Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems

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A R T I C L E   I N F O

A B S T R A C T

Habitat stability of coastal ecosystems, such as marshes and mangroves, depends on maintenance of soil elevations relative to sea level. Many such systems are characterized by limited mineral sedimentation and/or rapid subsidence and are consequently dependent upon accumulation of organic matter to maintain elevations. However, little field information exists regarding the contribution of specific biological processes to vertical accretion and elevation change. This study used biogenic mangrove systems in carbonate settings in Belize (BZ) and southwest Florida (FL) to examine biophysical controls on elevation change. Rates of elevation change, vertical accretion, benthic mat formation, and belowground root accumulation were measured in fringe, basin, scrub, and dwarf forest types plus a restored forest. Elevation change rates (mm yr^{-1}) measured with Surface Elevation Tables varied widely: BZ-Dwarf (−3.7), BZ-Scrub (−1.1), FL-Fringe (0.6), FL-Basin (2.1), BZ-Fringe (4.1), and FL-Restored (9.9). Root mass accumulation varied across sites (82–739 g m^{-2} yr^{-1}) and was positively correlated with elevation change. Root volumetric contribution to vertical change (mm yr^{-1}) was lowest in BZ-Dwarf (1.2) and FL-Fringe (2.4), intermediate in FL-Basin (4.1) and BZ-Scrub (4.3), and highest in BZ-Fringe (8.8) and FL-Restored (11.8) sites. Surface growth of turf-forming algae, microbial mats, or accumulation of leaf litter and detritus also made significant contributions to vertical accretion. Turf algal mats in fringe and scrub forests accreted faster (2.7 mm yr^{-1}) than leaf litter mats in basin forests (1.9 mm yr^{-1}), but similarly to microbial mats in dwarf forests (2.1 mm yr^{-1}). Surface accretion of mineral material accounted for only 0.2–3.3% of total vertical change. Those sites with high root contributions and/or rapid growth of living mats exhibited an elevation surplus (+2 to +8 mm yr^{-1}), whereas those with low root inputs and low (or non-living) mat accumulation showed an elevation deficit (−1 to −5.7 mm yr^{-1}). This study indicates that biotic processes of root production and benthic mat formation are important controls on accretion and elevation change in mangrove ecosystems common to the Caribbean Region. Quantification of specific biological controls on elevation provides better insight into how sustainability of such systems might be influenced by global (e.g., climate, atmospheric CO_2) and local (e.g., nutrients, disturbance) factors affecting organic matter accumulation, in addition to relative sea-level rise.

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1. Introduction

Global mean sea-level rose almost 0.2 m during the twentieth century (Jevrejeva et al., 2008), but is predicted to rise by 0.6 m or more by 2100 (Parry et al., 2007). A scenario of accelerated sea-level rise suggests that many coastal ecosystems are vulnerable to submergence and subsequent degradation (Ellison and Farnsworth, 1996; Cahoon et al., 2006). Those systems with limited mineral sedimentation and/or undergoing rapid subsidence are most vulnerable to submergence. Many coastal ecosystems, including marshes and mangroves, are characterized by highly organic substrates, suggesting the major role of biological processes in soil development and controls on accretion and elevation change (Nyman et al., 2006; McKee et al., 2007; Neubauer, 2008). Furthermore, habitat stability of many wetlands in relation to sea-level rise is thought to be dependent on a feedback relationship between hydro-edaphic conditions and plant growth contributing to organic matter accumulation (Nyman et al., 2006; McKee et al., 2007; Mudd et al., 2009). Water movement brings in sediment and nutrients and flushes out salts and phytotoxins, actions that promote plant growth and biomass production (Mendelssohn and Morris, 2000). Buildup of soil organic matter occurs where plant matter input is high and/or decomposition rates are slow. Flooding and anaerobic soil conditions influence both biomass production and decomposition rates, which determine organic matter accumulation. Recent work has

further shown that elevated concentrations of atmospheric CO_2 can accelerate elevation gain in some coastal marshes by stimulating belowground production and upward expansion of the soil surface (Langley et al., 2009).

Quantification of rates and patterns of organic matter deposition as well as relative contribution of specific biological processes to elevation change is required to understand and predict habitat stability, particularly of coastal wetlands characterized by biogenic soil formation (Neubauer, 2008; Mudd et al., 2009). Contributions of organic matter to soil volume and vertical accretion in marsh and mangrove wetlands have been inferred from analysis of sediment cores (e.g., Turner et al., 2006; Sanders et al., 2008). However, few empirical studies have directly linked biotic processes to rates of vertical accretion and surface elevation change (e.g., Nyman et al., 2006; McKee et al., 2007; Langley et al., 2009), two of the critical processes controlling habitat stability in coastal wetlands.

The objective of this study was to investigate biophysical mechanisms contributing to surface and subsurface deposition of organic matter and to quantify elevation change rates in relationship to these processes. In this investigation, I used mangrove forests in a carbonate setting as a model biogenic system. Although the sites selected for this study do not represent the entire range of sedimentary settings in which mangroves occur, they include forest types typical of those found throughout the wider Caribbean Region. These forest types, which include fringe, basin, scrub, and dwarf (Lugo and Snedaker, 1974) forests plus a restored forest, represent a broad range of hydrologic energy, tree physiognomy, and productivity. In addition, the two study areas used in this investigation, Belize and southwest Florida, provided additional differences in terms of site history, geology, freshwater and nutrient input, and other characteristics.

The following questions were addressed in this work:

(1) What are elevation change rates in mangrove forests dominated by biogenic soil formation and do they vary among forest types or geographic location?
(2) Are both surface and subsurface processes important in controlling elevation change in biogenic mangrove forests?
(3) Do root accumulation rates vary among mangrove forest types? Do mangrove roots contribute significantly to soil volume and subsurface change? Are fine roots more important than coarse roots to this process?
(4) Do benthic mats make a significant contribution to vertical accretion? What are the major components of benthic mats and does their composition vary among forest types? Do benthic mats mainly contribute through accumulation of organic matter or do they also trap inorganic (mineral) material?
(5) What is the relative contribution of surface and subsurface biophysical processes to elevation change and does this vary with location and/or forest type?

2. Methods

2.1. Study sites

The study sites in Belize were located on a 75 ha range of islands called Twin Cays in the MesoAmerican Barrier Reef Complex. This island range is located 2.3 km west of the reef crest and 12 km from the mainland (16°50′ N latitude, 88°06′ W longitude). Based on corings and radiocarbon dates, Twin Cays is underlain by 8–10 m of peat atop a Pleistocene limestone platform and is 7000–8000 yr old (McKee et al., 2007). Twin Cays and other mangrove islands in the region have built vertically through accumulation of biogenic

material, primarily mangrove peat with lenses of calcareous sand (McKee et al., 2007). Due to distance from the mainland, Twin Cays receives no appreciable inputs of terrigenous sediment or freshwater. This area is also microtidal (mean range = 20 cm) with semidiurnal tides. The entire island range is intertidal, although some areas are flooded less frequently than others (e.g., on spring tides). The climate in Belize is subtropical, with an average minimum temperature of 20 °C in December and an average maximum temperature of 31 °C in August. Monthly rainfall varies from 23 mm in March to 335 mm in November. Vegetation and edaphic conditions have been described previously (McKee, 1995a,b; Woodroffe, 1995). The dominant vegetation is red mangrove (*Rhizophora mangle* L.), which forms dense fringing stands along the shoreline and reaches tree heights of 4–7 m. The fringe zone (BZ-Fringe) transitions through a scrub zone (BZ-Scrub) (tree height = 2–4 m) to extensive stands of dwarf *R. mangle* in the island interior (BZ-Dwarf) (tree height < 2 m).

Another set of study sites was located in southwest Florida, USA adjacent to the Gulf of Mexico. Southwest Florida is subtropical with an annual mean temperature of 23.6 °C and a temperature range from a mean monthly low of 14 °C in January to an August high of 28 °C. The annual precipitation is ~1350 mm, falling primarily during the wet season from May through October. Seven study sites were located in the Rookery Bay National Estuarine Research Reserve (RBNERR) (26°3′N, 81°42′W) and along Naples Bay (26°7′N, 81°47′W), which included three basin forests, three fringe forests, and one restored forest. Detailed descriptions of most of these forest stands and hydro-edaphic conditions have been reported previously (Twilley et al., 1986; Cahoon and Lynch, 1997; McKee and Faulkner, 2000a). The fringe forests used in this study have not been described previously, but are similar in structure and other characteristics to that described in Cahoon and Lynch (1997). The main features of each study site are summarized in Table A1 (Supplementary material).

2.2. Experimental design

The objective of this study was to examine the contribution of biophysical processes to accretion and elevation change in mangrove forests using data collected at multiple sites representing different forest structures, environmental conditions, and site histories (total plots in Belize = 12, Florida = 32). The same methods were used across sites to determine elevation change (Surface Elevation Tables), surface accretion (marker horizons), root production (in-growth bags), and benthic mat development (surface screens) (methods described below). Benthic mat development was assessed at all sites (total of 44 plots), whereas elevation change and vertical accretion (above feldspar) were determined at a subset of sites (25 plots). Although the study sites used in this investigation were established at different times and represent different record lengths for accretion and elevation change, measurements within a site were conducted concurrently. The record length for elevation change was at least 3 yr and for accretion above marker horizons or surface screens (benthic mat development) was 1.5–3.75 yr.

Each forest type by location combination was treated as a separate level in the ANOVA analysis, and comparisons among regions (BZ vs. FL), forest types (fringe, scrub, basin, dwarf, restored) or benthic mat types (turf algae, microbial, leaf litter) were made using Post-ANOVA contrast analysis (*t*-test). Correlations among variables were examined with correlation analysis. Data were transformed as needed to conform to normality or homogeneity of variance assumptions prior to statistical analysis.

2.3. Analyses

2.3.1. Elevation change, vertical accretion, subsurface change

Surface Elevation Tables (SETs) were used to measure elevation change. Benchmark rods (Belize) or aluminum pipe (Florida) were driven by hand to the point of refusal and fixed with cement. Total depth of the benchmarks varied from 9 to 12 m in Belize and 1 to 3 m in Florida. At Rookery Bay, the original style SET measuring arm was employed with 9 pins arrayed in a 3 × 3 pattern through a plate at the end of the arm (Cahoon et al., 2002a). The portable arm was attached to the benchmark capped with a six- or eight-notch receiver. In Belize, the newer Rod SET measuring arm was used in which the 9 pins were arrayed in a straight line along the arm axis (Cahoon et al., 2002b). Four measurement directions were established by compass bearing, and at each measurement time fiberglass pins were lowered through the measurement arm to the soil surface. Height of pins relative to the arm was recorded at intervals. At Fringe 2 and Basin 2, two directions per SET were used, giving a total of 90 elevation observations per time interval (2 directions × 9 pins × 5 replicate SETs). At all other sites, four directions were used, giving a total of 108 observations (4 directions × 9 pins × 3 replicates).

Simultaneously with SET measurements, deposition above marker horizons was also determined to give vertical accretion (Cahoon and Lynch, 1997). Feldspar clay (Florida) or white sand (Belize) was sown on the soil surface in a $0.25 \, m^2$ marked area near each SET. Both clay and sand were deposited in triplicate plots to a depth of ∼1 cm at all plots. On each sampling date, 2 cm diameter cores were taken through the marker horizon with a knife, and the depth of deposit was measured to the nearest millimeter at four different positions around the core, averaged, and plotted over time. Values from the triplicate marker horizons were then averaged to give a mean value per SET. The difference between elevation change (SET) and vertical accretion (marker horizon) was used to estimate subsurface change. Duplicate soil cores were collected on the last sampling date to the depth of the marker horizon (but away from the feldspar or sand plots) for analysis of percent organic matter and ash (Loss on Ignition). These values were used to calculate accretion rates of organic and mineral matter.

Relative sea-level rise (RSLR) values for Florida were based on mean sea-level trends measured in Naples, FL (NOAA, gauge #8725110); values for Belize were estimated based on tide gauge records at Key West, FL (NOAA, gauge #8724580).

2.3.2. Belowground accumulation of mangrove roots

Relative accumulation rates of mangrove roots were determined with the implanted mass technique (McKee et al., 2007). Other methods (e.g., sequential coring) were not feasible due to excessive disturbance to the study plots and other logistical considerations. In-growth bags (4.5 cm diameter × 30 cm long) constructed of loose nylon mesh ($3 \, mm^2$, J&M Industries, Ponchatoula, LA) and a prepared substrate were inserted into holes (5 cm diameter × 30 cm deep) cored adjacent to each SET plot. The bags were pre-filled with a substrate that provided a similar bulk density and organic matter content to the native soil. In Belize, where the substrate is composed of mangrove peat (>75% organic matter), commercial, finely-milled peat was used; native peat was not feasible because it consisted primarily of mangrove roots. In Florida, a mixture of commercial peat and mineral sediment collected from tidal creeks was used to simulate the substrate at each site. The bags were secured with a plastic pin across the top of the hole and tethered with monofilament to a nearby prop root. Bags were collected by re-coring and replaced at 4-month or 6-month intervals. Soil surrounding the excavated bags was cut away, and roots were severed at the bag surface. In-grown root material was washed over a sieve ($1 \, mm^2$) with tapwater to separate from

sediment and other debris and then rinsed with deionized water. All recovered roots were considered to have been produced during the time interval. Roots were separated into two size categories (coarse, >2 mm diameter, and fine, ≤2 mm diameter), dried at 70 C, and weighed. The roots retrieved at intervals were summed to give an annual total accumulation (net result of production, turnover, and decomposition). Root volume was calculated using previously determined values for root specific volume (volume per unit mass) measured with a pycnometer (McKee et al., 2007).

2.3.3. Benthic mat development

The biological processes contributing to surface accretion were assessed more closely with mesh screens placed on the soil surface. The objective was to determine composition of benthic mats and relative rate of development in different forest types. Note that accretion above mesh screens was not necessarily measured during precisely the same time interval as feldspar horizons (described above) and may not be directly comparable. Sub-plots were established between aerial roots at replicate sites, and the soil surface at t_0 was marked by placement of Fiberglas® mesh screens (24 cm × 24 cm). The mesh material (1 mm mesh openings and 0.32 mm thick) provided a thin, inert marker horizon that allowed deposition of organic and inorganic sediment on top as well as penetration of roots from below into sediment deposited above the screen. The soil surface was first prepared by removal of loose litter, which was replaced after screen deployment. The screens were pressed flat onto the soil surface, and the four corners and center were secured with plastic paper clips inserted at an angle into the soil. At intervals, 2 cm diameter cores were collected with a sharpened cork borer through the screen and into the soil beneath. The cores were extruded from below to avoid compression of the material deposited on the screen surface. One core was examined under magnification to identify major components (leaf, algal, or microbial matter). A second core was used to calculate depth and physical characteristics of the deposit. Thickness of the fresh material deposited above the screens was measured at four positions with digital calipers and averaged for a single value per screen. The fresh core was weighed, then dried at 105 °C, and reweighed to determine water mass and dry bulk density. The dried material was subsequently ashed in a muffle furnace (550 °C) to determine percent ash and organic matter contents of solids. These values were used to calculate surface accretion rates of organic and mineral matter at each site. Table A2 (Supplementary material) summarizes the formulae used to calculate mat characteristics.

Shear strength (the torque required to shear or deform the material) of benthic mats was determined *in situ* (adjacent to mesh screens) with a Torvane device (H-4212 1, Humbolt Manufacturing Company, Durham Geo-Enterprises, Inc).

3. Results

3.1. Elevation change, vertical accretion, and subsurface change

Elevation change rates varied from -5.4 to $10.9 \, mm \, yr^{-1}$ across 25 mangrove plots and differed significantly by site (Table 1). Rates were higher overall in FL ($3.1 \, mm \, yr^{-1}$) than BZ ($-0.23 \, mm \, yr^{-1}$) (1 df contrast, t-ratio $= -3.51$, $P = 0.0025$). Elevation losses occurred in dwarf and scrub forest types, whereas elevation gains occurred in fringe (ave. $= 1.9 \pm 1.5 \, mm \, yr^{-1}$) and basin (ave. $= 2.1 \pm 0.8 \, mm \, yr^{-1}$) types (1 df contrast, t-ratio $= -7.10$, $P < 0.0001$). Elevation gain was highest in the restored mangrove forest compared to other sites (1 df contrast, t-ratio $= 5.33$, $P < 0.0001$). Vertical accretion rates (marker horizons) also varied significantly across mangrove sites from 0.72 to $7.6 \, mm \, yr^{-1}$ (Table 1). Accretion was higher in FL ($5.64 \, mm \, yr^{-1}$) than BZ ($1.47 \, mm \, yr^{-1}$) (1 df contrast, t-ratio $= -5.79$, $P < 0.0001$).

Table 1
Comparison of elevation change and related processes across study sites instrumented with SETs. Subsurface change was calculated as the difference between elevation change and accretion (above a feldspar marker horizon) to indicate net compaction ($-$) or expansion ($+$). Root input was calculated based on annual root accumulation (g m^{-2} yr^{-1}) and specific root volume of fine (20 cm^3 g^{-1}) and coarse (10 cm^3 g^{-1}) roots. Vertical change due to other processes (physical compaction, decomposition, and hydrodynamics) was calculated as the difference between subsurface change and root inputs. Elevation deficit/surplus = $A + VC_{root} + VC_{other} - RSLR$, where A is accretion, VC_{root} and VC_{other} are vertical changes due to root input and other processes, and RSLR is relative sea-level rise. Values are the mean $\pm$ 1 SE; all units are mm yr^{-1}; results of a one-way ANOVA with site as the grouping factor are indicated by F-ratios; significance is indicated by *$P \leq 0.05$, ***$P \leq 0.001$, ****$P \leq 0.0001$, ns = not significant.

Site	n	RSLR	Elevation change	Accretion	Total subsurface change	Change due to root input	Change due to other processes	Elevation deficit ($-$) or surplus ($+$)	
								+ Roots	− Roots
BZ-Fringe	3	2.00	4.05 ± 2.22	1.64 ± 0.69	2.42 ± 2.90	8.77 ± 0.81	-6.36 ± 2.24	2.05 ± 2.22	-6.72 ± 1.60
BZ-Scrub	3	2.00	-1.05 ± 1.49	2.03 ± 1.25	-3.08 ± 2.59	4.28 ± 1.31	-7.36 ± 1.34	-3.05 ± 1.49	-7.33 ± 0.75
BZ-Dwarf	3	2.00	-3.70 ± 0.96	0.72 ± 0.34	-4.42 ± 1.11	1.24 ± 0.71	-5.66 ± 1.82	-5.70 ± 0.96	-6.94 ± 1.65
FL-Basin 1	3	2.08	3.85 ± 0.90	2.00 ± 0.35	1.86 ± 0.58	8.49 ± 0.57	-6.63 ± 1.00	1.78 ± 0.94	-6.71 ± 1.34
FL-Basin 3	5	2.08	1.06 ± 0.88	7.55 ± 0.94	-6.48 ± 0.80	1.54 ± 0.23	-8.02 ± 0.58	-1.02 ± 0.88	-2.56 ± 0.77
FL-Fringe 3	5	2.08	0.61 ± 1.84	5.74 ± 0.78	-5.13 ± 2.01	2.40 ± 0.26	-7.53 ± 2.13	-1.47 ± 1.84	-3.87 ± 1.91
FL-Restored	3	2.08	9.93 ± 0.50	5.97 ± 0.45	3.96 ± 0.78	11.81 ± 0.65	-7.85 ± 0.56	7.85 ± 0.49	-3.96 ± 0.21
ANOVA			7.61****	10.83****	10.04****	44.29****	0.28^{ns}	7.55***	1.96^{ns}

Accretion was highest at restored, basin (ave. = 5.5 ± 1.2 mm yr^{-1}), and fringe (ave. = 4.2 ± 0.9 yr^{-1}) sites and lowest at dwarf and scrub sites (1 df contrasts, $P < 0.01$) (Table 1). Shallow subsurface change also varied significantly among locations (Table 1). Four sites were characterized by subsidence (ave. = -4.8 ± 0.8 mm yr^{-1}), but three sites showed subsurface expansion (ave. = 3.3 ± 0.9 mm yr^{-1}).

Elevation change varied in concert with surface and subsurface processes (Table 1). The site with maximum elevation gain (FL-Restoration) was characterized by high surface accretion and high subsurface expansion. Two other sites gaining elevation (BZ-Fringe, Fl-Basin 1) had low accretion rates, but were undergoing subsurface expansion rather than subsidence. Sites showing little or no elevation gain (Fl-Basin 3, FL-Fringe 3) had high surface accretion, but also high subsidence rates. Sites losing elevation (BZ-Dwarf, Scrub) exhibited low accretion and high subsidence rates.

3.2. Belowground root accumulation

Mangrove root accumulation was a major contributor to soil development, adding 82–797 g m^{-2} yr^{-1} of organic matter annually (Fig. 1). Fine root accumulation was higher in Florida (264 ± 31) than Belize (143 ± 34) (1 df contrast, $t = -3.03$, $P = 0.0045$), but there was no difference in coarse root accumulation. Both fine and coarse root accumulation were higher in the FL-Restored site than in other sites ($P < 0.05$) and lower in BZ-Dwarf sites than in other sites ($P < 0.01$). Elevation change was positively correlated with fine and coarse root accumulation (Fig. 2).

3.3. Benthic mats

Benthic mats developed rapidly atop the surface screens pinned to the forest floor. Initially, development was patchy, but the entire screen was usually covered within 1 yr at most sites (Fig. A1, Supplementary material). Each forest type was characterized by a distinct benthic mat dominated by turf algae (fringe, scrub, restored), leaf litter (basin), or microbial matter (dwarf) (Table A3, Supplementary material). Filamentous algae were major components of sites with turf mats. Even sites dominated by leaf litter mats contained filamentous algae (Rhodophyta). The microbial mats, often laminated, contained mixtures of cyanobacteria, diatoms, and other microalgae, and amorphous organic matter. In most cases, the benthic mats contained other components, such as mangrove roots, leaf or wood fragments, or mineral sediment. In Belize, for example, benthic mats contained up to 30% by volume of live mangrove roots (K.L. McKee, unpublished data).

Turf mats accreted faster (2.7 mm yr^{-1}) than leaf litter mats (1.9 mm yr^{-1}) (1 df contrast, $F = 2.04$, $P = 0.0494$), but similarly to microbial mats (2.1 mm yr^{-1}). However, rates of mat accretion within mat type were highly variable across sites (Fig. 3). The organic nature of the material accreting on the soil surface in these mangrove forests was evidenced by the organic matter content of mat solids, which varied from 56 to 77%. Organic matter accumulation, calculated from mat accretion rates and organic density, varied from 56 to 509 g m^{-2} yr^{-1} across sites (Table 2), but rates did not differ by mat type ($P > 0.05$).

Physical characteristics of benthic mats, such as bulk density and total pore space, also differed among sites (Table 3). Mineral and organic solids accounted for a small proportion of mat volume; the bulk of mat volume was water contained in pore space and associated with organic matter. However, the amount of organic matter (by volume) was 1–3 times greater than inorganic material. The ratio of organic to mineral contributions to accretion was higher in Belize (2.5) than FL (1.5) (t-ratio = 7.22, $P < 0.0001$), and highest in microbial mats (3.4) compared to turf (1.9) or leaf (1.4) mats ($P < 0.001$).

Qualitative observations indicated that filamentous algae (and mangrove roots) not only contributed directly to the volume of accreting material in turf mats, but formed a strong matrix on the soil surface that aided in trapping and retention of detrital particles and mineral sediment. An analysis of covariance with
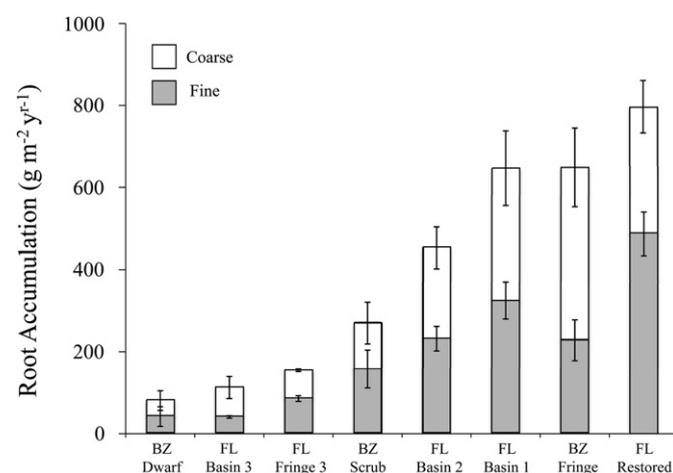

Fig. 1. Belowground accumulation of fine and coarse roots in different mangrove forest types in Florida (FL) and Belize (BZ). Values are the mean and SE (n = 3–9).
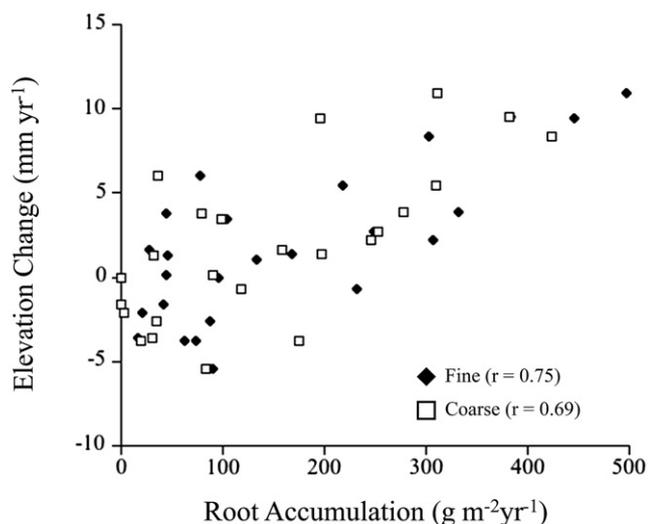
Fig. 2. Elevation change in relation to rates of fine and coarse root accumulation at mangrove sites in Belize and Florida. The *r* value indicates the strength of the relationship.

mat type (within region) as the covariate was conducted to determine if mat type influenced the relationship between accretion rates of organic and inorganic solids (by volume). The slopes of the relationships differed significantly from zero (Fig. 4)

and from each other ($F = 12.75$, $P < 0.0001$, mat type $\times$ organic accretion interaction), indicating that some organic mats accumulated relatively more inorganic material than others. FL-turf mats accumulated 1.1 mm yr^{-1} of inorganic matter for every 1 mm yr^{-1} of organic matter accreted. BZ-turf and FL-leaf mats also accumulated inorganic material, but less so than FL-turf mats. BZ-microbial mats showed no significant relationship between organic and inorganic accretion (slope not significantly different from zero).

3.4. Elevation change and relative importance of surface and subsurface processes

Contributions of surface and subsurface processes to vertical change were compared to better understand controls on elevation (Table 1). Root input contributed from 1.2 to 11.8 mm yr^{-1} to vertical change across study sites. In comparison, surface accretion contributed 0.7–7.6 mm yr^{-1}. To maintain elevations within the intertidal zone, vertical change must balance RSLR (subsurface losses plus eustatic SLR). To gauge the capacity of each site to match RSLR, an elevation deficit/surplus was calculated (Table 1). The elevation deficit/surplus varied across sites from −5.7 (BZ-Dwarf) to 7.9 (FL-Restored) mm yr^{-1}. Without root inputs, however, there would be an elevation deficit at all sites.

The relative contribution of all processes to vertical change (calculated as a percent of the total change) provided a clearer picture of how important surface and subsurface contributions
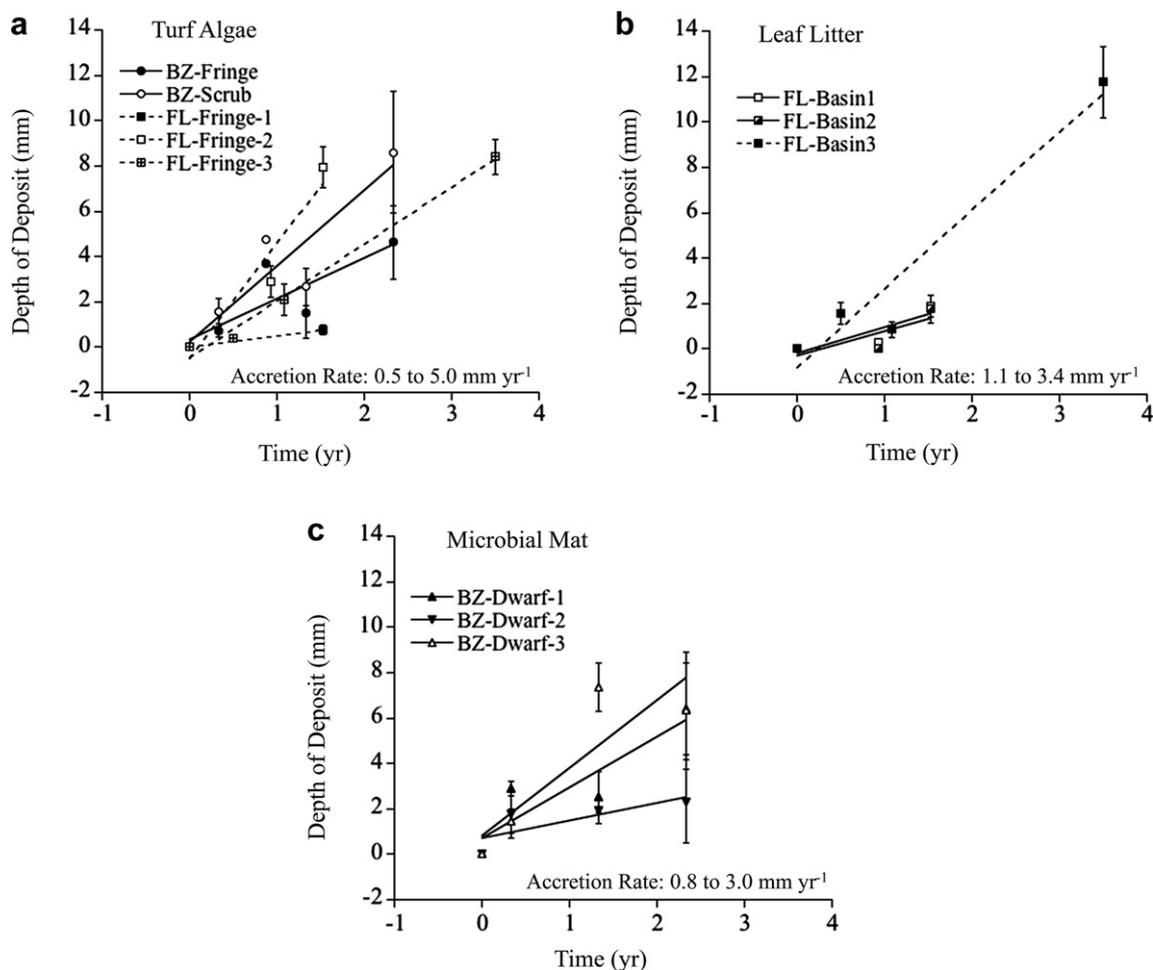

Fig. 3. Accretion of benthic mats in mangrove forests in Florida (FL) and Belize (BZ) dominated by different mat types: A. turf algae, B. microbial, and C. leaf litter. Values are the mean and SE ($n = 3–5$).

Table 2
Summary of benthic mat contributions to accretion (above mesh screens), organic matter content (by mass), and organic matter accumulation in different mangrove forest types in Belize (BZ) and Florida (FL). Mat type indicates the primary component of the mat, but other biotic components, including mangrove roots and detritus, may have contributed to mat volume. Organic matter accumulation was estimated based on vertical accretion rates × organic density (Table 3) of accreting material. Values are the mean ± SE; n = total number of replicate plots per site. Results of a one-way ANOVA with site as the grouping factor are indicated by F-ratios ($P \leq 0.0001$).

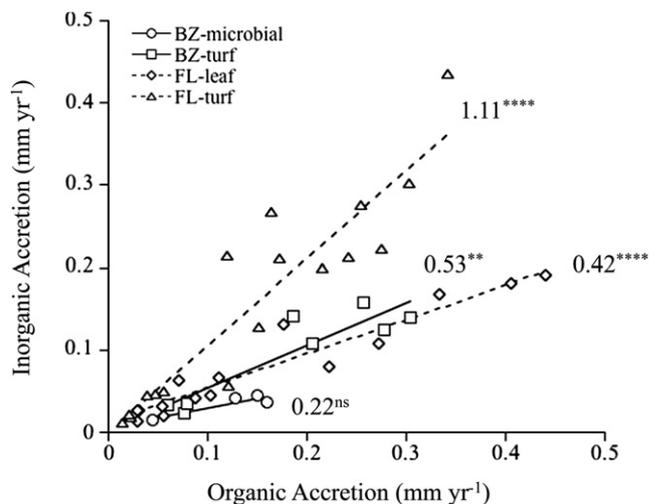| Site	n	Mat type	Accretion rate (mm yr^{-1})	Organic Matter (%)	Organic matter accumulation (g m^{-2} yr^{-1})
BZ-Fringe	4	Turf algal	2.48 ± 0.78	69 ± 3	277 ± 93
BZ-Scrub	4	Turf algal	3.90 ± 0.89	64 ± 3	377 ± 88
BZ-Dwarf	4	Microbial	2.05 ± 0.46	77 ± 2	205 ± 44
FL-Basin 1	5	Leaf	1.15 ± 0.29	57 ± 2	111 ± 28
FL-Basin 2	5	Leaf	1.06 ± 0.36	71 ± 1	174 ± 58
FL-Basin 3	5	Leaf	3.44 ± 0.45	67 ± 3	583 ± 81
FL-Fringe 1	5	Turf algal	0.49 ± 0.14	50 ± 1	56 ± 12
FL-Fringe 2	5	Turf algal	5.02 ± 0.59	46 ± 2	509 ± 62
FL-Fringe 3	5	Turf algal	2.50 ± 0.26	49 ± 4	376 ± 52
FL-Restored	2	Turf algal	1.46 ± 0.53	61 ± 8	162 ± 54
ANOVA			9.46	15.92	8.56

Fig. 4. Relationship between accretion of organic and inorganic solids (by volume) above surface screens pinned to the soil surface in mangrove sites dominated by different mat types in Florida (FL) or Belize (BZ): BZ-microbial (microbial mat), BZ-turf (turf algae), FL-leaf (decaying leaf litter), FL-turf. The slopes of the linear relationship are shown and whether they differed significantly from zero: **$P < 0.001$, ****$P < 0.0001$, ns = not significant.

were to the direction and rate of elevation change (Fig. 5). Processes leading to elevation loss (i.e., compaction due to decomposition and decreased pore space) accounted for 31–74% of total elevation change across sites, and where these processes exceeded organic matter inputs, elevation loss occurred. At BZ-Scrub and BZ-Dwarf sites, root contributions were important (14–33%), but insufficient to balance subsidence (53–76%); these sites exhibited elevation deficits of −3.1 and −5.7 mm yr^{-1}, respectively (Table 1). At three of seven sites (FL-Restored, BZ-Fringe, FL-Basin 3), root contribution to total vertical change was 45% or greater, and it was these sites that exhibited an elevation surplus. At two sites (FL-Fringe 3 and FL-Basin 3), accretion was high, but root contributions were significantly lower than other sites (Fig. 3). These latter sites showed an elevation deficit (Table 1).

4. Discussion

In wetland habitats with low inputs of mineral sediment, especially in geological settings characterized by high rates of RSLR, organic matter accumulation determines whether the system is sustainable, i.e., elevation change equals RSLR. Organic matter accumulation and contribution to soil formation is widely recognized, and the processes controlling it have been well studied in many habitats. The organic matter content of surficial material at sites in Belize (71 ± 2%) and Florida (52 ± 2%), in combination with

the occurrence of deep peat deposits (e.g., 8–10 m thick in Belize, McKee et al., 2007), suggested the biogenic nature of soil formation in these mangrove ecosystems. The relative contribution of organic solids to surface accretion was one to three times that of inorganic solids across study sites and also pointed to biological, rather than mineral controls on vertical accretion.

Organic matter is often the main structural component in coastal wetland soils. It accounts for over 90% of soil volume even in mineral sedimentary settings (Bricker-Urso et al., 1989; Nyman and DeLaune, 1990; Nyman et al., 1993) and four times more volume contribution to soil accretion than an equivalent mineral mass (Neubauer, 2008). Modeling studies also have shown the key role of organic matter contributions in wetland elevation change (Rybczyk and Cahoon, 2002; Cahoon et al., 2003; Mudd et al., 2009). A few studies have investigated indirect effects of vegetation on mineral sediment deposition (e.g., Gleason et al., 1979; Leonard et al., 1995; Rooth and Stevenson, 2000; Krauss et al., 2003). Those investigations focused on how plant shoots (marshes) or aerial roots (mangroves) altered sedimentation rates by baffling water movement or trapping sediment. A few experimental studies have directly linked specific biological processes to vertical accretion and surface elevation change in wetlands (McKee et al., 2007; Langley et al., 2009).
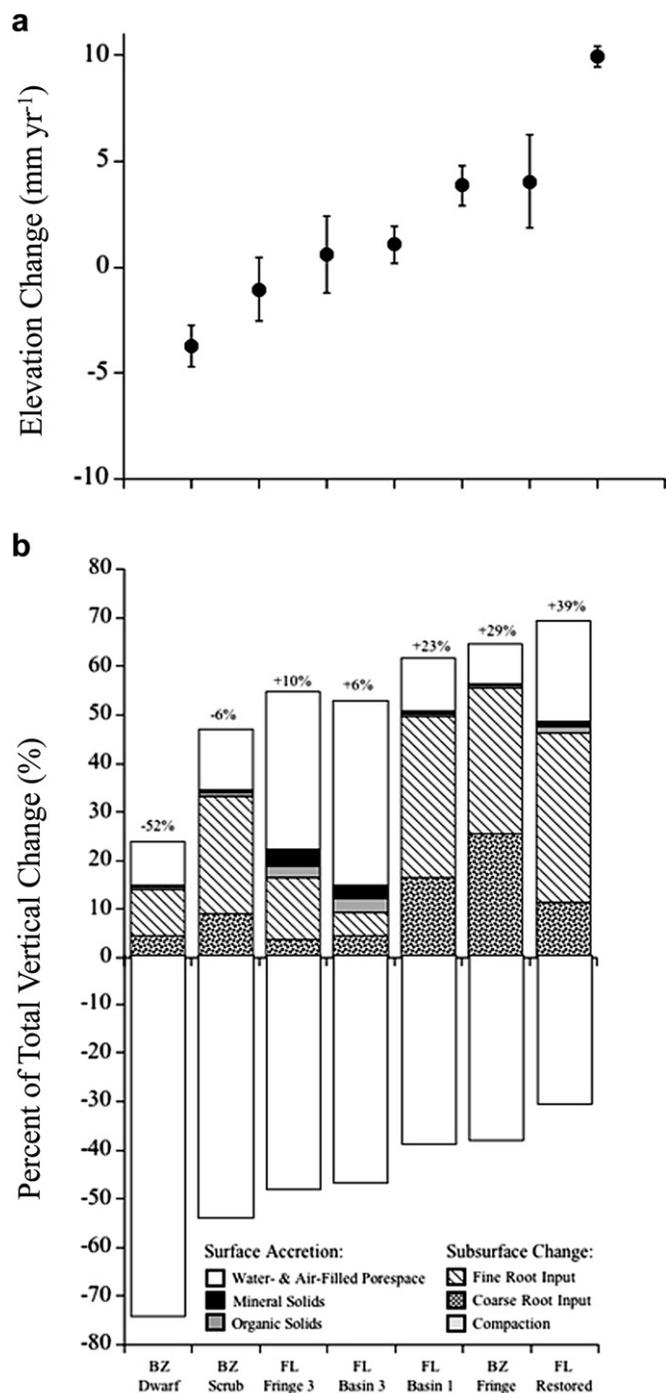
Table 3
Physical characteristics of benthic mats in Belize (BZ) and Florida (FL). Mat type (T = turf algal, M = microbial, L = leaf) indicates the primary component of the mat, but other biotic components, including mangrove roots and detritus, may have contributed to mat volume. See Table A2 for calculations. Values are the mean ± SE; results of a one-way ANOVA with site as the grouping factor are indicated by F-ratios; significance is indicated by *$P \leq 0.05$, ***$P \leq 0.001$, ****$P \leq 0.0001$.

Site	Mat type	Bulk density (g cm^{-3})	Relative saturation (%)	Organic density (g cm^{-3})	Mineral density (g cm^{-3})	Particle density (g cm^{-3})	Total pore space (%)	Organic matter by volume (%)	Mineral matter by volume (%)	Organic to mineral ratio by volume
BZ-Fringe	T	0.16 ± 0.01	92 ± 1	0.11 ± 0.01	0.05 ± 0.01	1.78 ± 0.02	91 ± 1	6.1 ± 0.2	2.8 ± 0.4	2.3 ± 0.4
BZ-Scrub	T	0.15 ± 0.01	92 ± 1	0.10 ± 0.01	0.06 ± 0.01	1.82 ± 0.03	91 ± 1	5.5 ± 0.6	3.0 ± 0.3	1.8 ± 0.2
BZ-Dwarf	M	0.13 ± 0.01	94 ± 1	0.10 ± 0.01	0.03 ± 0.00	1.72 ± 0.10	92 ± 1	5.9 ± 0.3	1.8 ± 0.2	3.4 ± 0.3
FL-Basin 1	L	0.17 ± 0.01	91 ± 1	0.09 ± 0.00	0.08 ± 0.01	1.89 ± 0.02	91 ± 1	5.1 ± 0.3	3.9 ± 0.3	1.3 ± 0.1
FL-Basin 2	L	0.24 ± 0.03	88 ± 2	0.17 ± 0.02	0.07 ± 0.01	1.77 ± 0.01	86 ± 2	9.7 ± 1.2	4.0 ± 0.4	2.4 ± 0.1
FL-Basin 3	L	0.25 ± 0.01	87 ± 1	0.17 ± 0.01	0.08 ± 0.01	1.80 ± 0.02	86 ± 1	9.4 ± 0.6	5.0 ± 0.4	2.1 ± 0.2
FL-Fringe 1	T	0.24 ± 0.03	87 ± 2	0.12 ± 0.01	0.12 ± 0.02	1.95 ± 0.01	88 ± 1	6.1 ± 0.5	6.1 ± 0.8	1.0 ± 0.1
FL-Fringe 2	T	0.22 ± 0.01	88 ± 1	0.10 ± 0.01	0.12 ± 0.00	1.99 ± 0.03	89 ± 1	5.1 ± 0.4	5.9 ± 0.2	0.9 ± 0.1
FL-Fringe 3	T	0.31 ± 0.03	81 ± 3	0.15 ± 0.01	0.17 ± 0.03	1.97 ± 0.04	84 ± 1	7.5 ± 0.5	8.3 ± 1.3	1.0 ± 0.1
FL-Restored	T	0.19 ± 0.03	90 ± 2	0.11 ± 0.00	0.08 ± 0.03	1.86 ± 0.07	90 ± 1	6.1 ± 0.0	4.1 ± 1.3	1.6 ± 0.5
ANOVA		7.21****	9.76****	7.71****	4.69****	22.52****	7.46***	3.10*	29.81****	21.9****

Fig. 5. A. Comparison of elevation change rates across mangrove forest types in Belize (BZ) and Florida (FL). Values are the mean and SE ($n = 3$–5). B. Relative contributions of processes to elevation change. Values are the mean percent of total vertical change due to accretion of organic and inorganic solids and pore space aboveground and accumulation of fine and coarse roots belowground. Compaction (subsurface change − root inputs) is plotted as a negative percent for comparison with inputs. The difference between inputs and losses (% surplus or deficit) is indicated above each bar.

Previous work has shown that the main component of peat in biogenic mangrove forests is refractory mangrove roots (Parkinson et al., 1994; McKee and Faulkner, 2000b; McKee et al., 2007). Even in muddy coastal environments where mineral sediment deposition contributes to vertical accretion, the soil binding capacity of mangrove roots has been noted (Scoffin, 1970). Despite the general

recognition that variation in root production may influence soil volume (Cahoon and Lynch, 1997; Rybczyk and Cahoon, 2002), few direct measures of root contributions (or losses through decomposition) have been made in conjunction with elevation change in mangrove ecosystems. Work in Honduras following Hurricane Mitch showed that rapid soil collapse occurred in a mangrove forest that experienced total mortality and lack of root production (Cahoon et al., 2003). In other work, belowground root accumulation in mangrove sites was found to be highly correlated with elevation change (Cahoon et al., 2006; McKee et al., 2007). In the current study, root inputs could account for at least 1 mm yr^{-1} of subsurface expansion and as much as 12 mm yr^{-1} (FL-Restored). Since mangrove roots are relatively more refractory than leaves (Middleton and McKee, 2001) and are also produced belowground where anaerobic conditions would limit decomposition of organic matter, differences in above- vs. belowground plant partitioning may influence elevation change.

Another biological process that has received little attention relative to accretion is the development of benthic mats. Other workers have noted their potential role in sediment trapping in mangrove forests (Cahoon and Lynch, 1997), and the current study found that accumulation of decaying leaves or formation of living benthic mats were important mechanisms controlling surface accretion in the mangrove forests studied. Mat type differed among forest types and presumably reflected conditions supporting growth of turf algae, microbial communities, or accumulation of leaf litter. The accumulation of plant litter in Caribbean mangrove forests can vary substantially depending upon litterfall rates, consumption by macrodetritivores, microbial decomposition rates, and tidal flushing (Middleton and McKee, 2001). Basin forests, which form in depressional areas, are less frequently flushed by tides than exposed shorelines and are characterized by deep layers of decaying leaves. In fringe forests in Belize, less litter accumulates due to frequent removal by ebb tides and detritivore feeding (Middleton and McKee, 2001). The latter areas were characterized by growth of turf algae, which formed thick, living mats over the soil surface. Such mats, which are common throughout the Caribbean region (K. McKee, pers. obs.), have high shear strength relative to other organic or mineral surfaces in mangrove forests (Table A4, Supplementary material).

Microbial mats are another type of benthic community easily overlooked due to their nondescript color (Joye and Lee, 2005). Although microbial mats superficially resembled mineral sediment, a high organic content (77%) attested to their biotic origin, and examination under magnification revealed a complex community of cyanobacteria, diatoms, and other microorganisms. Microbial mats were common in dwarf mangrove forests and shallow, protected ponds where the tree canopy was open or absent and the soil surface remained flooded.

Mass accumulation rates of turf algal and microbial mats were remarkably high (56–509 g m^{-2} yr^{-1}, Table 2) and rivaled that of leaf litter production by mangroves (280–896 g m^{-2} yr^{-1}, Table A1). While accumulation of leaf litter led to vertical accretion rates of 1.0–3.4 mm yr^{-1}, the rapid growth of turf algae and/or microbial mats resulted in similar or higher accretion rates (0.5–5.0 mm yr^{-1}) (Table 2). These accretion rates are in the same range as found with feldspar/sand horizons (0.72–7.5, Table 1), but are not exactly the same (within location) due to different measurement intervals and slightly different sampling locations. Taken together, accretion rates above screen and feldspar/sand suggest that mat development and contribution to vertical accretion is somewhat variable both spatially and temporally. Within- and among-site variation in mat accretion is likely attributable to variation in factors such as microtopography and canopy openness and their respective influences on edaphic and light conditions.

Mat development may also fluctuate over time as environmental conditions influencing growth and decomposition change.

Nonetheless, accretion rates of algal mats are comparable to those occurring in habitats with high mineral sedimentation (e.g., $3.3–7.1$ mm yr^{-1}; Cahoon et al., 2000). Also, the relationship between organic and inorganic accretion, which differed among mat types (Fig. 4), suggests that turf and leaf litter mats trap mineral sediment. The mechanism whereby benthic mats may trap and/or retain mineral sediment is unclear and beyond the scope of this study. However, structures such as plant shoots or aerial roots may slow water velocities (causing settlement of particles) or increase water turbulence (causing erosion) (Spenceley, 1977; Krauss et al., 2003). Other work has shown that as plant litter on the soil surface was varied experimentally, the amount of trapped sediment increased exponentially and contributed to accretion (Rooth et al., 2003). The greater surface area created by a turf algal mat may promote even greater trapping of suspended sediment and also minimize resuspension. Further work is needed to quantify the sediment trapping potential of benthic mats and possible synergistic effects of organic and inorganic processes on accretion.

A comparison of surface and subsurface contributions to elevation change (Fig. 5) indicated that the relative importance of biophysical processes varied not only among, but within forest types. Accumulation of roots was clearly a major contributor to elevation change at some sites, accounting for up to 55% of vertical change. Where root contributions were high, volume inputs exceeded losses, even when surface accretion of material was low (e.g., BZ-Fringe). Surface accretion by benthic mats was also important and accounted for 9–35% of total vertical change. Only 0.6–2.8% of vertical change could be attributed to organic accretion, but these proportions reflect the amount of dry solids and do not include the pore space associated with fresh material. Total pore space was high in material accreting on the soil surface, and some was undoubtedly associated with living mat components (algae, roots, and microorganisms) and decaying organic matter. Virtually all the water in sediment cores from Rhode Island marshes was associated with the organic fraction (4–15% of dry solids); consequently, most of the vertical accretion (91–96%) was attributed to organic production (Bricker-Urso et al., 1989). In future studies, determination of specific volume of mat components would improve the estimate of surface organic contributions to elevation change.

Although this study focused on organic inputs to soil formation and elevation change, volumetric losses due to compaction processes were clearly important (Fig. 5). Soil compaction results from the combination of organic matter decomposition and the reduction of soil pore space (Ewing and Vepraskas, 2006; Turner et al., 2006). Compaction of pore space varies with porosity of deposited material and soil depth (mass of material above) (Ewing and Vepraskas, 2006). In the current study, total pore space of benthic mats varied from 84 to 92%, suggesting the potential for variation in physical compaction of surficial material as it becomes buried. Mangrove roots also have a high air-filled porosity (20–60%) due to the presence of an aerenchymatous cortex needed for root aeration (Pi et al., 2009). Variation in inputs of roots belowground and benthic mats aboveground should influence the rate of compaction due to differential physical compression as well as differential rates of decomposition (Middleton and McKee, 2001). In the current study, decomposition rates of organic components were unknown, but relative contributions of leaves, roots, algae, and other organic material could influence overall decomposition rates due to differences in constitutive refractory compounds. For example, relative decomposition rates of mangrove roots, leaves, and wood measured in Belize indicated that decaying mangrove roots had a turnover time of about 10 yr,

whereas leaves had a turnover time less than 1 yr in some locations (e.g., fringe forests) (Middleton and McKee, 2001). The buildup of decaying leaves in basin forests (Fig. 3), however, showed that where conditions minimized physical removal by tides, slow decomposition rates were likely important in promoting surface accretion of organic matter. Further information about decomposition rates of organic matter in mangrove forests, both above- and belowground, is needed to fully understand variation in compaction rates.

5. Conclusions

Biotic processes such as root production and benthic mat development clearly contribute to soil volume in mangrove forests, and consequently may allow sediment-poor ecosystems to keep pace with sea-level rise. Some workers have predicted widespread collapse of mangroves in the Caribbean region under accelerated sea-level rise (2.3–4.0 mm yr^{-1}) (Ellison and Stoddart, 1991). However, other studies suggest that mangroves are keeping pace with or are expanding under these rates (Cahoon and Lynch, 1997; Cahoon et al., 2006; McKee et al., 2007). Discrepancies among studies are partly due to methodological differences (Cahoon and Lynch, 1997), but may also reflect local and regional differences in processes controlling elevation change. Subsurface peat accumulation has been suggested to be the dominant process contributing to vertical development of mangrove soils in carbonate settings (Parkinson et al., 1994; McKee et al., 2007). The current study suggests that the process is more complicated than previously recognized and that development of benthic mats can also contribute to accretion in these mangrove forests.

The finding that biotic processes are important controls on accretion and elevation change in mangrove ecosystems has implications for other coastal wetlands in sediment-deficient environments. Obviously, removal or degradation of the biological components contributing to organic matter production could have negative consequences for habitat stability, especially given sea-level rise scenarios (Parry et al., 2007). Other work suggests that increases in atmospheric CO_2 may stimulate belowground root production and rates of elevation gain in some marshes, countering sea-level rise (Cherry et al., 2009; Langley et al., 2009). Information about biological processes will be essential to predict wetland sustainability as atmospheric CO_2, climate, sea-level, and other global factors change in the future. Changes in local conditions such as eutrophication, toxic spills, and storm events that disrupt plant production may also affect the capacity of the wetland to keep pace with sea-level change. The potential feedback interactions among resources (nutrients, light, CO_2), primary producers, and organic matter accumulation suggest a complex suite of controls on wetland elevation that are just beginning to be investigated (Mudd et al., 2009). This study has highlighted the importance of biological processes specific to mangrove forests in carbonate settings, but comparable information is needed for other coastal wetlands.

Mendelssohn, and two anonymous reviewers. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecss.2010.05.001.

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