-driven accretion (Coldren et al., 2019) as seen in the simulations. The results of sensitivity analyses (Table S3 in Supporting Information S1) illustrate the complexity of feedback among relative elevation, tree growth rate (time-to-maturity), root turnover, and RSLR. It is important to note that biologic processes (e.g., organic matter production and decay) are primarily responsible for the differences between *A. germinans* and *S. alterniflora* simulation results rather than the physical environment which suggests that these results should apply to other locations.

Gains in surface elevation in coastal wetlands span from mostly organically-driven accretion on peat-based islands, for example, (McKee, 2011) to mostly mineral-driven (Callaway et al., 1997; Nyman et al., 1990). Though both *S. alterniflora* saltmarshes and *A. germinans* wetlands showed organically-driven accretion, in both wetland types the importance of mineral inputs increased toward the end of the century at the higher RSLR. Due to the massive accumulation of soil organic matter through root growth and turnover, pioneer mangroves can: (a) accrete to a position above their ideal elevation (Figure 2c) and (b) can collapse very rapidly with significant loss of elevation (Figure 1f) because of the large inventory of labile organic matter and its decomposition over and above the belowground biogenic input as flooding stress (waterlogging) becomes excessive. This scenario is akin to simulations in which peat-based mangrove islands are predicted to collapse by the year 2070 (Lovelock et al., 2015). However, in predicting submergence outcomes, it is important to consider mangroves at different life stages, particularly in ecotones where colonizing mangrove ages will likely be dynamic over the next 50 years. Indeed, mature trees may collapse more quickly than pioneers (Figures 1f and 3) due to the ability of wetlands colonized by pioneers to rapidly gain elevation and large amounts of live biomass.

The ability of mangroves to outperform marshes in accretion at low to moderate SLR (Tables 1 and 2) has important implications for wetland sustainability in ecotones and restoration. As pioneer mangrove trees colonize marshes, they provide initial gains in elevation, but these may be followed by rapid declines in elevation under high SLR scenarios, as they fail to keep pace with sea level toward the end of the century and the inventory of soil carbon declines. Conversely, if severe freezes become less frequent over the next 80–100 years, the presence of *Rhizophora mangle* (red mangrove) in these coastal wetlands also likely will increase, and this species establishes well in those flooded, lower elevations and may build peat faster than *A. germinans* due to root architecture (Gill & Tomlinson, 1977; McKee & Faulkner, 2000). Thus, we conclude that the time frame in which mangroves encroach into southeastern U.S. marshes, by natural processes or with assistance, may determine a wetland's ability to maintain elevation. Further, our results also have implications for restoration studies and, with reparameterization, may allow us to predict elevation gain in restored coastal wetlands around the world where young mangroves are being planted (Friess et al., 2019).

Many saltmarshes in NE FL are experiencing rapid encroachment and expansion of mangroves, and *A. germinans* has encroached northward into saltmarshes to the south bank of the St. Mary's River on the border with Georgia, U.S.A (Cavanaugh et al., 2019). Further expansion into Georgia and South Carolina likely will be determined by a combination of environmental drivers, including dispersal limitation to suitable habitats (Yando et al., 2021) and frequency and severity of freeze events (Cavanaugh et al., 2019; Kennedy et al., 2020), which can differentially affect the life-history stage (C. Pickens et al., 2019; C. N. Pickens & Hester, 2011). Although these factors were not specifically addressed in the CWEM, the effect of these freeze events is particularly important to consider, as they can directly affect above- and belowground productivity and biomass partitioning. Freeze damage effects can range from partial dieback to death of aboveground tissue in extreme cases. Although *A. germinans* is often able to resprout from epicormic shoots, vertical growth is very slow and growth is dominated by lateral spread, which maintains the shrub architecture characteristic of mangroves in this ecotone (Chapman et al., 2021).

Tropical storms and Nor'easters can also be important dispersal vectors for mangrove propagules and these severe storm events can episodically increase elevation or cause erosion (McKee et al., 2020). Thus, the combination of extreme climate events, such as tropical storms and freezes from polar vortices, both of which are likely changing, will determine whether mangroves are dispersed to, establish in, and survive to mature adults, at higher latitudes. From previous MEM model runs, Morris et al. (2021) found that the maximum vertical accretion rate of *S. alterniflora* marshes typical of the southeastern United States is about 3.0 mm yr⁻¹, which is nearly equal to the current RSLR as seen in Charleston, SC (Morris & Renken, 2020). This limit suggests that saltmarshes are nearing a tipping point where further increases in the RSLR will begin to lower productivity and, hence the rate of

vertical accretion. The accelerating rate of SLR that coastal marshes in the southeastern United States are encountering raises the question of how coastal wetlands should be optimally managed for longer-term stability and what role active management, including proactive planting of mangroves and human-assisted dispersal, should play in long-term planning for enhanced coastal wetland resilience to SLR.

6. Conclusions

We investigated the consequences of an invasion of *A. germinans* mangrove trees into saltmarshes dominated by the saltmarsh grass *S. alterniflora* at a subtropical ecotone in NE Florida, USA. The objective of our empirical studies and modeling of this vegetation shift was to determine the consequences of the transition for ecosystem sustainability, vertical accretion, and resilience in the face of rising sea level. We used the Coastal Wetland Equilibrium Model (CWEM) to simulate vegetation survival and changes in sediment elevation in the two habitats. We found black mangroves, *A. germinans*, can build soil elevation at 8 mm yr⁻¹, four times greater than saltmarshes at the same site, a finding that is broadly consistent with field measurements of elevation change. Mangroves build elevation more rapidly than saltmarshes by producing much greater volumes of root biomass, but when mangroves drown, their soils abruptly lose elevation due to the large volume of quickly decomposing necromass following flood-induced mortality. Young mangroves grow root mass faster than mature trees and, therefore, can gain elevation more rapidly, but neither saltmarshes nor *Avicennia* mangroves of any age survived a centenary sea-level increase of 100 cm.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

- CWEM is the successor to MEM. CWEM can simulate the growth of mangrove trees, hence the name change. There is a user guide that explains the parameter inputs required to run the model. CWEM comes with examples of hard-wired estuaries that can be selected by highlighting a radio button. The model is free to use.
- CWEM-9.01
- v9.01
- <https://doi.org/10.5281/zenodo.7044963>
- <https://github.com/tilbud/CWEM-9.01>

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