

How Plants Influence Resilience of Salt Marsh and Mangrove Wetlands to Sea-Level Rise

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Abstract

This review evaluates the importance of plants and associated biological processes in determining the vulnerability of coastal wetlands to sea-level rise. Coastal wetlands occur across a broad sedimentary continuum from minerogenic to biogenic, providing an opportunity to examine the relative importance of biological processes in wetland resilience to sea-level rise. We explore how plants influence sediment accretion, elevation capital (vertical position in the tidal frame), and compaction or erosion of deposited material. We focus on salt marsh and mangrove wetlands, which occupy a similar physiographic niche and display similar physical and biological controls on resilience to sea-level rise. In both habitats, plants stabilize emergent mudflats and help sustain the wetland position in the tidal frame relative to ocean height through both surface and subsurface process controls on soil elevation. Plants influence soil elevations by modifying (1) mineral sediment deposition and retention, (2) organic matter contributions to soil volume, and (3) resistance to compaction and erosion. Recognition of the importance of plants in coastal wetland resilience to sea-level rise is key to accurate predictions about the future fate of salt marshes and mangrove forests and for development of effective management and restoration plans.

Keywords Accretion · Elevation capital · Erosion · Resilience · Sedimentation · Wetland loss

Introduction

Sea-level rise, a known consequence of global warming, will modify shorelines worldwide and cause major changes in coastal ecosystems and the human communities reliant on them (IPCC 2014). Because of their low-lying position at the land-sea interface, coastal wetlands are particularly vulnerable to submergence and lateral erosion caused by rising sea level, as well as sea-level extremes and wave activity during storm surges (Nicholls 2004; Lovelock et al. 2015; Roman 2017; Leonardi et al. 2018). To persist in a particular location, these ecosystems must maintain sufficient elevation capital (vertical position in the tidal frame, see Fig. 1) by accreting at a rate equal to the

relative rise in sea level (Cahoon et al. 2019). Coastal wetlands must also resist lateral erosion at the seaward edge, especially if landward migration is blocked by natural or artificial barriers (Mariotti and Fagherazzi 2013; Ganju et al. 2015). Further, some wetlands mitigate storm surge impacts (van Coppenolle et al. 2018; Armitage et al. 2019; van Coppenolle and Temmerman 2020). Although some investigations have focused exclusively on physical processes such as mineral sedimentation and erosion (e.g., Fagherazzi et al. 2013; Ganju et al. 2015; Ganju 2019), there is increasing evidence that plants play a key role in vertical land development and capacity of coastal wetlands to keep pace with sea-level rise (reviewed by Friess et al. 2012; Krauss et al. 2014; Woodroffe et al. 2016). Plants may contribute to soil accretion and upward expansion of the soil surface in two general ways: (1) indirectly by slowing water flow and turbulence (allowing sediment particles to settle) and by trapping and binding mineral sediment (Bird 1986; Leonard et al. 1995; Christiansen et al. 2000; Krauss et al. 2003; Li and Yang 2009; Mudd et al. 2010; McKee 2011; Chen et al. 2018) and (2) directly through production and accumulation of organic matter, primarily plant roots, and rhizomes (McKee et al. 2007; Cherry et al. 2009; Langley et al. 2009; McKee 2011; Baustian et al. 2012; Morris et al. 2016; Morris and Callaway 2018; Coldren et al. 2019; Rogers et al. 2019). Plant roots and rhizomes also contribute to soil shear strength, which aids in

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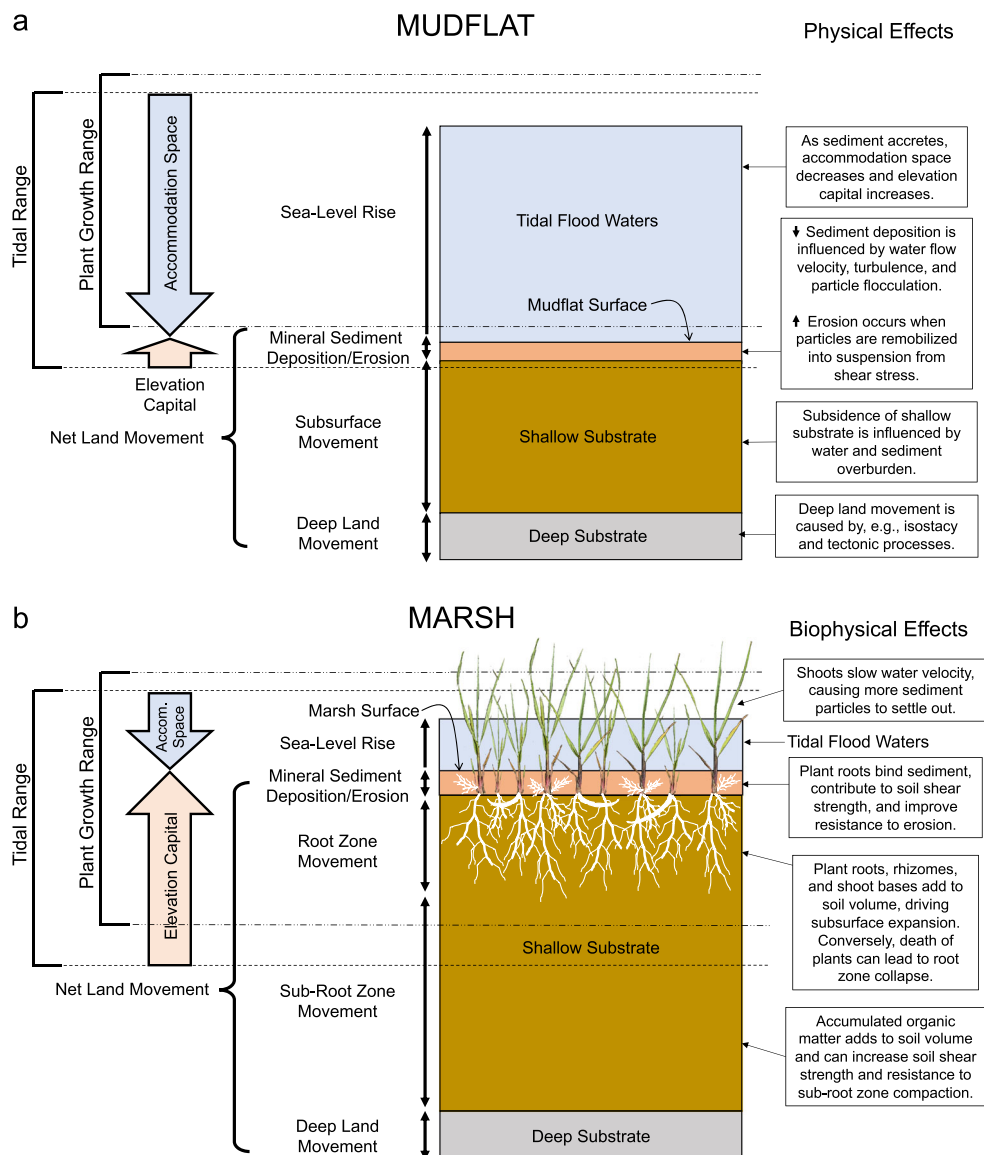
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Fig. 1 Conceptual diagram showing how plants can improve resilience of coastal wetlands to sea-level rise by increasing elevation capital (vertical position in the tidal frame). **a** Profile view of physical substrate dynamics and net land movement in a mudflat where accommodation space for sediment accretion is high and elevation capital is negligible because the mudflat surface elevation lies below the growth range of emergent vegetation. **b** Profile view of macrophytes and associated biophysical processes in a marsh (lower accommodation space and higher elevation capital) environment (vis-à-vis an unvegetated mudflat), which modify the physical processes shown in **a**, except for Deep Land Movement. Plants such as salt marsh grasses or mangrove trees and shrubs enhance vertical substrate development in response to sea-level rise by increasing (1) deposition and retention of mineral sediment, (2) soil volume and subsurface expansion, and (3) soil shear strength and resistance to compaction



resistance to compaction and erosion (Cahoon et al. 2003; McKee and Vervaeke 2009; Graham and Mendelsohn 2014; Sasser et al. 2018; Coleman and Kirwan 2019).

Acceleration in the rate of sea-level rise threatens the sustainability of coastal wetlands if it exceeds the capacity of the wetland to maintain optimum vertical position within the tidal frame (Lovelock et al. 2015; Horton et al. 2018). Although some global-scale assessments conclude that coastal wetlands such as salt marshes will be overwhelmed by rising seas (Crosby et al. 2016; Spencer et al. 2016), others project lower losses of global wetlands (Kirwan et al. 2016) or even gains, especially if adaptation measures take into account certain drivers of resilience (Ganju 2019). Discrepancies among estimates of coastal vulnerability may reflect differences in the key mechanisms used to model persistence of coastal wetlands under sea-level rise. In particular, failure to incorporate

biological feedbacks in such models may lead to overestimates of losses to sea-level rise (Kirwan et al. 2010; Ganju 2019). Further complicating the prediction of sea-level-rise effects on wetland loss is the local and regional variation in relative sea-level rise rates and local factors such as plant species, geomorphology, sediment supplies, hydrology, shallow and deep subsidence, and human activities (Cazenave and Le Cozannet 2014; Davidson 2014; Kelleway et al. 2017; Rodriguez et al. 2017; Doughty et al. 2019). In addition, co-occurring drivers of vegetation change such as elevated atmospheric CO₂ and climate warming may lead to interactive and complex responses by species and ecosystems to sea-level rise (McKee and Rooth 2008; McKee et al. 2012; Osland et al. 2016; Carey et al. 2017; Coldren et al. 2019; Lu et al. 2019).

This review focuses on two types of coastal wetlands that develop in a similar physiographic setting: salt marshes and

mangroves. Salt marshes are typically dominated by herbaceous plants (grasses, rushes, succulents, and forbs) dominating temperate latitudes as far north as the Arctic, whereas mangroves comprise mostly of tree and shrub species limited to tropical and subtropical regions (Mendelssohn and McKee 2000). The two vegetation types may co-exist in subtropical latitudes forming an ecotone (Mendelssohn and McKee 2000). Despite floristic and distributional differences, salt marshes and mangroves share many features. Both vegetation types occupy the most seaward zone along low-lying coastlines and develop most extensively in areas protected from wave action such as shallow bays, estuaries, lagoons, and behind offshore islands (Mendelssohn and McKee 2000). The plant species found in salt marshes and mangrove forests are tolerant of salinity and flooding, and many exhibit similar morphological, anatomical, and physiological adaptations to the intertidal habitat (e.g., foliar salt glands, aerenchymatous tissues, anaerobic root respiration) (Ball 1988; Colmer and Flowers 2008). Existing salt marshes and mangroves began developing between 8000 and 4000 years before present when sea-level rise slowed (Redfield and Ruben 1962; Woodroffe et al. 1985; Gehrels 1999). Both maintain their relative positions in the intertidal zone through similar mechanisms governing vertical land building (Cahoon et al. 2006; Krauss et al. 2014; McKee and Vervaeke 2018) and both have similar influences on stability of the system (Kakeh et al. 2016).

This synthesis evaluates the role plants and associated biological processes play in resilience of salt marshes and mangrove forests to sea-level rise. The role and importance of physical factors such as hydrology, sediment supplies and transport, and lateral erosion have been described in numerous studies and reviews of mangrove (e.g., Woodroffe et al. 2016) and marsh (e.g., Fitzgerald et al. 2008; Weston 2014; Morris et al. 2016) wetlands and, consequently, will not be emphasized in this review except as they relate to plant processes. We explore the linkages and feedbacks between physical and biological processes in the resilience and long-term sustainability of coastal wetlands by reviewing the following:

- The active role of plants in land formation (vertical accretion and lateral expansion)
- Plant influences on elevation adjustment to changes in relative sea level
- Minerogenic versus biogenic coastal wetlands
- Importance of vegetation dynamics and biophysical feedbacks to wetland management and restoration

The Active Role of Plants in Land Formation

The contribution by plants to land formation is readily evident in the soils of coastal wetlands, which are often composed of both inorganic sediment and organic matter derived from the

vegetation (Adam 1990; Woodroffe et al. 2016). Although inorganic sediments predominate in some sedimentary settings such as river deltas, many coastal wetland soils contain substantial organic matter (Bricker-Urso et al. 1989; Bescansa and Roquero 1990; Nyman et al. 1990; Nyman et al. 1993; Osland et al. 2018). In sediment-deficient environments, peats ($\geq 40\%$ organic content) composed of refractory plant matter can accumulate in thick deposits, e.g., beneath Atlantic coast marshes (Redfield and Ruben 1962; Redfield 1965; Niering et al. 1977) and oceanic mangrove islands (Cameron and Palmer 1995; McKee et al. 2007). Radiocarbon dating of such peat deposits, typically composed of partially decayed plant roots, rhizomes, and shoots (Niering et al. 1977; McKee and Faulkner 2000a), has shown how organic matter accumulation drove vertical land development as sea level rose over thousands of years. For example, offshore mangrove islands in Belize, which receive no terrigenous sediment, are underlain by more than 10 m of peat that has accumulated over 7000 to 8000 years (Cameron and Palmer 1995; Macintyre et al. 1995; McKee et al. 2007). In that setting, peat formation closely tracked variation in sea-level rise rates (McKee et al. 2007), in agreement with a recent study of Holocene sea-level change in the wider Caribbean Region (Khan et al. 2017). In fact, because coastal peats accrete in concert with changing sea level, they are used to reconstruct historical rates of sea-level rise (e.g., Redfield and Ruben 1962; Rampino 1979; Belknap et al. 1989; Khan et al. 2017).

The direct role of plants in land formation can also be seen in the process of mudflat conversion to vegetated marsh (Fig. 1). Emergent mudflats develop from subaqueous (water bottom) sediment surfaces through the physical processes of mineral sediment accumulation (Cahoon et al. 2011). Change in the elevation of the mudflat surface is influenced by the net flux of sediment to the surface (i.e., sediment deposition is influenced by water flow velocity, turbulence, and particle flocculation versus remobilization of sediment particles into suspension by erosion from shear stress) and the compaction of the mudflat substrate by the water and sediment overburden (Fig. 1a). Deep land movement from isostatic and tectonic processes also influences the mudflat elevation. The space available for sediment accumulation is termed “accommodation space” and is delineated in the vertical dimension by the distance between the soil surface and the uppermost tide level (Jervey 1988). As sediment accretes, accommodation space decreases and elevation capital increases (Fig. 1a, b). When the height of the mudflat within the tidal frame reaches the height of the growth range of emergent vegetation, then plants colonize the mudflat, converting it to emergent marsh (Fig. 1b). Typically, the growth range of the vegetation approximates the local tidal range (e.g., *Spartina alterniflora*, McKee and Patrick 1988). When the wetland first forms, the height of the soil surface is at the lower end of the growth range, and therefore has low elevation capital (Cahoon et al. 2019). As the wetland surface

elevation continues to increase in relation to sea-level, the elevation capital increases (Fig. 1b).

Once colonized by plants, elevation change of the newly developed wetland surface is thereafter influenced by both physical and biological processes, and these biophysical effects occur both above and below the soil surface (D'Alpaos and Marani 2016; Gonneea et al. 2019). The plant canopy slows water velocity, which enhances sediment particle settlement; the plant root and rhizome mass anchors the mineral sediment in place, enhancing particle retention; roots, rhizomes, and shoot bases directly increase soil volume; and the network of roots and rhizomes increases resistance to soil compaction and surface erosion (Fig. 1b). The stability of the wetland system (the relative heights of the marsh plain, mudflat, and marsh creek) is now controlled by the productivity and health of the vegetated surface in addition to mineral sediment supply and transport processes. Accretion and elevation change across the marsh landscape from the creek-side levee margin to the marsh interior henceforth reflects the interplay among flooding; vegetation production (aboveground and belowground); organic matter decomposition; and sediment supply, transport, and trapping (by vegetation) (Nyman et al. 1993; Turner et al. 2000; Belliard et al. 2016; D'Alpaos and Marani 2016; Roner et al. 2016). Further, the biologic-geomorphic feedbacks influence spatial variation in organic and inorganic deposition and retention. For example, a study of southeastern Australian salt marshes found that *Juncus* assemblages in the upper marsh (less flooding) were characterized by autochthonous organic deposition, whereas lower marsh (more flooding) with succulent (*Sarcocornia*) and grass (*Sporobolus*) assemblages was dominated by minerogenic inputs (Kelleway et al. 2017). There was high retention of organic inputs in the *Juncus* assemblage, but substantial redistribution of material deposited in the low marsh assemblages. In another study of coastal wetlands in Queensland, Australia, sediment retention was influenced by geomorphological setting (seaward fringe mangroves, landward scrub mangroves, and high intertidal salt marsh/cyanobacterial mat) (Adame et al. 2010).

Plant Influences on Wetland Elevation Adjustment

Coastal wetlands may resist, adapt, or succumb to sea-level rise. We define resilience to sea-level rise as the capacity to adjust to a change in sea level, e.g., through the accumulation of inorganic sediments and plant organic matter such as roots and rhizomes. Although inorganic sediment supply and growth of plant roots and rhizomes affect resilience of wetlands to sea-level rise, the contribution of plants and attendant processes to wetland resilience becomes increasingly important if sediment supplies diminish. Plants enhance overall

resilience of coastal wetlands to sea-level rise by (1) improving mineral sediment trapping and retention, which is especially important when and where supplies are low; (2) contributing organic matter to soil volume, which allows continued vertical expansion, within limits, even when mineral sediment is deficient; and (3) aiding in resistance to compaction and erosion of deposited sediment by increasing soil shear strength (Fig. 1). Also, plant presence means that surface accretion and subsurface expansion may be modified by co-occurring factors such as elevated CO₂ that increases production of refractory organic matter (Cherry et al. 2009; Langley et al. 2009) or temperature that drives a shift in dominant plant species (Osland et al. 2016) and may increase the rate of organic matter decomposition (Carey et al. 2017). Thus, plants influence wetland vertical position in the tidal frame relative to ocean height through both surface and subsurface process controls on elevation.

Plant Influences on Surface Sediment Deposition

Plants can influence vertical accretion and elevation change by altering deposition of both inorganic and organic material on the soil surface (Fig. 1). Aboveground biomass that subsequently senesces and accumulates on the soil surface plus exogenous organic matter imported by the tides can be important contributors to accretion in both marshes (DeLaune et al. 1983; Callaway et al. 1997; Turner et al. 2000; Kelleway et al. 2017) and mangrove forests (McKee 2011; Breithaupt et al. 2017). However, the relative amount of organic material that accumulates varies, for example in mangrove forests, with tidal flushing, litterfall rates, consumption by macrodetritivores (crabs, snails), and microbial decay rates (McKee and Faulkner 2000b; Middleton and McKee 2001). In basin mangroves of southeastern Florida, which form in depressions and are infrequently flushed by tides, leaf litter accumulates in thick layers on the forest floor and accounts for accretion rates of 1.1 to 3.4 mm year⁻¹ (McKee 2011). In salt marshes, however, aboveground biomass tends not to contribute substantially to accretion because it is often decomposed in situ and/or is flushed out by tidal action (Teal 1962). Instead, accretion in salt marshes has been attributed primarily to mineral sediment and allochthonous sources of organic matter or to root and rhizome inputs (discussed below) (Howes et al. 1985; Morris et al. 2016).

In addition to being the source of organic matter that is deposited on the soil surface, the standing vegetation can influence transport, deposition, and retention of inorganic sediment carried by tidal action in both mangrove (Bird 1986; Kumara et al. 2010; Kamal et al. 2017; Phillips et al. 2017; Sanchez-Nunez et al. 2019) and salt marsh (Leonard et al. 1995; Li and Yang 2009; Mudd et al. 2010) wetlands. The height, density, and morphology of plant shoots (marsh) and aerial roots (mangrove) can affect sediment deposition during

a tidal cycle by reducing water flow velocity (Shi et al. 1996; Mazda et al. 1997; Tempest et al. 2015), wave action (Möller et al. 2014), and turbulence (Christiansen et al. 2000; Leonard and Croft 2006), which allows particles to settle onto the soil surface (Leonard and Luther 1995). However, some species promote sediment deposition through this baffling effect more than others (Krauss et al. 2003; Kelleway et al. 2017; Wang et al. 2017; Chen et al. 2018) or may have no apparent effect (Moskalski and Sommerfield 2012). Short, dense plant structures such as mangrove pneumatophores may even enhance turbulence close to the sediment surface (Norris et al. 2019). Sediment also can adhere to living plant surfaces (Li and Yang 2009), fallen plant litter (Rooth et al. 2003), or benthic algae (McKee 2011) and later be incorporated into the soil. For example, a study conducted in the Yangtze delta (China) estimated that vegetation-trapped sediment accounted for more than 10% of the depositional rate in *S. alterniflora* marshes (Li and Yang 2009). A study of mangroves in the Caribbean Region (Belize and southwest Florida, USA) found that surface growth of turf-forming algae and accumulation of leaf litter and other organic detritus not only contributed directly to vertical accretion, but promoted trapping and deposition of mineral matter (McKee 2011). Also, in some subtropical regions where mangrove and salt marsh vegetation co-exist (e.g., Louisiana, USA), sediment accretion occurs at similar rates in side-by-side stands of *A. germinans* and *S. alterniflora* (Perry and Mendelsohn 2009; McKee and Vervaeke 2018). These studies suggest that despite differences in aboveground structure, both mangrove and salt marsh plants interact with physical processes in similar ways to promote sedimentation.

Plant Influences on Soil Volume

A second way that plants can influence resilience to sea-level rise is through belowground contribution of plant biomass to soil volume, which drives upward expansion of the soil surface in both biogenic and minerogenic settings (Fig. 1b). The importance of biological processes in soil volume expansion in mangrove and salt marsh wetlands is most clearly indicated by the occurrence of thick peat deposits in both habitats (Redfield 1972; Niering et al. 1977; Cameron and Palmer 1995; McKee et al. 2007) where conditions support peat formation (Redfield 1965; Middleton and McKee 2001). Peat generally accumulates in wetlands where organic matter production exceeds decomposition, and input of mineral sediment is low or absent, such as conditions found on oceanic mangrove islands in the Caribbean Region (McKee et al. 2007) and in some New England salt marshes, USA (Redfield 1972). Production of roots and rhizomes are also important in minerogenic salt marshes and mangrove forests because they aid in sediment retention and make a substantial contribution to soil volume (Fig. 1).

Subsurface Expansion

Field investigations of elevation change trends in a minerogenic salt marsh soil on the Norfolk coast of England (Cahoon et al. 2000) and biogenic mangrove soils on the islands of Roatan, Honduras (Cahoon et al. 2003), and Twin Cays, Belize (McKee et al. 2007), and in a mangrove forest in Homebush Bay, Sydney, Australia, with limited mineral sediment input (Rogers et al. 2005) revealed that elevation gain was greater than surface accretion, indicating subsurface expansion from accumulation of root and rhizome biomass. Root zone expansion in a salt marsh in Chesapeake Bay, USA, was greater than shallow subsidence occurring below the root zone, and thus contributed positively to surface elevation change (Blum et al. 2020). Manipulative experiments conducted in both the greenhouse and field have further confirmed that root and rhizome matter accumulation contributes to the upward expansion of the soil surface in marsh- and mangrove-dominated ecosystems (McKee et al. 2007; Cherry et al. 2009; Langley et al. 2009; Davis et al. 2017; Coldren et al. 2019). For example, phosphorus additions to subsiding mangrove areas in Belize greatly stimulated root production, which led to subsurface expansion and dramatic gains in soil surface elevation (McKee et al. 2007). Similarly, fertilization of microtidal salt marshes in North Carolina, USA, caused increases in aboveground standing biomass and rates of surface elevation gain (Davis et al. 2017). Warming of plots in a subtropical wetland in Florida, USA, increased soil elevation, which was driven by increases in mangrove root production (Coldren et al. 2019). Manipulative field and greenhouse experiments with brackish marsh species have shown that elevated concentrations of atmospheric CO₂ can increase belowground production and accumulation of organic matter, accompanied by upward expansion of the soil surface (Cherry et al. 2009; Langley et al. 2009). The marsh response was mainly caused by growth stimulation of the C₃ species (*Schoenoplectus americanus*) rather than the C₄ grass (*Spartina patens*) and was modified by salinity and flooding levels (Cherry et al. 2009). These studies suggest that both mangrove and salt marsh plants can produce sufficient refractory biomass belowground to influence soil volume and upward expansion of the soil surface.

Subsurface Collapse

Conversely, vegetated wetland surfaces are also vulnerable to elevation loss through non-lethal declines in plant productivity. For example, vegetation grazing in marshes by mammals can significantly reduce belowground production, soil elevation, and expansion of the root zone, thereby negatively affecting soil building processes (Ford and Grace 1998). Furthermore, death of the vegetation can lead to abrupt elevation loss through root/rhizome death and collapse of the root

zone. (See the discussion of peat collapse in the section below on soil compressibility.) Excess nitrate can also have a negative effect on peat stability, leading to marsh loss (Deegan et al. 2012). In some cases, however, marsh response to nutrients is dependent upon elevation, as reported for North Carolina, USA, salt marshes fertilized with nitrogen and phosphorus (Davis et al. 2017) and a Long Island, New York, USA, salt marsh exposed to wastewater (Krause et al. 2019).

Model Projections

Plant root and rhizome growth contributes directly to elevation gain through increases in soil volume, and a simple back-of-the-envelope calculation demonstrates how important this is. First, the volume occupied by a dry gram of pure soil organic matter is almost 12 cm^3 ; i.e., its self-packing density is 0.085 g cm^{-3} (Morris et al. 2016). From this, the vertical accretion that derives from organic production may be computed. Assuming only belowground production contributes to growth of soil volume, a hypothetical rate of belowground production of $2000 \text{ g m}^{-2} \text{ year}^{-1}$ gives a vertical accretion rate of $0.235 \text{ cm year}^{-1}$. Note that some estimates of belowground productivity in salt marshes are considerably greater (Valiela et al. 1976). This calculation further assumes that only a fraction of that production is actually preserved and creates new volume, apparently related to the lignin fraction (Goñi and Thomas 2000). The lignin content of *Spartina* roots and rhizomes was estimated conservatively to be 10% (Hodson et al. 1984; Wilson et al. 1986). Therefore, the refractory organic matter contribution to soil should be about $200 \text{ g m}^{-2} \text{ year}^{-1}$, or $0.02 \text{ g cm}^{-2} \text{ year}^{-1}$, and dividing this by the density (0.085 g cm^{-3}) gives the vertical rate. This organic contribution is sufficient to allow a marsh to keep pace with rates of sea-level rise that characterized most of the twentieth century.

How does this compare with vertical accretion from mineral sediment? Another calculation shows that the difference is significant. Assuming a marsh surface floods 704 times annually (semidiurnal tide) with a suspended sediment concentration of 20 mg l^{-1} to an average water depth of 10 cm, the maximum mineral sediment load is $0.1408 \text{ g cm}^{-2} \text{ year}^{-1}$. Dividing this by the density of dry mineral sediment, 1.99 g/cm^3 (Morris et al. 2016), gives a vertical accretion of $0.07 \text{ cm year}^{-1}$, which is almost insignificant in comparison to the organic contribution.

The result in the previous example depends, of course, on the assumptions. Physical variables that differ among estuaries and are important to vertical accretion are suspended sediment concentration, tides, and depth of flooding. The importance of the latter two variables is illustrated (Fig. 2) using a model that describes feedbacks that equilibrate the marsh surface with mean sea level (Morris et al. 2002; Morris and Callaway 2018). The mineral contribution to accretion is

proportional to the depth and frequency of flooding, and the suspended sediment concentration (Krone 1987). The organic contribution is a nonlinear function of flood depth (Fig. 3). There is a vertical range between about mean sea level (MSL) and mean high water (MHW) that will support vegetation (McKee and Patrick 1988), with an optimal elevation in the middle of this range that supports maximum growth (Morris et al. 2002; Morris et al. 2013). Permutations of MHW in the range of most micro- and meso-tidal estuaries (5–120 cm) and flood depths spanning a range of tidal amplitudes (0–130 cm) result in a response surface (Fig. 2a) with maximum vertical accretion of 0.6 cm year^{-1} at the highest MHW (120 cm) and flood depth of 86 cm. At this combination of depth and MHW, the contributions of organic production to vertical accretion ($0.28 \text{ cm year}^{-1}$) and mineral sedimentation ($0.32 \text{ cm year}^{-1}$) are similar. However, for flood depths less than 80 cm, the organic contribution dominates vertical accretion (Fig. 2b).

In these virtual marshes, as noted above, maximum growth occurs in the mid-range (Fig. 2c), and it is in this mid-range where maximum organic accretion occurs. At super-optimal elevations (higher than the optimum), biogenic volume production dominates, while at suboptimal elevations, mineral sedimentation begins to dominate at depths that dampen organic production. Marsh restoration by a method known as thin-layer sediment placement can move the elevation of a marsh from a position that is suboptimal for the vegetation, where vegetation has a diminishing role as sea level rises, to a position higher in the tidal frame, where vegetation has a dominant role, is flooded less often, and responds positively to rising sea level (Ford et al. 1999; Cahoon et al. 2019).

Plant Influences on Soil Shear Strength and Compressibility

A third way that plants can influence movement of the wetland surface is to alter soil shear strength and resistance to compaction (Fig. 1). Precisely how plant-driven mechanisms affect soil strength and compaction is not fully understood, but such processes can potentially affect elevation dynamics in coastal wetlands (Ameen et al. 2017; Jafari et al. 2019; Zoccarato et al. 2019). At the soil surface, plant roots and benthic algae bind soil particles, thereby creating a strong matrix that resists shearing forces such as waves and tidal currents (De Battisti et al. 2019) (Fig. 1b). Variation in soil shear strength has been correlated with live root biomass or productivity in both marsh- and mangrove-dominated wetlands (Cahoon et al. 2003; Graham and Mendelssohn 2014; Sasser et al. 2018; Coleman and Kirwan 2019; Silliman et al. 2019) and with the presence of filamentous algal mats growing on the soil surface in mangrove forests (McKee 2011). In a study of eleven coastal marsh types in Louisiana, live belowground biomass explained the most variation in soil shear strength across sites with soils ranging from organic to mineral

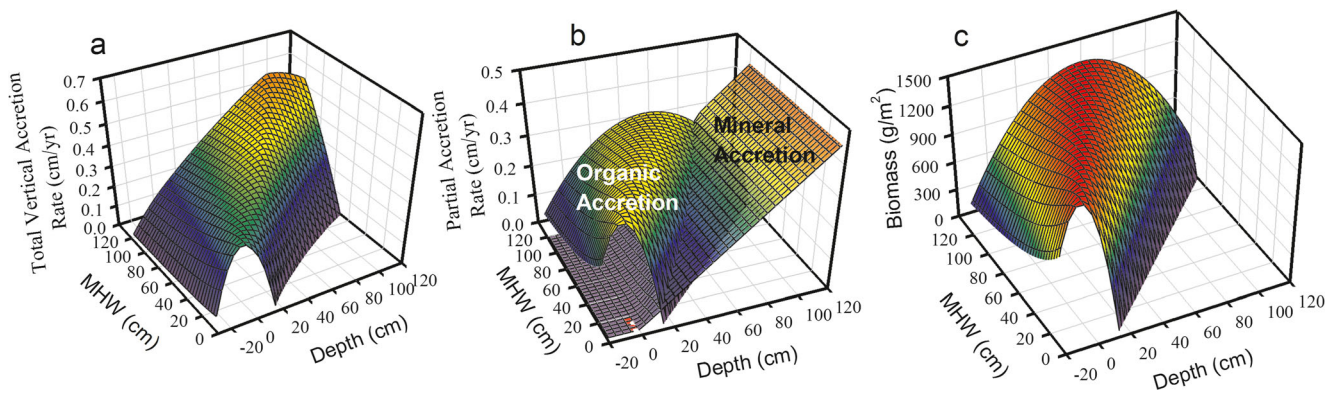


Fig. 2 Response surfaces generated by the Marsh Equilibrium Model (MEM) showing the total **a** and partial **b** vertical accretion rates and standing biomass **c** resulting from permutations of mean high water level (MHW) and average flood depth (Morris et al. 2016; Morris and Callaway 2018). Standing biomass at optimum depth was set conservatively at 1500 g m⁻² across all simulations, the ratio of roots

and rhizomes to shoots at 2:1, the refractory fraction of belowground production at 0.1, and suspended sediment concentration of 20 mg l⁻¹. Permutations of MHW and depth gave rise to the total vertical accretion rates shown in **a**, the partials, or contributions from mineral and organic accretion in **b** and standing biomass in **c**. The partials in **b** sum to give the totals in **a**

(Sasser et al. 2018). Shear strength also decreases with soil depth and fewer live roots (Cahoon et al. 2003; Comeaux 2010; Turner 2011; Graham and Mendelsohn 2014), further implicating the influence of plant roots on soil strength. Studies of disturbance caused by hurricanes (Cahoon et al. 2003) or humans (McKee and Vervaeke 2009) have also shown that soil shear strength in mangrove forests declines significantly in high-mortality areas compared to reference

sites. In a greenhouse study comparing *A. germinans* and *S. alterniflora* growth in different soil substrates (topsoil, beach sand, and soil collected from a natural marsh and a restored marsh), both species significantly increased soil shear strength relative to unvegetated controls through ingrowth of roots and rhizomes (Feher and Hester 2018). Tensile strength of individual wetland plant roots, which was highly correlated with root morphometrics (diameter, cross-sectional area,

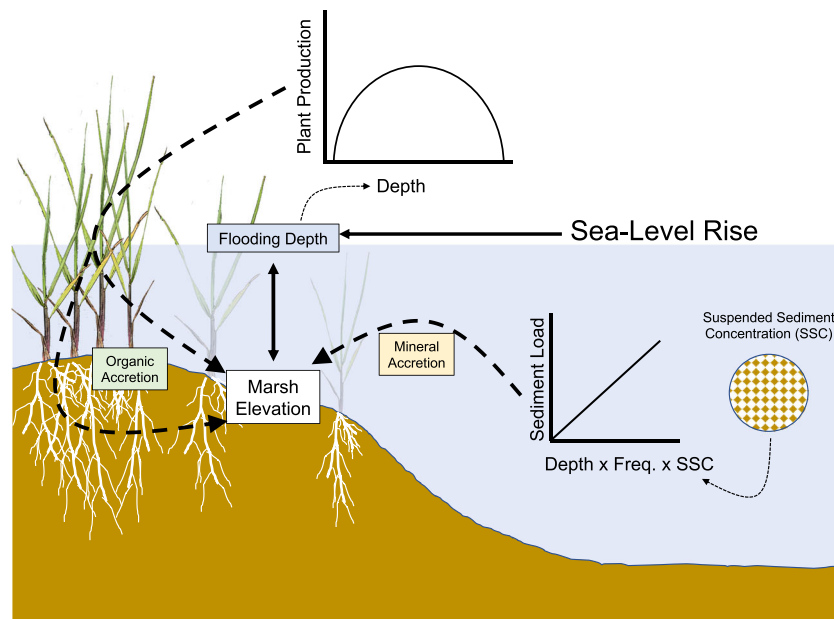


Fig. 3 Conceptual diagram of the dominant processes controlling relative marsh elevation or vertical accretion. Mineral deposition or sediment load increases with the depth of water flooding the marsh/mangrove surface, the frequency of flood events, and the suspended sediment concentration (SSC). The accretion of organic matter (i.e., plant shoot and root/rhizome material) is proportional to primary production, which is a parabolic function of flood depth (Morris et al. 2002). There is a range of flooding depth that supports a marsh/mangrove community. At one extreme, too great a depth of flooding results in hypoxia and drowning,

and at the other extreme too little flooding results in osmotic stress. If the depth is suboptimal, i.e., less than optimal flooding, then a rise in sea level will increase production and organic accretion, raising the surface elevation. An equilibrium with mean sea level will ensue, provided the rate of sea-level rise does not exceed a tipping point. Beyond the tipping point, the equilibrium elevation will fall to the super-optimal side of the growth curve (too much flooding) where continued increases in the rate of sea-level rise will decrease primary production and organic accretion, with a drowning marsh being the end result.

volume) (Hollis and Turner 2018), may be a key trait, along with soil factors, influencing soil shear strength.

In addition to soil shear strength, live plant roots and rhizomes can also alter resistance to subsurface compaction. The evidence for the role of plants in soil compaction and elevation change comes primarily from observations of peat collapse or elevation loss following mortality of the vegetation in marshes (Delaune et al. 1994; Cahoon et al. 2004; Day et al. 2011; Baustian et al. 2012; Lane et al. 2016; Coleman and Kirwan 2019) and mangrove forests (Sherman et al. 2000; Cahoon et al. 2003; Whelan 2005; Lang'at et al. 2014; Krauss et al. 2018). The term “peat collapse” implies a sudden loss in elevation caused by a decrease in soil strength or structural integrity of a highly organic soil and is distinct from that of soil erosion (although the two processes may occur together) (for an in-depth review and discussion, see Chambers et al. 2019). However, the cause of mortality and rate of elevation loss varies among studies. For example, elevation of hummocks in a coastal marsh decreased almost 15 cm in 2 years after plant mortality caused by excessive flooding (Delaune et al. 1994). In another study, experimental girdling and cutting of mangrove trees at Gazi Bay, Kenya, led to a subsidence rate of 3 cm year⁻¹ (compared to an elevation gain of 0.4 cm year⁻¹ in control plots) (Lang'at et al. 2014). Such examples indicate that while plants may improve soil shear strength, their presence also increases vulnerability of the wetland to sudden loss of elevation upon disturbance of the vegetation. Such studies also suggest that the mechanisms involved in elevation loss are related, at least in part, to the death of roots and rhizomes and consequent loss of soil volume and structural support. Possible mechanisms leading to loss of elevation of an organic soil include (1) loss of turgor upon death of roots and rhizomes and collapse of gas-filled aerenchyma tissue; (2) compression of gas-filled voids in the soil created, for example, by animal burrows (Xiong et al. 2019); (3) loss of organic mass through decomposition; and (4) dissolution and dispersion of undecomposed material no longer held in place by a live root matrix (modified from Chambers et al. 2019). Although the relative contribution of these mechanisms to loss of wetland elevation following plant mortality is not known, they suggest, in general, that plant roots influence the overall compressibility of the soil.

The role of live plant roots and rhizomes in altering resistance to subsurface compaction has also been suggested from comparisons of elevation dynamics on vegetated and unvegetated wetland surfaces. In a study of a crevasse splay in the Mississippi River delta, shallow subsidence rates varied with elevation from 2 to 5 cm year⁻¹ in the open water habitat to 1.5 cm year⁻¹ in the low marsh to 0.2–0.5 cm year⁻¹ in the forested wetland (Cahoon et al. 2011). This inverse relationship between subsidence rate and elevation occurred despite the additional overburden of mineral and organic material at the low marsh and forested wetland sites (43, 79 cm,

respectively). Thus, these thicker, vegetated soils with extensive root systems consolidated more slowly than the unvegetated water bottom sediments. Further, in a comparison of vegetated and unvegetated experimental pots placed along an elevation gradient in a temperate salt marsh, the soil surface in the vegetated pots subsided significantly less than that in the unvegetated pots (Payne et al. 2019). The authors hypothesized that the root network infilled the pore space of the potted soils, thereby adding to the resistance of subsurface compaction.

Functional Similarities of Mangrove and Salt Marsh Influences on Elevation

Despite obvious differences in physiognomy and other plant traits, mangrove and salt marsh plants appear to influence sedimentation, soil volume expansion, and soil strength in fundamentally similar ways (Friess et al. 2012; Kakeh et al. 2016). The reason for this correspondence likely reflects broadly similar functional traits of growth (e.g., for the acquisition of light and nutrients) and persistence (e.g., dispersal, recruitment, and recovery from disturbance) (Mendelsohn and McKee 2000). Both vegetation types produce aerial structures (shoots or aerial roots) that act like baffles to modify water velocity (Shi et al. 1996; Mazda et al. 1997) and hence sediment deposition. Both produce belowground biomass (roots and/or rhizomes) that periodically senesces and either decomposes or accumulates, depending on environmental conditions and tissue chemistry (van der Valk and Attiwill 1984; Hackney 1985; Middleton and McKee 2001; Huxham et al. 2010). Both display a similar array of adaptation strategies for avoidance or tolerance of flooding and salinity stress, e.g., adventitious rooting, aerenchyma, lenticels, succulence, and salt glands (Ball 1988; Colmer and Flowers 2008). Like most plants, mangrove and salt marsh species also exhibit plasticity, i.e., response to the environment through changes in morphology or physiology (Waller 1991). For example, canopy height, morphology, and productivity of both mangrove and salt marsh species can vary substantially across environmental gradients (Anderson and Treshow 1980; Mendelsohn and Morris 2000; Lovelock et al. 2005; Vovides et al. 2014). These universal plant features are the reason that mangrove and salt marsh vegetation influence resilience to sea-level rise similarly (even though the magnitude of their effects may differ within and between these two vegetation types).

Minerogenic Versus Biogenic Coastal Wetlands

The conceptual sediment model of wetland resilience to sea-level rise recently proposed by Ganju (2019) concludes, for

wetlands in general, that mineral sediment supply and transport control resilience, and vegetation contributions to resilience are unimportant or even detrimental. However, this mineral sediment-based model, which is most suitably applicable to mineral-rich estuarine systems, does not account for the fact that coastal wetlands, on a global scale, occur along a mineral sediment continuum from (1) sediment-rich estuaries and deltas (Cahoon et al. 2011; Swales et al. 2015) to (2) sediment-poor coasts (low-energy, back-barrier, lagoonal marshes (e.g., Cedar Island, NC (Cahoon et al. 1995)) or low-energy, karst, groundwater-dominated salt marshes (e.g., St. Mark's, FL (Cahoon et al. 1995)) and mangroves (Whelan et al. 2005), to (3) wetlands with little or no mineral sediment available such as oceanic mangrove island settings (e.g., Twin Cays, Belize (McKee et al. 2007)). In these low-sediment or sediment-lacking settings, the conceptual model proposed by Ganju (2019) is less explanatory, or not relevant, in describing coastal wetland resilience to sea-level rise. Plant contributions to soil volume are an important component of resilience for all wetlands along the entire continuum, but especially for wetlands where there is little to no mineral sediment or where wetland formation and vertical development depend entirely on accumulation of plant organic matter. For example, at biogenic soil settings (e.g., carbonate platform mangroves in south Florida, USA), the role of soil organic matter accumulation is vital to wetland survival relative to sea-level rise and is a better indicator of vertical accretion than mineral sediment accumulation (Breithaupt et al. 2017). At oceanic reef mangroves (no terrigenous sediment), there are no mudflats, and mangrove vertical development is driven primarily by autochthonous accumulation of organic matter that is highly sensitive to nutrient enrichment effects (McKee et al. 2007). Examples of the role of vegetation in surface elevation dynamics and contributions to wetland resilience are presented for extreme end members of the continuum: a minerogenic deltaic marsh and a biogenic mangrove setting.

Minerogenic Wetland: Mississippi River “Birdsfoot” Delta

Active crevasse splays are riverine-dominated coastal environments with a high sediment supply and efficient sediment transport mechanisms (Coleman et al. 1998). A study of the accrual of elevation capital and wetland formation dynamics at the Brant Pass splay (Cahoon et al. 2011), located at the mouth of the Mississippi River, reveals the changing roles of mineral and organic matter accumulation as the splay undergoes three stages of development: mineral sediment infilling, vegetative colonization of emerging mudflats, and development of a mature wetland community. The initial stage of splay development is mineral sediment infilling of the subaqueous water bottom of the receiving basin, as

conceptualized in Fig. 1 a. Mineral sedimentation and shallow subsidence rates are highest during this stage. Eventually, mineral sediment accumulation leads to development of an emergent (subaerial) mudflat, which is rapidly colonized by vegetation (Fig. 4). Plant root and rhizome development stabilizes the loosely consolidated mineral sediment within the first growing season (Cahoon et al. 2011), which leads to increased soil shear strength (Ameen et al. 2017). In addition, when sediment is transported onto the deltaic islands during floods and storms, the emergent vegetation enhances sediment retention (by approximately 10%) by actively trapping mineral sediment on the wetland surface (Olliver et al. 2020). From this time forward, as the newly emergent wetland converts from low marsh to high marsh and finally to forested wetland, elevation capital and belowground biomass increase (compared to the subaqueous habitat). Further, deltaic vegetation structure (e.g., stem height and density) directly influences mineral sedimentation, with intermediate values of relative vegetation height and density being optimal for enhancing both sand and mud deposition (Nardin and Edmonds 2014; Nardin et al. 2016). Thus, in contrast to the unvegetated mudflat, vertical development and resilience to sea-level rise of the wetland is controlled by both mineral and organic matter accumulation, which is also influenced by vegetation structure, as conceptualized in Fig. 1 b.

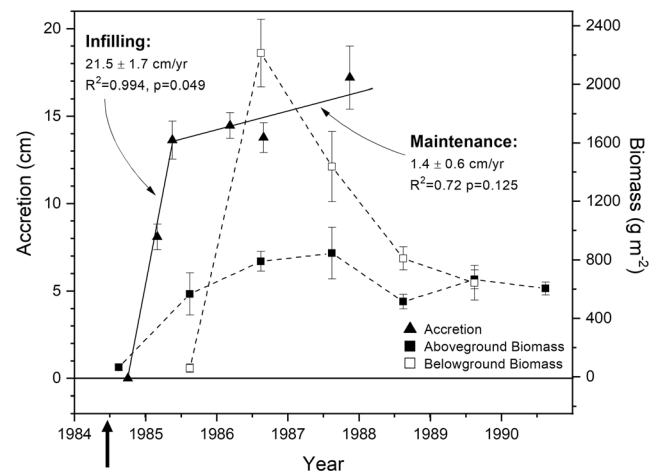


Fig. 4 Accretion and aboveground and belowground plant biomass at the shallow open water leading edge of a splay at Brant Pass at the mouth of the Mississippi River (modified from Cahoon et al. 2011). The arrow on the x-axis indicates the timing of high river discharge (spring) that led to a rapid infilling phase and creation of a subaerial mudflat that was quickly colonized by emergent vegetation during the subsequent year and converted to low marsh habitat, at which time the sedimentation rate decreased (i.e., maintenance phase). Initial high levels of belowground biomass ($> 2000 \text{ g m}^{-2}$) stabilized the substrate, after which belowground biomass decreased ($\sim 600 \text{ g m}^{-2}$). As flooding and sediment delivery at these higher elevation habitats (low marsh, high marsh, and forested wetland) decreased relative to the mudflat and open water habitats, the role of belowground biomass in maintaining soil volume and elevation capital became critical (Cahoon et al. 2011)

Biogenic Wetland: Twin Cays, Belize

The archipelago called Twin Cays, Belize, which is located in the Meso-American Barrier Reef in the western Caribbean Sea, is an example of a mangrove ecosystem that has kept pace with rising sea level for millennia through accumulation of organic matter. Deep cores (Fig. 5) collected from Twin Cays and nearby mangrove islands show continuous peat deposits over 10 m thick, which document a depositional history characterized by gradual accrual of organic matter (Cameron and Palmer 1995; Macintyre et al. 2004). Wetland formation began at Twin Cays when mangroves colonized a Pleistocene limestone platform about 8000 years ago when sea level was 9 to 10 m lower than that at present (Macintyre et al. 2004). Once mangroves were established, peat formation proceeded as undecomposed leaves, wood, and roots accumulated in the low-nutrient, waterlogged environment (Middleton and McKee 2001). Although some calcareous sand has been deposited periodically at the island periphery (Macintyre et al. 1995), vertical land development at Twin Cays has occurred

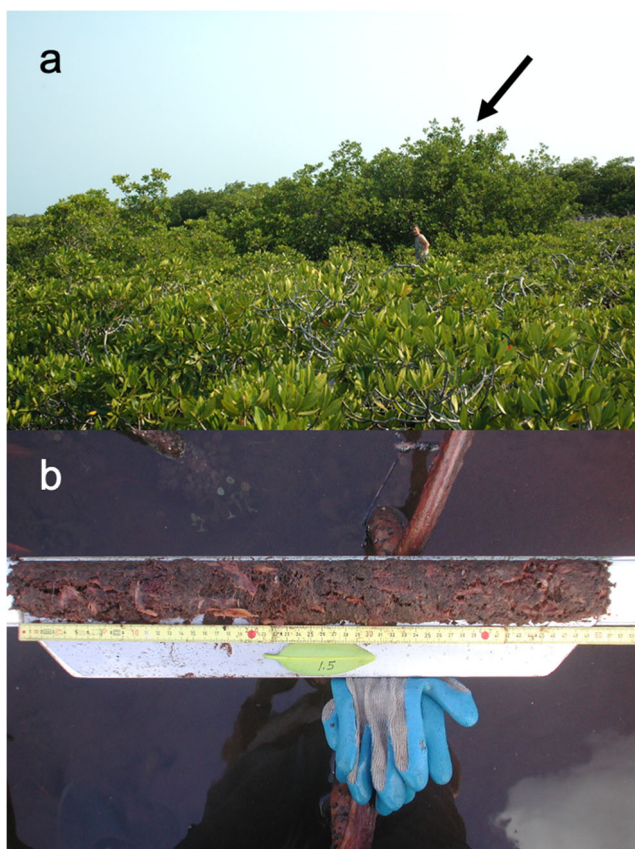


Fig. 5 Oceanic mangrove islands in Belize have kept pace with sea-level rise for 7000 to 8000 years through vertical accumulation of 10 to 12 m of peat. **a** Ground view of Twin Cays showing stunted red mangrove stands in the island interior (foreground). Plots fertilized with phosphorus had taller trees (arrow), higher root production, and faster rates of elevation gain than unfertilized control plots (McKee et al. 2007). **b** Example of a peat core (1.0- to 1.5-m depth) collected at Twin Cays showing refractory remains of red mangrove roots and other organic matter

primarily through continuous peat production in response to relative sea-level rise. Subsequent experiments conducted at Twin Cays showed that (1) surface elevation gain or loss was directly correlated with subsurface change (subsidence or expansion) and (2) nutrient additions (nitrogen (N) and phosphorus (P)) caused significant changes in mangrove root accumulation, which influenced both the rate and direction of elevation change (McKee et al. 2007). Stunted mangrove stands in the island interior with low root accumulation were characterized by subsidence and elevation loss, but more productive stands along the shorelines exhibited subsurface expansion and elevation gains. Fertilization of stunted mangrove plots with P stimulated root production and led to a dramatic gain in elevation (Fig. 5a, b, 7 cm in 3 years). These results provided evidence for the important role of plant roots in driving soil volume expansion and elevation gain in sediment-deficient settings.

Importance of Biophysical Feedbacks to Wetland Management and Restoration

In both the minerogenic and biogenic settings described above, vegetation plays a foundational role in the transformation of mudflat and shallow open water habitats into healthy wetland ecosystems, with their associated ecosystem services (Barbier 2019). In minerogenic wetlands, the feedback between mineral sedimentation and vegetation growth determines elevation capital and controls wetland development and maintenance (Fig. 1b). In biogenic settings, such as oceanic carbonate platforms, vegetation growth determines elevation capital and controls development and maintenance (Krauss et al. 2017; Osland et al. 2020). Given the fundamental difference between the minerogenic and biogenic settings, each setting requires a different management approach. Successful management of a biogenic system like Twin Cays can beneficially focus more on vegetation health than on mineral sedimentation. In this type of setting, which is dependent upon organic matter accrual, the removal (e.g., clearcutting (McKee and Vervaeke 2009)) or mortality (e.g., hurricanes (Cahoon et al. 2003)) of mangroves stops peat formation while subsidence and sea-level rise continue. Conversely, greater emphasis on sustaining or improving mineral sedimentation is required for minerogenic systems to maintain habitat stability (e.g., sediment diversions, thin-layer deposition of dredged material (Ford et al. 1999; Allison and Meselhe 2010; Cahoon et al. 2019). However, as discussed above, plant root systems are also important in sediment-rich settings, which means that proper management requires attention to both inorganic sediment delivery and plant productivity.

Efforts to manage healthy wetlands for targeted ecosystem services (Lee et al. 2014), restore degraded wetlands (Adam

2019), or create new wetlands (Broome et al. 2019) can beneficially focus on maintaining the dominant vegetation within its optimum growth range (McKee and Patrick 1988; Cahoon et al. 2019). Managing wetlands for targeted ecosystem services is often done through water level management using structures (levees and water control gates), sometimes described as structural marsh management (Cahoon 1994). In this approach, water level management manipulates the tidal frame and flooding of the wetland surface (i.e., artificially maintained elevation capital) to favor growth of the target plant species that supports target secondary producers, such as birds (Cahoon and Groat 1990), while largely limiting sediment transport to the wetland surface and soil organic matter accumulation (Cahoon 1994). Restoration of degraded wetlands can be done by restoring natural tidal exchange. If this is not possible, restoration is achieved by either implementing reduced tidal exchange, a form of structural management (Vandenbruwaene et al. 2011; Oosterlee et al. 2018), or mineral sediment is introduced and deposited in a thin layer to restore optimum elevation capital (Cahoon et al. 2019), as described above. When creating a new wetland, building the correct elevation (i.e., elevation capital) that will support the target dominant vegetation is crucial to creation success (Broome et al. 2019).

Conclusions

Biogenic habitats such as coastal wetlands, seagrass beds, oyster reefs, and coral reefs are vulnerable to changes in sea level because of their intertidal or subtidal positions, but they also have the capacity to keep pace through buildup of organic and/or inorganic material (Dullo 2005; Baustian et al. 2012; Krauss et al. 2014; Potouroglou et al. 2017; Ridge et al. 2017). The participation of the biota in adjustment to sea-level rise is most obvious in those habitats constructed by invertebrates (e.g., coral reefs and oyster reefs) where vertical accretion of the reef is directly attributable to growth of the reef-forming organisms (Dullo 2005; Beetham et al. 2017; Ridge et al. 2017). However, in vegetated habitats receiving allochthonous sediment (e.g., seagrasses, mangroves, and salt marshes) (Baustian et al. 2012; Krauss et al. 2014; Potouroglou et al. 2017), biotic contributions to vertical adjustment may be less apparent and more difficult to quantify. For example, root contributions to soil volume are not as readily observed as is mineral sedimentation on the soil surface and may require long-term, manipulative experiments to demonstrate their effects on vertical land movement (e.g., McKee et al. 2007; Langley et al. 2009). Even without such experiments, the contribution of salt marsh and mangrove plants to land formation processes is evidenced by the accumulation of organic matter (e.g., roots and rhizomes) in the soil as well as plant colonization of and subsequent conversion of mudflat to vegetated

wetland. When a mudflat becomes an emergent, vegetated wetland through plant colonization, the resilience of that wetland to sea-level rise is thereafter controlled by the biophysical feedbacks between mineral sediment supply (and transport) and vegetation growth dynamics (Fig. 1).

Plants enhance wetland resilience by improving mineral sediment trapping and retention, contributing organic matter to soil volume, and resisting compaction and erosion of wetland soils by increasing soil shear strength. In so doing, plants help sustain wetland vertical position (i.e., elevation capital) within the tidal frame. However, plant presence means that surface accretion and subsurface contributions to elevation may be modified positively or negatively by co-occurring factors (e.g., elevated CO₂ may increase refractory organic matter in the soil leading to elevation gain (Langley et al. 2009), whereas herbivory by mammals may reduce root production leading to elevation loss (Ford and Grace 1998)).

The occurrence of salt marshes and mangroves along a continuum from sediment-rich (i.e., minerogenic) to sediment-poor (i.e., biogenic) settings means that the role of plants may vary globally. In minerogenic settings, plants play an important role in maintaining wetland elevation capital by promoting mineral sediment trapping and retention, although vegetation may have modest effects on elevation dynamics (e.g., McKee and Vervaeke 2018). In settings with mixed deposition of organic and inorganic material, the biotic contribution to vertical accretion may not be fully appreciated unless calculations are conducted to quantify it. In sediment-deficient settings, soil organic matter accumulation is vital to wetland survival, and changes in plant production can have dramatic effects on vertical accretion and elevation gain (e.g., Morris et al. 2002; Cahoon et al. 2003; McKee et al. 2007).

Understanding the importance of plants in promoting wetland resilience to sea-level rise is essential to accurate predictions about the future fate of salt marshes and mangrove forests and the development of effective management and restoration strategies. Future research can seek a better understanding of (1) linkages and feedbacks between physical and biological processes driving vertical land movements, (2) mechanisms by which plants affect soil strength and compressibility, and (3) how co-occurring drivers of vegetation change such as elevated atmospheric CO₂ and climate warming may interact with responses by species and ecosystems to sea-level rise.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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