RESEARCH PAPER

Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation

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ABSTRACT

Aim The long-term stability of coastal ecosystems such as mangroves and salt marshes depends upon the maintenance of soil elevations within the intertidal habitat as sea level changes. We examined the rates and processes of peat formation by mangroves of the Caribbean Region to better understand biological controls on habitat stability.

Location Mangrove-dominated islands on the Caribbean coasts of Belize, Honduras and Panama were selected as study sites.

Methods Biological processes controlling mangrove peat formation were manipulated (in Belize) by the addition of nutrients (nitrogen or phosphorus) to *Rhizophora mangle* (red mangrove), and the effects on the dynamics of soil elevation were determined over a 3-year period using rod surface elevation tables (RSET) and marker horizons. Peat composition and geological accretion rates were determined at all sites using radiocarbon-dated cores.

Results The addition of nutrients to mangroves caused significant changes in rates of mangrove root accumulation, which influenced both the rate and direction of change in elevation. Areas with low root input lost elevation and those with high rates gained elevation. These findings were consistent with peat analyses at multiple Caribbean sites showing that deposits (up to 10 m in depth) were composed primarily of mangrove root matter. Comparison of radiocarbon-dated cores at the study sites with a sea-level curve for the western Atlantic indicated a tight coupling between peat building in Caribbean mangroves and sea-level rise over the Holocene.

Main conclusions Mangroves common to the Caribbean region have adjusted to changing sea level mainly through subsurface accumulation of refractory mangrove roots. Without root and other organic inputs, submergence of these tidal forests is inevitable due to peat decomposition, physical compaction and eustatic sea-level rise. These findings have relevance for predicting the effects of sea-level rise and biophysical processes on tropical mangrove ecosystems.

Keywords

Accretion, decomposition, elevation change, habitat stability, Holocene, nutrients, radiocarbon, *Rhizophora*, subsidence.

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INTRODUCTION

Mangrove wetlands offer important ecological and societal benefits along tropical and subtropical coastlines. Mangroves provide nursery grounds and refuge for commercially important marine organisms (Primavera, 1998; Mumby *et al.*, 2004), act as buffers against hurricanes and tsunamis (Dahdouh-Guebas *et al.*, 2005; Danielsen *et al.*, 2005), and filter terrestrial sediment and nutrients, minimizing their input into more sensitive systems such as seagrass beds and coral reefs (Alongi & McKinnon, 2005). Mangroves and other tidal, saline wetlands such as salt marshes also have the capacity to sequester carbon into soil faster than in terrestrial ecosystems (Chmura *et al.*, 2003). The habitat stability of mangroves and other coastal wetlands ultimately depends on the capacity of the system to maintain soil elevations relative to sea level. Plants contribute directly to soil formation

through input of organic matter, but no empirical information directly links specific biotic processes to elevation change in coastal systems. This type of information is necessary, however, to accurately predict the future responses of coastal wetlands to sea-level rise and their interactions with other factors affecting biological processes, e.g. nutrients.

Mangroves develop in a wide range of sedimentary environments, from alluvial habitats with abundant mineral input to oceanic islands with little or no allochthonous contributions of sediment. Oceanic mangrove systems dependent upon the biogenic processes of vertical land building are common throughout the Caribbean region and total over 780,000 ha (FAO, 2003). Caribbean mangrove forests are often underlain by deep peat deposits formed by the gradual accumulation of organic matter (Woodroffe, 1983; Parkinson *et al.*, 1994; Cameron & Palmer, 1995; McKee & Faulkner, 2000a; Middleton & McKee, 2001; Toscano & Macintyre, 2003; Macintyre *et al.*, 2004). These mangrove forests are fundamentally different from those receiving mineral sediment (e.g. in alluvial habitats) and thus represent a model system for the study of biotic contributions to elevation change.

Although the biogenic nature of these and other peat-forming systems is generally recognized, the processes controlling the accumulation of organic matter have not been directly linked to elevation change. In addition, little information exists on how peat formation and elevation change may be affected by eutrophication, a major threat to mangrove systems globally (Valiela *et al.*, 2001). Recognition of the biotic contributions to elevation change is essential for the development of models that can better predict the responses of coastal wetlands to sea-level rise and climate change. An understanding of the central role of mangroves in controlling soil elevation is also critical to the conservation and management of tropical coastlines worldwide.

To better understand the rates and processes of mangrove peat formation, we examined the rates of elevation change and accumulation of root matter in a mangrove ecosystem in the Meso-American Barrier Reef of Belize. This ecosystem contains hundreds of mangrove-dominated islands, and together with mainland mangroves totals 65,767 ha (FAO, 2003). These Belizean islands were selected as representative of peat-forming mangrove systems found throughout the Caribbean (Woodroffe, 1983, 1995; Toscano & Macintyre, 2003; Macintyre *et al.*, 2004) with some of the deepest (10 m) and oldest deposits of peat (>7000 years) (Macintyre *et al.*, 1995, 2004; Toscano & Macintyre, 2003). In addition, these islands have experienced less human interference than many other locations [loss of mangrove area in Belize is *c.* 12 % of the total reported in 1980 compared with a loss of 21% over the same period for the Americas (FAO, 2003)]. To compare modern changes in elevation with past peat development, geological rates of peat accumulation were determined using radiocarbon dating of peat cores from Belize, Honduras and Panama. The results were compared with a sea-level curve for the western Atlantic (Toscano & Macintyre, 2003) as well as with peat accumulation in other locations throughout the Caribbean region. We then used the results to predict how peat-forming mangroves

may respond to future scenarios of sea-level rise. Our approach is applicable to other coastal wetlands, particularly those in which elevational dynamics are dominated by biological processes.

METHODS

Study sites

The Meso-American Barrier Reef system extends 220 km from the southern part of the Yucatan Peninsula to the Bay Islands of Honduras and contains the longest unbroken reef in the Western Hemisphere. A manipulative experiment was conducted from February 2001 to August 2004 at Twin Cays, a 75-ha archipelago located in the central part of the barrier reef system and about 2 km west of the reef crest (see Figs S1 & S2 in Supplementary Material for maps and photographs of the study sites). Twin Cays has been the focus of research by the Smithsonian Institution since the early 1970s (Rützler & Feller, 1996). These mangrove islands are far from the mainland, and peat cores contain no terrigenous sediment (Cameron & Palmer, 1995; McKee & Faulkner, 2000a; Purdy & Gischler, 2003; Macintyre *et al.*, 2004). The only source of fresh water is rainfall, and the entire system is intertidal [mean tide range (neap) = 0.2 m]. The vegetation is dominated by *Rhizophora mangle* (red mangrove), which is the most common species in the Caribbean region.

Peat cores were collected from Twin Cays and Cat Cay, Belize; the Bay Islands of Roatán and Guanaja, Honduras; and Isla San Cristóbal, Panama. Cat Cay is a 15-ha mangrove island in the Pelican Cays archipelago located 21 km south of Twin Cays (McKee & Faulkner, 2000a). The Bay Islands of Roatán and Guanaja lie 30–50 km north of the Caribbean coast of Honduras (Cahoon *et al.*, 2003). Roatán is the largest (133 km^2) and contains a 400-ha tract of mangroves on the eastern extension of the island. Guanaja is smaller (57 km^2) with *c.* 300 ha of mangrove forest prior to Hurricane Mitch. Isla San Cristóbal occurs on the Caribbean coast of the Republic of Panama within the Bocas del Toro archipelago (Lovelock *et al.*, 2005). All of these sites were dominated by *R. mangle*, and the organic matter content of the soil was 60% or higher, i.e. peat.

Manipulative experiment

We specifically tested the hypothesis that accumulation of refractory mangrove roots contributes directly to soil volume and hence elevation. Root dynamics were manipulated experimentally by the addition of nitrogen (N) or phosphorus (P), and the effects on elevation change were followed for 3 years. Previous work showed that mangrove shoot growth varied spatially and was stimulated by N (fringe), P (interior) or both N and P (transition) (McKee *et al.*, 2002; Feller *et al.*, 2003a). Experimental plots were established at three replicate sites in the Twin Cays archipelago. At each replicate site, three transects were established from the shoreline to the island interior across a tree height/productivity gradient (distance = 30–40 m). Permanent walkways were installed in 2000 across the entire length of each transect to minimize soil disturbance. Three vegetation zones relative to
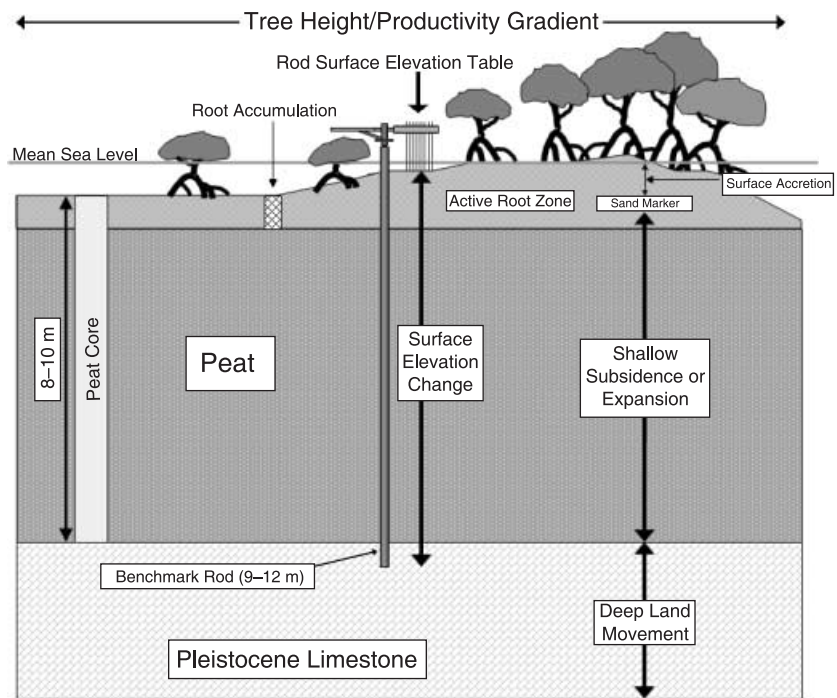
Figure 1 Rod surface elevation tables (RSETs) were used to measure elevation change across a tree height/productivity gradient at Twin Cays, Belize; deposition of material above marker horizons was simultaneously measured to give surface accretion. The difference between elevation change and surface accretion yielded subsurface subsidence (negative) or expansion (positive). In-growth bags were used to measure rates of root accumulation adjacent to RSETs. Peat cores were collected and sections radiocarbon dated to determine geological rates of accretion. Figure not drawn to scale.

the shoreline were designated based on previous work: Fringe (tree height = 5–7 m; litterfall = 700 g m^{-2} year^{-1}), Transition (tree height = 2–4 m; litterfall = 450 g m^{-2} year^{-1}) and Interior (tree height = 1–1.5 m; litterfall = 280 g m^{-2} year^{-1}) (Koltes *et al.*, 1998). Each of the three transects per site was randomly assigned to a treatment (N-fertilized, P-fertilized and unfertilized controls) (McKee *et al.*, 2002; Feller *et al.*, 2003a). This approach was taken to minimize the possibility of cross-contamination of plots due to tidal movement across zones. Fertilizer in the form of urea (45:0:0) or superphosphate (0:45:0) was applied below ground at 6-month intervals from 1997 until the end of the study in August 2004 (Feller *et al.*, 2003a). Individual trees were targeted, and fertilizer (150 g) contained in dialysis tubing was placed in two holes (3 cm diameter × 30 cm deep) cored into the substrate beneath the drip line on opposing sides of the tree and sealed with peat. Control sites were cored and sealed, but no fertilizer was added. Thus, there were 27 total plots; $n = 3$ for each treatment–zone combination. Treatments significantly increased the bioavailability of porewater $NH_4 + NO_3$-N or PO_4-P (measured with resin bags), respectively, from 0.117 or 0.011 μg (g resin)$^{-1}$ day^{-1} to 0.218 (N-fertilized, $F = 5.71$, $P < 0.01$) or 0.030 (P-fertilized, $F = 6.39$, $P < 0.01$) μg (g resin)$^{-1}$ day^{-1} (see Table 3 in McKee *et al.*, 2002). Porewater nutrients indicated there was no migration of fertilizer into adjacent experimental plots (data not shown).

Elevation change, surface accretion and subsurface change

A rod surface elevation table (RSET), which consisted of a benchmark rod and a portable measuring arm, was used to determine elevation change over time (Cahoon *et al.*, 2002) (see

Fig. 1 & Fig. S2 in Supplementary Material). This technique, which has been used in multiple studies worldwide, provided a measure of change in surface elevation relative to the base of a benchmark rod driven to the point of refusal (see http://www.pwrc.usgs.gov/set for a detailed description of the technique and a list of publications based on this method). The RSET measurement area (*c.* 2 m in diameter) was situated adjacent to each fertilized tree but did not overlap the point of fertilizer application. RSET installation and measurements were conducted while standing on mangrove prop roots or on portable platforms. In February 2001, a benchmark rod, in threaded sections, was driven with a slide hammer in each of 27 experimental plots; the total depth of the rods to the Pleistocene limestone base varied from 9–12 m. Baseline measurements of elevation were conducted 1 month later to allow recovery from rod installation. Four measurement directions were established, and at each measurement time, nine fibreglass pins were carefully lowered through the measurement arm to the soil surface ($n = 36$ per RSET and measurement interval). The height of pins relative to the arm was recorded at 6-month intervals to give the change in elevation of the soil surface over time. Consequently, movement of the soil surface as a result of all processes occurring in the entire soil profile to the Pleistocene limestone was measured for 3 years. One person conducted all elevation measurements to minimize operator error. In addition, strict protocols, extensive notes, field markers and photographs were employed to ensure consistency and to identify problematic data points.

At the same time, the deposition of material (organic and inorganic) above marker horizons of sand was determined adjacent to the RSET plots to give surface accretion (Cahoon & Lynch, 1997). White carbonate sand was collected from a nearby beach and placed in a marked area (0.1 m^2) near each RSET plot

to a depth of 1 cm. Cores were subsequently collected through the sand horizon, and the depth of deposited material was measured with a ruler at four positions and averaged. Differences between elevation change and surface accretion were used to calculate shallow subsidence (negative difference) or expansion (positive difference) (Fig. 1).

Accumulation of mangrove root material

Relative rates of accumulation of root matter were determined adjacent to each RSET using the implanted mass technique (Fig. 1). The objective was to measure the relative accumulation of roots (live and dead) and their potential contribution to peat formation, rather than absolute rates of root production. In-growth bags containing a standardized organic substrate were used in all plots since there was minimal variation in organic content of mangrove peat across zones (70–76%). Native peat could not be used because it is composed primarily of mangrove roots, making separation of in-grown roots impossible. Sphagnum peat provided a standardized material that is commercially available and similar to mangrove peat in bulk density (0.12 vs. 0.14 g cm^{-3}) and contents of organic matter (95 vs. 74%), total carbon (47 vs. 42%) and total nitrogen (0.7 vs. 0.8%). Duplicate in-growth bags (5 cm diameter × 30 cm length) made of flexible mesh material and containing sphagnum peat were installed in cored holes near each experimental tree. Bags were retrieved at 6-month intervals, and accumulated root mass was separated by condition (live, dead) and diameter class (fine, ≤ 2.5 mm; coarse, > 2.5 mm), dried in an oven (80 °C) and weighed. Annual accumulation of root matter was calculated by summing the mass during each sampling interval; annual root mortality was estimated based on the mass of dead roots. Dead roots were identified based on loss of structural integrity, colour and signs of decomposition. Live plus dead root biomass was used to estimate total root matter that accumulated during each interval. The contribution of root biomass to soil volume was calculated using specific root volume (volume per unit mass) of *R. mangle* fine and coarse roots. Specific root volume was determined with a 25-ml pycnometer. This approach allowed relative comparisons of root matter accumulation across treatments and zones in relation to concomitant changes in soil surface elevation and accretion.

To independently determine the effects of external nutrients on decomposition rates, roots of *R. mangle* were collected from a common (unfertilized) area, separated into size classes, air-dried to a constant mass, enclosed in mesh bags (1 mm) and buried in the root zone in each plot. Since the primary objective was to determine the accumulation of refractory matter, bags were retrieved after 1 year in the ground and the contents were dried (80 °C) and weighed to calculate the mass remaining.

Peat composition and geological rates of peat accumulation

Six peat cores (up to 10 m in length) were collected from Twin Cays, and a wood sample was also collected from a dead tree stump exposed at the peat surface. Cores were also collected from Cat Cay (two cores), Roatán (three cores), Guanaja (one core) and Isla San Cristóbal (two cores). Cores were extracted by hand in 50-cm sections with a Russian peat corer, which causes no vertical compaction of the sample (see Fig. S3 in Supplementary Material). The corer was carefully washed between extractions to avoid contamination. Cores were exposed in the field, photographed, sectioned (10-cm increments) and transported to the laboratory in water-tight plastic bags where they were kept refrigerated until analysis. Subsamples from every 10-cm section from each core were analysed for percentage organic content and examined under magnification to determine the proportion of mangrove roots as a component of peat. The percentage organic and mineral contents of samples were determined by loss-on-ignition. Subsamples were dried in an oven (70 °C) to constant mass, weighed into porcelain crucibles, ashed in a muffle furnace for 8 h at 400 °C and reweighed after cooling to room temperature in a desiccator. Radiocarbon dating [radiometric-standard delivery, radiometric with extended counting or accelerator mass spectrometer (AMS)] was conducted on selected peat sections, wood and shell (Beta-Analytic Radiocarbon Dating Laboratory, Miami, FL, USA). Measured radiocarbon ages were corrected using ^{13}C/^{12}C ratios and calibrated to calendar dates (Talma & Vogel, 1993; Stuiver *et al.*, 1998).

One peat core (8.3 m long) collected from an unvegetated flat in the interior of Twin Cays with stumps of mangroves, indicating dieback and no modern root production, was examined in detail to assess peat composition. A subsample of each 10-cm section was examined under magnification to identify major components of the peat (based on comparison with modern material and decomposing material from mesh bags). Seven selected sections (0.4–8.0 m) were manually sorted under magnification into four components: fine roots (≤ 2.5 mm), coarse root fragments, wood and leaf fragments (> 200 µm) and residual organic matter (≤ 200 µm).

Statistical analyses

Elevational data (surface elevation relative to the initial baseline) were averaged (*n* = 36 pins) for each RSET (= experimental unit) on each sampling date over a 3-year period. A linear model was fitted to the data for each RSET separately and the slopes of the relationship were tested. The same approach was used to analyse deposition above a marker horizon (surface accretion). The r^2 value was used to assess the linear fit to the data, and a *t*-test was used to determine whether the slope was significantly different from zero, i.e. if there was a significant change in elevation or accreted material over time. The individual slopes (*n* = 3) were used to test for treatment and zone effects as described below.

Elevational data and root accumulation, mortality and decomposition data were analysed by a simple split-plot analysis of variance (ANOVA) in which fertilizer treatment (Control, N and P) was the main plot and zone (Fringe, Transition and Interior) was the subplot (SAS, 2002). Data were transformed prior to analysis when necessary to meet variance homogeneity and normality assumptions for ANOVA. Relationships among variables were examined by correlation analysis. A step-wise
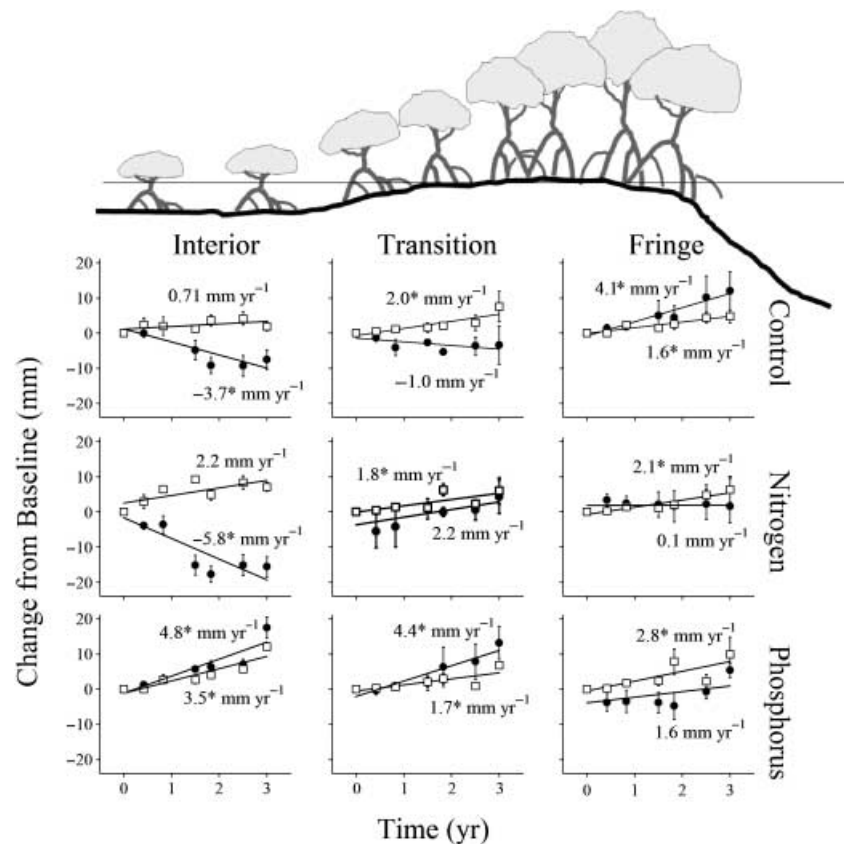
Figure 2 Elevation change (●) and surface accretion (□) across mangrove zones (Fringe, Transition, Interior) at Twin Cays, Belize and in response to nutrient treatments (Control, Nitrogen, Phosphorus); mean ± 1 SE (*n* = 3). Slopes of lines fitted to the data are shown; an asterisk indicates that the slope is significantly different from zero.

regression analysis was conducted in which the dependent variable was elevation change and the independent variables were vertical change due to surface deposition (accretion), root input and subsidence (physical compaction plus decomposition).

RESULTS AND DISCUSSION

Modern rates of accretion and elevation change

Few data exist reporting modern rates of elevation change in mangrove ecosystems, but are clearly important for understanding how such systems may respond to future sea-level rise. At Twin Cays, accretion and elevation change indicated the direction and rate of soil surface movement relative to the base of a benchmark, i.e. to the Pleistocene limestone underlying the study site (Fig. 2, Table 1). In several cases, slopes were significantly different from zero, indicating a gain or loss in elevation over time (Fig. 2). Fringe control plots with the largest trees showed an average gain in elevation of 4.1 mm year^{-1} and surface accretion of 1.6 mm year^{-1}, indicating subsurface expansion of 2.5 mm year^{-1}. In contrast, transition and interior control plots were subsiding and losing elevation at rates of −1.1 and −3.7 mm year^{-1}, respectively. These rates of accretion and elevation change are comparable with those reported for other mangrove forests (Cahoon & Lynch, 1997; Cahoon *et al.*, 2003, 2006; Krauss *et al.*, 2003; Whelan *et al.*, 2005).

Nutrient enrichment had different effects on elevation change depending on the tree zone and the nutrient added (Fig. 2, Table 1).

Compared with controls, fringe plots enriched with either N or P did not gain elevation and exhibited subsidence rather than expansion. The addition of nutrients to the transition zone caused no net change (N) or a gain (P) in elevation. The addition of N to the interior zone caused greater rates of elevational loss compared with controls, whereas the addition of P resulted in a gain in elevation. Peat expansion in P-fertilized interior plots was visually obvious and resulted in hummocks that were on average 7 cm higher than in the control plots at the end of the study. Addition of N or P thus altered vertical land building in this system, resulting in rates of change in elevation ranging from −7.7 to 8.4 mm year^{-1} across the 27 experimental plots.

These results indicate three important points: (1) modern rates of change in elevation can vary in both direction and magnitude within the same mangrove ecosystem; (2) change in elevation varies in conjunction with natural gradients in mangrove tree productivity; and (3) addition of nutrients can alter both the direction and rate of change of surface elevation. Below, we examine the relative role of surface and subsurface processes to better understand what controls elevation change in peat-forming mangrove systems.

Surface and subsurface processes controlling elevation change

Work in marshes has shown that fertilizer-induced increases in above-ground production and stem density of the marsh grass, *Spartina alterniflora*, more than doubled mineral accretion rates

Table 1 Elevation change (mm year^{-1}), surface accretion (mm year^{-1}), subsurface change (mm year^{-1}), fine and coarse root accumulation (g m^{-2} year^{-1}), annual root mortality (%) and decomposition (% mass after 1 year) of fine and coarse roots across zones (Z) and in response to fertilizer treatments (F): nitrogen (N) or phosphorus (P) addition or Control (C) applied to each transect (T). Values are the mean ± SE ($n = 3$). ANOVA F-ratios with significance indicated by: *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; ****$P \leq 0.0001$; n.s., not significant.

	Elevation change	Surface accretion	Subsurface change	Root accumulation		Root mortality	Root decomposition	
				Fine	Coarse		Fine	Coarse
Interior								
C	−3.7 ± 1.0	0.7 ± 0.3	−4.4 ± 1.1	43 ± 24	39 ± 24	0.0 ± 0.0	63 ± 5	29 ± 2
N	−5.8 ± 1.6	2.2 ± 1.2	−8.0 ± 2.7	37 ± 20	45 ± 17	17.2 ± 6.5	68 ± 4	28 ± 4
P	4.8 ± 1.0	3.5 ± 0.1	1.3 ± 0.9	339 ± 44	403 ± 69	5.1 ± 5.1	62 ± 1	24 ± 3
Transition								
C	−1.1 ± 1.5	2.0 ± 1.3	−3.1 ± 2.6	189 ± 73	205 ± 109	2.1 ± 2.1	63 ± 4	29 ± 7
N	2.2 ± 1.6	1.8 ± 0.9	0.3 ± 1.1	168 ± 42	132 ± 51	0.8 ± 0.8	63 ± 2	23 ± 1
P	4.4 ± 1.9	1.7 ± 0.3	2.7 ± 2.1	310 ± 52	194 ± 79	0.4 ± 0.4	63 ± 1	38 ± 3
Fringe								
C	4.1 ± 2.2	1.6 ± 0.7	2.4 ± 2.9	197 ± 34	328 ± 132	0.0 ± 0.0	61 ± 1	24 ± 5
N	0.1 ± 1.5	2.1 ± 1.2	−2.0 ± 1.0	164 ± 13	316 ± 25	0.5 ± 0.5	65 ± 4	32 ± 6
P	1.6 ± 0.7	2.8 ± 1.0	−1.2 ± 0.2	260 ± 51	163 ± 45	4.3 ± 4.3	62 ± 1	25 ± 4
ANOVA source:								
F	4.33(n.s.)	2.26(n.s.)	2.32*	12.4***	2.90(n.s.)	6.23*	1.51(n.s.)	0.67(n.s.)
T [F]	3.76*	0.50(n.s.)	2.47(n.s.)	1.83(n.s.)	0.58(n.s.)	0.32(n.s.)	1.16(n.s.)	0.36(n.s.)
Z	10.1**	0.08(n.s.)	5.50*	4.41*	5.73*	2.14(n.s.)	0.71(n.s.)	0.33(n.s.)
Z × F	10.1***	0.63(n.s.)	4.93**	3.95*	7.46**	2.28(n.s.)	0.64(n.s.)	0.22(n.s.)

(Morris *et al.*, 2002). Faster accretion of mineral material may be caused by the baffling effect of plant shoots (marsh) or aerial roots (mangrove) on water movement and sedimentation patterns. Spatial variation in above-ground plant structures has been correlated with sediment accretion and/or elevation change (Spenceley, 1977; Krauss *et al.*, 2003). Elevation change in the Twin Cays system, however, was not correlated with surface accretion ($r = 0.10$, $P > 0.05$). Accretion rates were also not significantly influenced by nutrient treatment or zone (Table 1). Surface deposition across most of the island consisted of algal/microbial mats and organic detritus. Carbonate sand accumulated primarily along leeward shorelines and did not contribute to surface accretion in experimental plots. Work in south-west Florida also found minimal influence of surface sedimentation/erosion processes in a riverine mangrove forest dominated by *R. mangle* (Whelan *et al.*, 2005). Instead, temporal changes in groundwater movement appeared to influence mangrove elevations through shrink–swell of peat deposits (Whelan *et al.*, 2005). Such considerations may be more important for riverine mangroves or areas with significant groundwater influence. The hydrology of the Twin Cays system is dominated by astronomical tides and has no rivers or groundwater sources of fresh water that might influence peat swelling (Wright *et al.*, 1991). In any case, such processes cannot explain the effects of fertilizer treatment on elevation change at Twin Cays.

Elevation change was significantly correlated with subsurface change ($r = 0.94$; $P < 0.0001$) at Twin Cays, indicating that below-ground processes were primarily responsible for the observed variation. Below-ground root accumulation, root mortality and root decomposition were consequently assessed to determine whether these biological processes may be influencing soil elevations here. Accumulation of root biomass varied from 82 (interior) to 525 (fringe) g m^{-2} year^{-1} across control transects (Table 1) and paralleled above-ground litterfall rates (Koltes *et al.*, 1998). The addition of P dramatically increased rates of accumulation of fine and coarse roots in transition and interior plots, but the addition of N had no effect in any forest zone. Low root accumulation in interior plots was probably due to flooding limitations on root growth (McKee, 2001, 2002). Root mortality was increased by the addition of N, and these losses may explain greater subsidence in N-fertilized plots (Table 1 and 1 d.f. contrast: t-ratio = −3.53, $P = 0.0123$). Few data exist for mangrove forests, but rates of root accumulation measured in this study are comparable with those found in Florida (McKee & Faulkner, 2000b) and Honduras (Cahoon *et al.*, 2003) using a similar in-growth method. Although the root in-growth method may over- or underestimate absolute rates of root production (due to growth into unoccupied substrate or damage to roots during installation), it provides an excellent way to compare the relative accumulation of root matter, especially in relation to change in elevation. This technique is also minimally destructive, which is essential in areas where change in elevation is to be measured.

In order for root matter to accumulate, the rate of root decomposition must be slower than the rate of root production. Mangrove root decomposition was very slow, with 30 to 60% of the original mass remaining after 1 year, but was unaffected by external nutrient treatment (Table 1). Fine roots were particularly resistant to decay (99% turnover time averaging 10 years), as
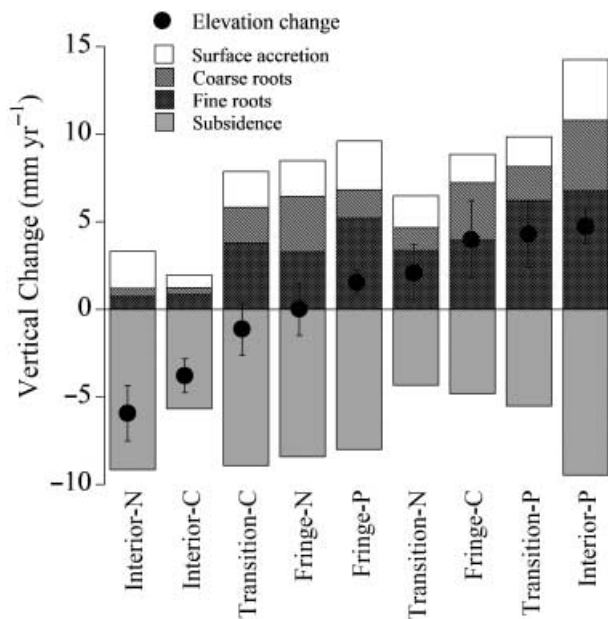
Figure 3 Variation in surface elevation change (●) relative to vertical change attributable to surface accretion, fine and coarse root production, and shallow subsidence (physical compaction and decomposition) across mangrove zones and nutrient treatments at Twin Cays, Belize; mean ± 1 SE ($n = 3$); SE not plotted on stacked bars for clarity.

reported previously for Belizean (Middleton & McKee, 2001) and Australian (van der Valk & Attiwill, 1984) mangroves. Slow decomposition and lack of response to external nutrient treatment probably reflected the inability of the microbial community to decompose refractory root tissues under flooded, anaerobic conditions (Middleton & McKee, 2001). Change in elevation was significantly correlated with fine ($r = 0.72$, $P < 0.0001$) and coarse ($r = 0.41$, $P = 0.03$) root accumulation, but was not correlated with root mortality ($r = -0.28$, $P > 0.05$) or root decomposition [$r = -0.02$ (coarse) or -0.15 (fine), $P > 0.05$]. Thus, change in elevation of these intertidal islands varied primarily with inputs of mangrove roots, which resist microbial decay due to their refractory nature and anaerobic conditions limiting decomposers.

Vertical change due to root volume inputs varied from 1.2 to 10.8 mm year^{-1} (Fig. 3). Surface deposition above a marker horizon, in comparison, ranged from 0.7 to 3.5 mm year^{-1} (Fig. 3). Loss of elevation to decomposition and physical compaction was calculated by subtraction of the root input from measured subsurface change. These processes, collectively termed 'shallow subsidence', caused losses ranging from -4.8 to -9.5 mm year^{-1} (Fig. 3). A step-wise regression analysis showed that fine root input explained 42% of variation in elevation change ($P \leq 0.001$), with subsidence, coarse roots and surface accretion explaining an additional 36, 10 and 2% of variation ($P \leq 0.05$). Thus, annual inputs of fine roots contributed substantially to soil volume and explained a significant amount of the variation in elevation change.

These findings indicate that modern rates of accretion and elevation change measured in Belizean mangrove forests were influenced by the deposition and accumulation of refractory mangrove roots. They further suggest that mangrove peat accumulation has been the primary process allowing this island system and similar peat-forming systems to keep pace with the rise in sea level over the Holocene. To examine these points further, we looked at the peat record at several sites in the Caribbean dominated by mangrove vegetation.

Peat stratigraphy and geological accretion

Cores collected from multiple sites on the Caribbean coasts of Belize, Honduras and Panama showed that mangrove systems in these areas accumulate deep deposits of organic material (see Fig. S4 in Supplementary Material for a graphic log of cores). Peat thickness varied across study sites: 0.4 m (Guanaja, Honduras), 1.8 m (Roatán, Honduras), 2.8 m (Isla San Cristobal, Panama), 0.9 m (Cat Cay, Belize) and 10.0 m (Twin Cays, Belize). Loss-on-ignition showed that the organic content of these deposits averaged 65%. In some cases, deposits of marine sand (from calcareous algae) were found beneath the peat layer or between two peat layers. However, continuous deposits of peat composed of mangrove roots indicated that all of these systems were built primarily through organic accumulation, rather than physical processes of mineral sedimentation. The depth range of mangrove peat found in these sites is comparable to that reported in other locations throughout the Caribbean region (Ellison, 1993; Macintyre et al., 1995, 2004; McKee & Faulkner, 2000a; Islebe & Sanchez, 2002; Gischler, 2003; Toscano & Macintyre, 2003; Ramcharan, 2004; Whelan et al., 2005). In particular, the peat deposits at Twin Cays are some of the thickest and oldest on record in the Western Hemisphere (Macintyre et al., 2004), which identifies this location as an important peat-forming system for the Caribbean region. Twin Cays has built up vertically by the accumulation of mangrove organic matter throughout its Holocene history, as reported previously (Cameron & Palmer, 1995; Macintyre et al., 2004). The entire profile of an 8.3-m long core (REU) was composed of mangrove (predominantly R. mangle) fine roots (40 ± 6%), coarse root fragments (9 ± 3%), wood and leaf fragments (22 ± 5%) and organic particles less than 200 μm (fine root fragments and microbial mat residue) (27 ± 6%). Cores from other sites at Twin Cays showed continuous peat deposits up to 10 m in thickness and were similarly composed of refractory mangrove roots and other organic particles.

Radiocarbon dating indicated that mangroves established at Twin Cays between 7000 and 8000 cal BP [cal BP = calendar years before present (1950); see Table 2 for calibration details) and that peat accumulation closely followed rates of sea-level rise (SLR) calculated for the western Atlantic (Fig. 4), based on a combined coral–mangrove peat record (Toscano & Macintyre, 2003). Mangroves did not exist at Twin Cays when SLR rates exceeded 5 mm year^{-1}, but appeared when rates slowed to about 3.5 mm year^{-1}. Once established, mangroves accumulated peat at rates of 3 mm year^{-1} (7600–7200 cal BP), 1.3 mm year^{-1} (7200–5500 cal BP) and 1.0 mm year^{-1} (5500–500 cal BP), showing that peat formation

Table 2 Calibration of radiocarbon age of mangrove wood (exposed tree stump), a shell and peat samples [relative to mean sea level (MSL)] to calendar years. Samples are from Twin Cays (TC) or Cat Cay (CC), Belize; Roatan (R) or Guanaja (G), Honduras; and Isla San Cristobal, Panama (PAN). A date (± 1 sigma statistic) or an age range (± 2 sigma statistic) is given; cal BP = calendar years before present (dates are referenced to AD 1950).

Sample number	Measured radiocarbon age (yr BP)	$^{13}C/^{12}C$ ratio (‰)	Conventional radiocarbon age (yr BP)	Calendar age (cal BP)
Wood				
TC-SSA (−0.4 m)	150 ± 50	−24.6	160 ± 50	300–0
Peat				
TC-REU 1-8 (−1.3 m)	1320 ± 40	−25.9	1410 ± 40	1360–1270
TC-REU 1-32 (−3.7 m)	3510 ± 40	−23.6	3530 ± 40	3900–3700
TC-REU 1-64 (−6.9 m)	6010 ± 40	−26.8	5980 ± 40	6900–6710
TC-REU 1-82 (−8.7 m)	6630 ± 40	−26.5	6610 ± 40	7580–7430
TC3-36B (−3.9 m)	4790 ± 80	−27.2	4750 ± 80	5620–5310
TC3-64B (−6.7 m)	6280 ± 40	−26.8	6250 ± 40	7260–7020
TC3-80B (−8.3 m)	6820 ± 70	−26.5	6790 ± 70	7740–7560
TC5-8B (−0.6 m)	430 ± 40	−27.2	390 ± 40	520–420
TC5-35B (−3.3 m)	4020 ± 100	−25.3	4010 ± 100	4830–4220
TC5-65B (−6.3 m)	5990 ± 40	−28.3	5940 ± 40	6860–6670
TC5-100B (−9.8 m)	6690 ± 90	−27.0	6660 ± 90	7670–7420
TC8-14B (−1.6 m)	2500 ± 90	−26.0	2480 ± 90	2760–2340
TC8-26B (−2.8 m)	2370 ± 60	−24.1	2390 ± 60	2720–2330
TC8-85B (−8.7 m)	6000 ± 40	−27.7	5960 ± 40	6880–6680
TC9-6B (−0.5 m)	650 ± 40	−26.4	630 ± 40	660–540
TC9-19 B (−1.8 m)	2850 ± 40	−24.4	2860 ± 40	3080–2870
CC10-7 (−0.6 m)	500 ± 40	−26.6	470 ± 40	530–500
CLI-1-9,10 (−1.0 m)	290 ± 60	−22.9	330 ± 60	510–290
CMS-2-10,11 (−0.9 m)	460 ± 50	−25.6	450 ± 50	540–440
CMI-4-18,20 (−1.7 m)	1520 ± 70	−24.7	1530 ± 70	1550–1300
PAN-5-29 (−3.0 m)	2610 ± 50	−26.6	2580 ± 50	2630–2500
PAN8-14 (−1.5 m)	700 ± 50	−26.5	670 ± 50	680–550
Shell				
CHI-4-20 (−1.9 m)	1170 ± 70	+3.2	1640 ± 70	1310–1050

closely tracked sea-level rise. Basal peat dates from Roatán, Honduras and Isla San Cristóbal, Panama indicated that mangroves established at those sites within the past 2000–3000 years when SLR was *c.* 1 mm year^{-1}. Mangroves became established at sampling sites at Cat Cay, Belize and Guanaja, Honduras within the past 500–600 years.

The predominance of mangrove root matter throughout most of these peat cores is consistent with previous work (McKee & Faulkner, 2000a; Middleton & McKee, 2001) as well as with data linking change in elevation with accumulation of mangrove roots (this study). Fossil fine roots of *R. mangle* were well preserved and often indistinguishable from modern fine roots (see Fig. S3 in Supplementary Material), in agreement with decomposition results indicating their refractory nature (Table 1). The peat record thus shows a remarkable history of island development through the slow accumulation of mangrove roots in concert with changing sea level. Calibrated peat data from multiple geographical locations further show that peat formation is an important process in other Caribbean mangrove systems, allowing them to keep up with SLR (Fig. 4 & Fig. S4 in Supplementary Material).

Previous workers have reported peat accretion rates of *c.* 1.1 mm year^{-1} for mangrove forests (Ellison & Stoddart, 1991; Ellison, 1993; Parkinson *et al.*, 1994; Cahoon & Lynch, 1997). Such rates were calculated based on radiocarbon dates of basal peat divided by the depth of the sample. However, these rates represent the average for the entire peat record and do not indicate variation during different time periods. Most importantly, geological accretion rates reflect the net result of peat building interspersed with intervals of no elevation gain or even loss and consequently do not reveal precise patterns of change in the peat surface over time. Modern measurements of elevation change across Twin Cays showed that rapid vertical development occurs where mangroves are more productive, but elevation losses occur where plant growth is low. These modern measurements suggest that peat development has varied in a similar pattern over the Holocene as fluctuating environmental conditions affected mangrove growth. Past disturbance events may have interrupted peat building in mangrove systems. For example, peat collapse (−11 mm year^{-1}) has been documented in a basin mangrove forest in Honduras that suffered total mortality after Hurricane Mitch (Cahoon *et al.*, 2003). Although the cause of dieback at one of the Belize coring sites (REU) is unknown, the 0.4–0.5 m lower elevation relative to surrounding vegetated areas indicates that the area has been sinking for some time. This elevation differential divided by a rate of loss of elevation of −2.1 mm year^{-1} (measured nearby) suggests that the site has been losing elevation for 190–240 years, which agrees with a modern date for *Avicennia germinans*
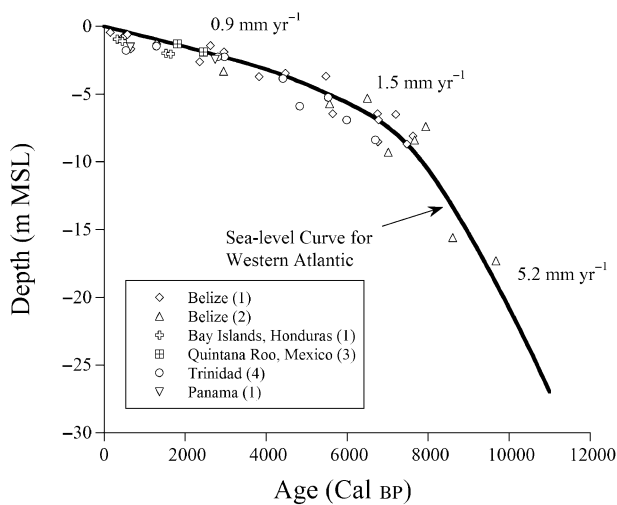
Figure 4 Time–depth plot of mangrove peat samples in relation to a sea-level curve for the western Atlantic. Data are from Twin Cays and Cat Cay, Belize; the Bay Islands of Roatán and Guanaja, Honduras; and Isla San Cristóbal, Panama (*1*) (this study); Lighthouse Reef, Turneffe Atoll and Glover's Reef, Belize (*2*) (Gischler, 2003); Quintana Roo, Mexico (*3*) (Islebe & Sanchez, 2002); and Trinidad (*4*) (Ramcharan, 2004). ^{14}C dates were calibrated to calendar years [cal BP = calendar years before present (1950)] as reported in the referenced sources. The sea-level curve is based on a separate set of calibrated mangrove peat and coral (*Acropora palmata*) dates from multiple sites (Antigua, Bahamas, Belize, Florida, Jamaica, Martinique, Panama, Puerto Rico, St Croix) (Table 4 in Toscano & Macintyre, 2003). Rates of SLR from three periods are indicated on the plot and show an initially rapid rate of 5.2 mm year^{-1} (10,600–7700 cal BP), decreasing to 1.47 mm year^{-1} (7700–2000 cal BP) and 0.93 mm year^{-1} (2000–400 cal BP).

tree stumps (< 300 cal BP). Revegetation of dieback areas with mangroves can occur (K.L.M. and I.C.F., personal observation), leading to new peat accumulation. Consequently, it is likely that these islands have undergone cycles of peat building and sinking as mangrove vegetation flourished, died back and recolonized.

These findings link the modern measurements of change in elevation and associated controls at Twin Cays to geological rates of accretion in this and other Caribbean mangrove systems. Thus, there has been a tight coupling between peat building in Caribbean mangroves and sea-level rise over the Holocene. The mechanism is likely to be related to feedback processes between mangrove root accumulation and elevation (presumably through flooding effects on production–decomposition processes).

Response to sea-level rise

Although mangrove systems at Twin Cays and other Caribbean locations have persisted for thousands of years, their continued existence depends on future rates of relative SLR. To avoid submergence, vertical building of these mangroves must equal relative SLR (eustatic rise plus local subsidence). Global mean rates of eustatic SLR, currently estimated at 1.5–2.0 mm year^{-1}, are predicted to increase with global warming over the next century,

with most model scenarios projecting rates of 3–5 mm year^{-1} (IPCC, 2001). Previous work has suggested future submergence of mangroves in the wider Caribbean region based on historical (caesium dating) and geological (radiocarbon dating) rates of peat accretion (Ellison & Stoddart, 1991; Parkinson *et al.*, 1994). As discussed above, rates of peat accretion may underestimate the potential of a mangrove system to build vertically, since they average over the entire record. Modern measurements of elevation change may overestimate it due to the short-term record.

Another approach is to compare rates of surface plus subsurface (root) accretion to estimate potential rates of vertical building with submergence rates. Since the Caribbean has a minimal degree of glacial isostatic adjustment and is thought to be tectonically relatively stable (Toscano & Macintyre, 2003), shallow subsidence plus eustatic SLR should give a minimum estimate of submergence. Assuming negligible deep subsidence and no root input, the submergence rate at Twin Cays is estimated to be 7–8.5 mm year^{-1} (eustatic SLR = 1.5–2.0 mm year^{-1}). Rates of surface plus subsurface (root) accretion in fringe, transition and interior zones at Twin Cays were 10.4, 6.3 and 2.0 mm year^{-1}. This comparison shows that transition and interior zones with low root production could not keep up with current submergence rates, consistent with observations that interior stands with stunted trees are flooded most of the time and interior areas with no vegetation are perennially flooded. However, fringe mangroves have kept up and could accommodate eustatic SLR rates of 4 mm year^{-1} if current accretion rates were maintained. If eustatic rates exceed 5 mm year^{-1} then these mangrove islands would not be likely to persist, assuming that all other conditions remain unchanged.

In addition to vertical building, mangrove forests may move laterally in response to sea-level changes (Snedaker, 1995). The landward retreat of mangroves in some locations may be limited because of natural and human barriers, but mangrove islands may expand and contract with changing conditions (McKee & Faulkner, 2000a). Lateral movement of these mangrove islands is evidenced by peat deposits offshore (Macintyre *et al.*, 1995, 2004) as well as by sand lenses in peat cores, indicating past shorelines. Dates of peat above and below sand lenses at Twin Cays show that sand was not deposited in a storm event, but was instead accumulated over thousands of years. For example, a transgression of lagoonal sand occurred 5000–6000 cal BP on the eastern island of Twin Cays; mangroves reoccupied these sites about 2000 cal BP and peat building resumed (see core TC-7, Fig. S4 in Supplementary Material).

CONCLUSIONS

The importance of plant production–decomposition processes in peat-forming systems is widely recognized and has been extensively studied. Early work described the role of mangroves in soil accretion and noted the contribution of mangrove roots to peat formation (e.g. Bird, 1971; Woodroffe, 1983; Parkinson *et al.*, 1994; Cahoon & Lynch, 1997; McKee & Faulkner, 2000a). The indirect effects of plants on sedimentation in mangrove and marsh systems have also been demonstrated in a few cases

(Bird, 1971; Spenceley, 1977; Morris *et al.*, 2002; Krauss *et al.*, 2003), presumably through the physical effects of vegetation on the trapping of mineral sediment. However, to our knowledge our work is the first to experimentally demonstrate *direct* biotic contributions to elevation change in a coastal ecosystem and to identify the biological process involved. We further linked modern elevation change due to root accumulation to past peat formation and the response of Caribbean mangrove systems to rising sea levels over the Holocene. These data provide direct evidence that mangroves are an integral and active component of the coastal landscape and thus represent a natural defence against submergence and wetland loss due to sea-level rise. Natural or anthropogenic disturbances that alter root dynamics may consequently impair the ability of such systems to accommodate sea-level rise.

The Caribbean region is an important reservoir of mangrove peat, with deposits up to 10 m thick. Belizean mangrove islands, including the Twin Cays archipelago, have formed some of the thickest peat deposits reported to date. Such peat-forming mangrove systems are particularly vulnerable to human interference. Their management consequently requires different strategies from those used in other sedimentary settings. Our work shows that removal of mangrove vegetation would stop soil accretion, while decomposition, physical compaction and erosion processes continue, ultimately leading to submergence and land loss. Other types of mangroves, e.g. riverine systems, may be better buffered against SLR due to high rates of mineral accretion. However, mangrove roots are important even in those settings to stabilize deposited sediment and prevent erosion (McKee & McGinnis, 2002).

Mangrove ecosystems are additionally subject to nutrient overloading, which has numerous and complex effects on structure and function (McKee *et al.*, 2002; Feller *et al.*, 2003a,b; Lovelock *et al.*, 2004). A change in the nutrient regime of peat-forming mangroves may alter the balance among biotic processes controlling the accumulation of organic matter and soil elevations relative to sea level, as demonstrated at Twin Cays. Even though nutrients temporarily enhanced peat formation by interior mangroves, eutrophication may have unforeseen consequences for the functioning and long-term stability of these biogenic systems. Given these insights, the challenge now is to incorporate this information into coastal management plans to minimize loss of ecosystem services, which mangroves and other coastal wetlands provide.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Maps of the study areas in Belize, Honduras and Panama.

Figure S2 Photographs of the study site at Twin Cays, Belize.

Figure S3 Photographs of a peat core and modern and fossil mangrove roots.

Figure S4 Graphic summary of dated peat cores collected in Belize, Honduras and Panama.

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