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Mangrove Peat Collapse Following Mass Tree Mortality: Implications for Forest Recovery from Hurricane Mitch

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Mass tree mortality leads to mangrove peat collapse at Bay Islands, Honduras after Hurricane Mitch

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Summary

1 We measured sediment elevation and accretion dynamics in mangrove forests on the islands of Guanaja and Roatan, Honduras, impacted by Hurricane Mitch in 1998 to determine if collapse of underlying peat was occurring as a result of mass tree mortality. Little is known about the balance between production and decomposition of soil organic matter in the maintenance of sediment elevation of mangrove forests with biogenic soils.

2 Sediment elevation change measured with the rod surface elevation table from 18 months to 33 months after the storm differed significantly among low, medium and high wind impact sites. Mangrove forests suffering minimal to partial mortality gained elevation at a rate (5 mm year^{-1}) greater than vertical accretion (2 mm year^{-1}) measured from artificial soil marker horizons, suggesting that root production contributed to sediment elevation. Basin forests that suffered mass tree mortality experienced peat collapse of about 11 mm year^{-1} as a result of decomposition of dead root material and sediment compaction. Low soil shear strength and lack of root growth accompanied elevation decreases.

3 Model simulations using the Relative Elevation Model indicate that peat collapse in the high impact basin mangrove forest would be 37 mm year^{-1} for the 2 years immediately after the storm, as root material decomposed. In the absence of renewed root growth, the model predicts that peat collapse will continue for at least 8 more years at a rate (7 mm year^{-1}) similar to that measured (11 mm year^{-1}).

4 Mass tree mortality caused rapid elevation loss. Few trees survived and recovery of the high impact forest will thus depend primarily on seedling recruitment. Because seedling establishment is controlled in large part by sediment elevation in relation to tide height, continued peat collapse could further impair recovery rates.

Key-words: Mangrove forest, rod surface elevation table, sediment elevation, subsidence, vertical accretion

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Introduction

For some mangrove forests in the Caribbean region, such as those located on low oceanic islands remote from continental sources of sediment, soil development occurs by the formation of peat (Cameron & Palmer 1995; Macintyre *et al*. 1995) that is composed primarily of mangrove roots (Woodroffe 1983; Cameron & Palmer 1995; McKee & Faulkner 2000; Middleton & McKee 2001). Soil build-up in these forests will occur as long as root production exceeds organic matter decomposition and thick mangrove peat can develop when sediment elevation continues to keep pace with local sea-level rise (e.g. Tobacco Range, Belize; Macintyre *et al*. 1995). Thus their long-term stability depends on sustained favourable conditions for root production and organic matter accumulation,

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but little is known about the balance between production and decomposition of soil organic matter in the maintenance of sediment elevation, or about the impact of tree mortality on sediment elevation dynamics.

Given the frequent hurricane activity of the Wider Caribbean Region (Reading 1990) and the tropical latitudes in general, and recent climate models that predict an increase in hurricane intensity of 5–10% (Giorgi *et al*. 2001), hurricanes can be forceful agents for change in mangrove ecosystems (Lugo 2000). Powerful storms have caused mass mortality of at least 10 Caribbean mangrove forests during the past 50 years (Jimenez *et al*. 1985; Armentano *et al*. 1995). The consequent cessation of root production should lead to a decrease in sediment elevation as decomposition of soil organic matter continues. Peat collapse should continue until such time as the rate of new root production from surviving mangrove trees and new recruits (propagules) once again exceeds the rate of peat decomposition. Despite a lack of quantitative empirical evidence that peat collapse occurs, Wanless *et al*. (1995; p. 125) hypothesized that peat collapse was responsible, in part, for the conversion of dead black mangrove forests in south-west Florida, USA, to mudflats after the Labor Day Hurricane in 1935 and Hurricane Donna in 1960. In the 2 years after Hurricane Andrew, H.R. Wanless (pers. comm.) observed a 20–30 mm year^{-1} decrease in sediment elevation in mangrove forests in south-west Florida killed by the storm. Sherman *et al*. (2000) attributed increased flooding in lightning gaps to collapse of the dense root mat. Similarly, Lugo (1997) attributed increased water depths in forests where trees had been removed to oxidation of the peat. Peat collapse could influence forest recovery rates by its effect on the establishment of new seedlings, which is controlled in large part by sediment elevation in relation to tide height.

We measured sediment elevation and accretion dynamics in mangrove forests of the Bay Islands, Honduras, impacted by Hurricane Mitch in 1998, where tree mortality ranged from negligible to *c*. 97% (Lebigre *et al*. 2000), to determine if peat collapse was occurring. Forest structure changes, relative rates of root production, and soil shear strength were also determined.

Study sites

The Bay Islands of Honduras are located between 30 km and 50 km to the north of the Caribbean coast of Honduras (Fig. 1). Guanaja and the neighbouring island of Roatan are the two most oceanic of the islands, receiving virtually no mineral sediment from the mainland. Roatan, the largest of the islands (133 km^2 including the eastward extensions of Santa Elena and Barbareta), is a long, narrow ridge orientated roughly east–west, with a maximum height above mean sea level of 233 m. Guanaja, 30 km to the west of Roatan, is a smaller island (57 km^2) with more pronounced relief (maximum height above mean sea level of 415 m). The climate is humid tropical with average annual rainfall between 2200 mm and 2500 mm and an average temperature of 27.6 °C.

Hurricane Mitch passed very near Guanaja and approximately 40 km to the east of Roatan as a category 4 hurricane (Guiney & Lawrence 1999) with estimated maximum surface winds of 240 km h^{-1} (NOAA, http://www.aoml.noaa.gov/hrd/Storm_pages/mitch 1998/wind.html) (Fig. 1). As the storm approached Guanaja, its forward progress slowed such that the

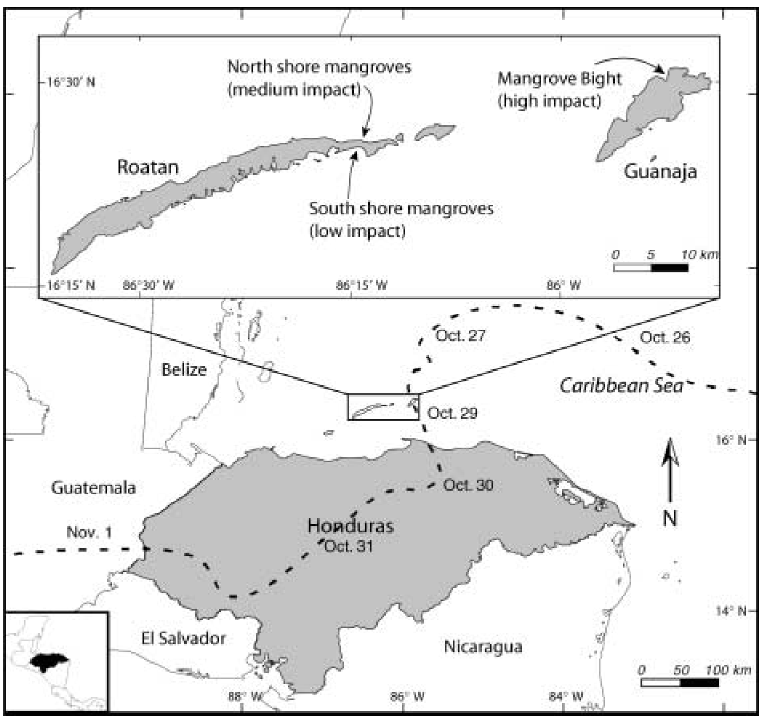

Fig. 1 Map of mangrove forest study sites in the Bay Islands, Honduras. Dashed line indicates the track of Hurricane Mitch.

Fig. 2 Photographs of dead forest at Mangrove Bight, Guanaja. Photos were taken 15 months after Hurricane Mitch (January 2000). Top panel: aerial view of Mangrove Bight mangroves. Live upland vegetation is indicated in darker shades. Bottom panel: close up view of dead mangroves.

island was exposed to hurricane force winds from 27 October to 29 October1998. Computer simulation models predicted maximum sustained north-west winds of 260 km h^{-1} at Mangrove Bight on the north shore of Guanaja (Doyle *et al*. 2003). The northern shoreline of the island of Roatan was directly exposed to on-shore tidal surge and storm winds simulated at 188 km h^{-1} (Doyle *et al*. 2003). We made an initial field reconnaissance to assess damage to the mangrove forests on Guanaja and Roatan in August 1999.

Mangrove forests cover the low-lying margins of Guanaja, such as Mangrove Bight and North-east Bight on the north shore (*c.* 190 ha). The red mangrove, *Rhizophora mangle* L. is the dominant here, with some black mangrove (*Avicennia germinans* (L.) Stearn) and lesser amounts of white mangrove (*Laguncularia racemosa* (L.) Gaertn.f), and buttonwood (*Conocarpus erectus* L.) also present, mostly in the basin forest. The two days of exposure to hurricane force winds caused nearly complete defoliation of the mangrove forests (Lebigre, J.M., Portillo, P. & Thompson, W., 2000, unpublished data), and the taller trees were either broken or uprooted (Fig. 2) and mortality was compounded by a tidal surge and storm waves that flooded low-lying areas. Prior to Hurricane Mitch, Guanaja had *c.* 311 ha of mangrove forests of which only 11 ha (3%) survived (Lebigre, J.M., Portillo, P. & Thompson, W. 2000, unpublished data). Surviving mangroves included a hydrologically isolated patch of red mangroves on the south-western end of the island (near the airport) about 10 km from Mangrove Bight and scattered buttonwood trees in basin forests. There was little or no evidence of sediment from either marine or terrigenous sources, apart from a 2-cm thick deposit of marl and calcium carbonate chips in a limited area of the fringe forest.

On Roatan, the largest tract of mangroves (*c.* 400 ha) lies on the eastern extension of the island (Fig. 1). The forest is dominated by red mangrove, although some basin forests have mixed red and black mangrove stands as well as locally dense populations of black mangrove (especially on the northern shore). White mangroves are also found in the basin forest, as are scattered individuals of buttonwood. Most mangroves on Roatan survived the combination of strong winds and tidal inundation associated with Hurricane Mitch, including the fringe forest on the north shore and the mangroves located on the more protected south shore where no wind damage was observed. However, extensive areas of the basin black mangrove forest on the north shore were killed by defoliation and toppling of trees. A narrow, shallow ridge of marl and calcareous algal chips located between the red mangrove fringe and the black mangrove basin forest on the north shore was apparently deposited during the storm. We observed 2–4 cm thick deposits of marl and calcium carbonate sediments throughout the fringe and basin forests on the north shore. There were no recent storm deposits in the mangrove forest on the southern shore.

Materials and methods

SAMPLING DESIGN

Mangrove forests were chosen to represent low, medium and high levels of wind impact (Fig. 1) with both fringe and basin forests sampled at each site. The medium impact basin plots on the north shore of Roatan were located in the ecotone between the dead *Avicennia* zone and the interior basin forest. Three replicate plots were randomly established in January 2000 within each impact × tidal zone combination to give 18 permanent sampling plots.

SEDIMENT ELEVATION MEASUREMENTS

In each plot, a single rod surface elevation table (RSET; Cahoon *et al.* 2002a) station was established in spring 2000 to monitor changes in sediment elevation over time (Fig. 3). The RSET works on the same principle as

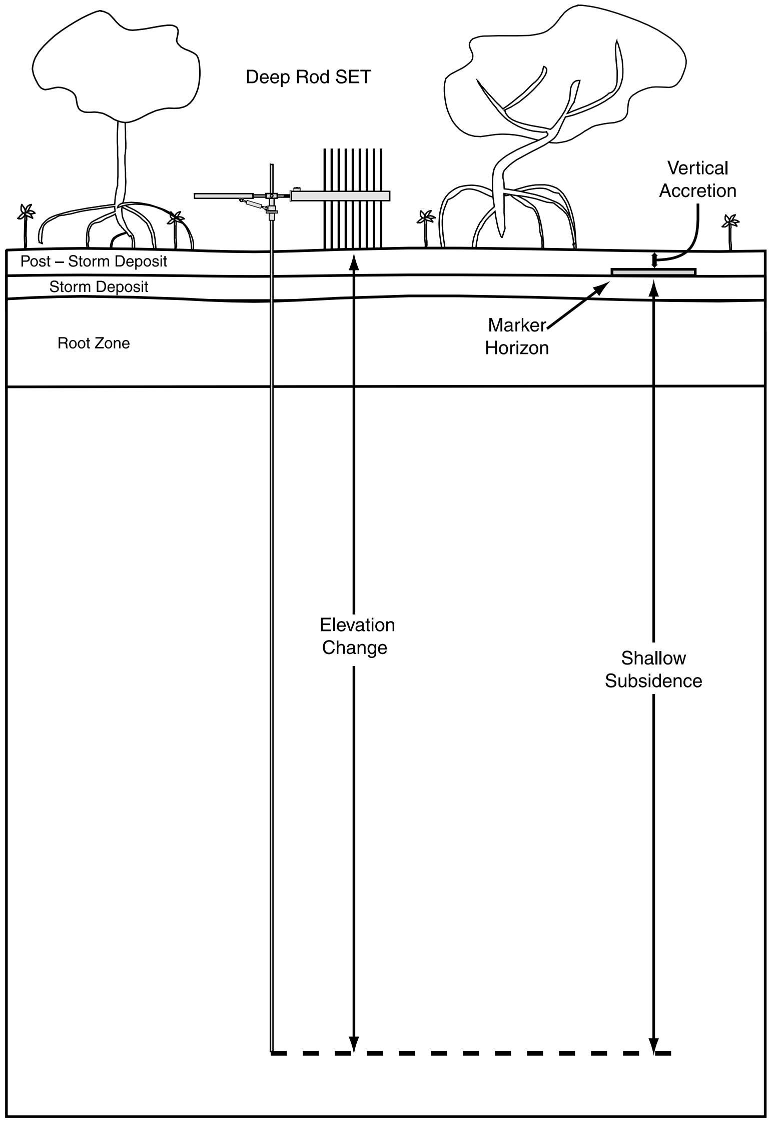

Fig. 3 A conceptual diagram (not to scale) showing that portion of the sediment profile measured by the Rod Surface Elevation Table and the marker horizon.

the surface elevation table (SET) (Cahoon *et al.* 2002b) used to measure changes in sediment elevation in mangrove forests in Florida, USA (Cahoon & Lynch 1997). Each benchmark for the RSET was constructed from stainless steel survey benchmark rods (in 1.2 m sections) that were sequentially inserted into the sediment by using a hand-held pile driver until the benchmark stopped moving. The benchmarks were driven to depths ranging from 4.3 m to 11.9 m. The RSET measures sediment elevation at eight positions around the benchmark. To avoid disturbing the sediment at measured positions, only five positions corresponding to a semicircle in front of a path of approach were sampled. After carefully levelling the RSET at each position, each of nine fibreglass pins was carefully lowered from the horizontal arm until it just touched the sediment surface, which was defined as the uppermost layer of material that was visibly incorporated into the sediment matrix. Litter not yet part of this matrix was moved aside to expose the underlying sediment surface and replaced after measurements were taken. Sediment elevation corresponded to the height of each pin remaining above the plane of the RSET horizontal arm.

SURFACE SEDIMENT ACCRETION MEASUREMENTS

The RSET measures all processes affecting sediment elevation over the depth of the rod benchmark. To separate below-ground processes (e.g. compaction, decomposition, root production and shrink/swell from water flux) from surface processes of accretion and erosion, artificial soil marker horizon plots were established in the vicinity of each RSET station (Fig. 3) (Cahoon *et al.* 1995). Three replicate 0.25 m^2 markers (local beach sand) were laid at the same time that the baseline RSET readings were taken (4–7 May 2000). Surface sediment accretion was measured from short cores collected from each marker horizon plot. Multiple measurements of depth from the sediment surface to the marker horizon were made within each core. As with the RSET, any material not yet incorporated into the sediment matrix was not considered as the sediment surface. The number of cores in which no marker horizon was recovered was recorded, and generally only one core was measured per horizon per sampling. RSET stations and marker horizons were read in May and August 2000 and January, April and August 2001. Shallow subsidence, or the influence of subsurface processes on sediment elevation, was calculated as surface sediment accretion minus elevation change (Cahoon *et al.* 1995).

FOREST STRUCTURE ASSESSMENT

Mangrove forest structure characteristics were obtained through a census of live and dead trees, recording mangrove species and trunk diameter, as well as seedlings and propagules within randomly chosen, marked 5 × 10 m quadrats, one within each of the 18 plots, conducted in January 2000 and 2001. Separate diameters were recorded for each main vertical trunk in multiple-trunk individuals (e.g. shoreline red mangrove). Diameters were recorded at the greater of either breast height (1.5 m), or above the highest prop root (in the case of the red mangrove). Tree density per plot was estimated for six age and diameter size classes: seedlings, < 2 cm, 2–4.9 cm, 5–9.9 cm, 10–19.9 cm and 20+ cm. Three additional plots were surveyed within the dead black mangrove zone along the north shore of Roatan in January 2001.

SOIL STRENGTH

Soil strength, defined as the torque required to shear or to deform the soil, was measured with a Torvane device (H-4212 1, Humbolt Manufacturing Company, Durham Geo-Enterprises, Inc.). Soil cores (12.5 cm diameter × 30 cm deep, 6 per site) were collected in January 2001 and cut in half vertically, creating the flat surface needed for measurement. Measurements were taken at the surface and at 5, 15 and 25 cm and the three subsurface values were averaged per core.

ROOT PRODUCTION

Relative root production rate (g m^2 $year^{-1}$) was determined using the implanted mass technique (Gallagher *et al.* 1984). A total of six soil cores (7.3 cm diameter × 30 cm deep) were removed from sites within each zone by impact combination with a coring device, and in-growth bags containing root-free, organic material were inserted in January 2000. The in-growth bags were constructed of loose nylon mesh (3 mm^2, J & M Industries, Ponchatoula, LA) and filled with milled sphagnum peat that approximated the bulk density and organic matter content of native mangrove peat. Native mangrove peat could not be used because it was primarily composed of fine roots, which would have been indistinguishable from in-grown roots. Bags were positioned with the tops level with the soil surface and tied with monofilament to a nearby prop root and exhumed in January 2001 with a 12.5-cm diameter corer. Soil and roots surrounding the excavated bags were carefully severed at the bag surface before transferring the contents to plastic bags for processing within 48 h of collection.

In-grown root material was washed and separated over a sieve (1 mm^2) with freshwater. Large, non-root particles were separated by hand, and roots and root fragments were separated by flotation. Roots were separated into two size categories (coarse, > 2 mm diameter; fine, < 2 mm diameter). Total recovery of root material was about 88% (based on subsamples processed to completion under magnification in the laboratory). Recovery of root fragments from bags deployed at the high impact site (i.e. where total mortality occurred) showed that dead roots could be physically transported into in-growth bags from the surrounding peat. Although these dead roots were not quantified, some of the un-recovered root fraction in other samples is probably attributable to this extraneous source. Root samples were air-dried in the field and later oven-dried in the laboratory at 70 °C and weighed.

STATISTICAL ANALYSES

Sediment accretion and elevation data resulted from a repeated measures, completely randomized treatment design, with the impact-by-zone treatment measured sequentially over time. The error structure was nested (pins within positions within plots, and cores within marker horizons within plots), and plots were the experimental unit for the treatment factor. Sediment elevation (RSET) and vertical accretion (marker horizon) data were analysed separately, although identical models were used. RSET data were calculated as cumulative change for each pin from the baseline reading. Average cumulative change was then calculated over the nine pins, then over the five positions within each RSET station. Marker horizon data were averaged per core, then per horizon and per plot. One sampling station (RSET with corresponding marker horizons) was lost in the medium impact basin before measurements could be taken, which resulted in an unbalanced design. Durbin-Watson tests (testing for significant first-order serial correlation) were non-significant, and analysis of covariance was therefore used, with time as the covariate (SAS Proc Reg, SAS©Version 8; SAS 1999). The data sets included zeros corresponding to the baseline readings or initial deployment of the marker horizons, and the models forced the intercept through the origin. Different slopes therefore corresponded to the different impact by zone treatment combinations. A stepwise regression procedure was invoked to select for the most efficient model, which grouped similar treatment levels according to their trends over time.

Mangrove mortality recorded in January 2000 was modelled as a logistic function of impact level, zone, and their interactions (Proc Logistic, SAS© Version 8; SAS 1999). Separate models considered all tree diameter size-classes, or only adult trees.

Soil strength and root production data were analysed as a 3 × 2 factorial design, where impact level and spatial position were grouping factors (two-way ANOVA; JMP© Version 4.0.2; SAS 2000). Data were log ($\ln(x + 1)$) or inverse ($1/(x + 1)$) transformed prior to analysis where necessary to reduce heterogeneity of variance and to reduce deviations from normality. Comparisons after the test among treatments were described with a Tukey HSD test or 1 degree of freedom contrasts for single comparisons of interest between two effects.

RELATIVE ELEVATION MODEL

The empirical elevation and accretion data sets described above incorporate not only the processes of sediment deposition and erosion, root growth, compaction and decomposition, but also feedback mechanisms on the processes themselves (e.g. a change in elevation alters flooding patterns that in turn affect rates of sediment deposition, decomposition and autogenic primary production). The short time scale (15 months) of these data sets, however, limits their usefulness in predicting the future relationship between sediment elevation and sea level on a longer time scale (e.g. decades) because compaction, decomposition and the feedback mechanisms are non-linear processes that change with time and elevation. For this reason, we used a previously published wetland sediment development model (Morris & Bowden 1986; Callaway *et al*. 1996; Rybczyk *et al*. 1998; Chen & Twilley 1999; Day *et al*. 1999; Rybczyk & Cahoon 2002) to examine changes in sediment elevation over longer time scales.

The model utilizes a cohort approach (tracking discrete packages of sediments through depth and time) to simulate sediment dynamics (organic and mineral matter accretion, decomposition, compaction and below-ground productivity). These dynamics produce model-generated changes in sediment characteristics including bulk density, organic matter volume and mass, mineral matter volume and mass and pore volume. The model yields total sediment height as an output. Sediment height is then balanced with eustatic sea-level rise and deep subsidence, both forcing functions, to determine wetland elevation relative to sea level. The model was programmed using STELLA iconographic modelling software (Richmond *et al*. 1987). An Euler numerical method, with $\Delta t = 1$ week, was used to solve the finite difference equations generated by the STELLA software. The model consists of three linked submodels or sectors: (i) primary productivity, (ii) sediment dynamics, and (iii) relative elevation. The sediment dynamics submodel was validated previously by Rybczyk *et al*. (1998) using the dimensionless statistic EF (modelling efficiency) described by Loague & Green (1991). EF parallels the coefficient of determination (R^2) except that the lower bound for the EF is negative infinity while the lower bounds for R^2 is zero. A perfect fit would be indicated by an EF value of 1, and values less than 0 would be indicative of a poor fit (Mayer & Butler 1993). For the sediment model used in this study, EF values ranged from 0.21 to 0.97.

We applied the model to the basin forest on Guanaja, which suffered virtually complete tree mortality and exhibited little potential for natural forest regeneration because there was no regrowth, propagule colonization or adjacent live forest to serve as a source of propagules. To simulate the effect of Hurricane Mitch in the interior forest on Guanaja, we first 'turned off' the primary production sub model and modified leaf, wood and root litter functions to reflect the instantaneous death of all primary production. All leaves were instantaneously pulsed to the forest floor, and all previously live roots were shunted to the soil litter pools (either as labile or refractory material). Wood, however, was fluxed to surface litter at a slower rate to reflect the observations that much remains as standing dead at the site. We ran the impact model for 10 years

Table 1 Initialization parameters for the Guanaja Basin Sediment Elevation Model

Parameter	Value	Source
Sea-level rise	0.15 cm year^{-1}	(Church *et al*. 2001)
Deep subsidence rate	0.17 cm/year^{-1}	Emery & Aubrey (1991)
Initial wetland elevation	37.5 cm above MLLW	This study
Mineral input	385 g/cm^2 year^{-1}	McKee & McGinnis (2003)
Root standing crop	15 000 g dw m^2	Chen & Twilley (1999)
Above ground standing crop	20 000 g dw m^2	Chen & Twilley (1999)
Sediment bulk density at surface	0.16 g dry soil cm^{-3}	McKee & McGinnis (2003)
Percent organic matter at surface	57.6%	McKee & McGinnis (2003)
Decomposition rate of deep refractory organic matter (*kdeep*)	0.0009 week^{-1}	By calibration
Decomposition rate of labile OM (*klab*)	0.025 week^{-1}	By calibration
Decomposition rate of surface labile OM (*klabsurf*)	0.30 week^{-1}	By calibration
Decomposition rate of refractory OM (*kref*)	0.0009 week^{-1}	Similar to Chen & Twilley (1999)
Labile fraction of above-ground biomass (*leaf_lab_frac*)	50%	By calibration

(simulated years 1998–2008) with no production inputs assuming current sea-level rise of 0.15 cm year^{-1} (Church *et al*. 2001).

We used elevation and accretion data collected as part of this study to initialize the model (Table 1). The model was calibrated by comparing observed percentage organic matter over depth (McKee & McGinnis 2003) with the simulated output of the same parameter. A full description of the model is provided in Rybczyk *et al*. (1998) and Cahoon *et al*. (2003). Because the primary production submodel was turned off, the sediment dynamics submodel, which simulates sediment collapse and decomposition of sediment organic matter, was the most important part of the model.

The sediment dynamics submodel has four state variables, each measured once in each of 18 soil cohorts (labile organic matter, refractory organic matter, mineral matter and live root biomass). Maximum mineral inputs (Table 1) are the only forcing functions in this submodel, as other inputs are model generated. This submodel simulates the decomposition of organic matter, the inputs of mineral matter, the distribution of root biomass, sediment compaction and the transfer of material from cohort to cohort. Changes within the cohort caused by decomposition, which is a function of model-generated depth, are calculated on a weekly basis. Sediment compaction, also calculated weekly, is a function of initial pore space (a forcing function) and the mass of material above a particular cohort. Measurements obtained from soil cores (e.g. bulk density, percentage organic matter and mineral matter), along with measurement of accretion rates derived from horizon markers, all collected as part of this study, provide the data which are used to calibrate the submodel.

Decomposition

The model separates all organic matter into labile and refractory pools, each with its own time-dependent decay rate. Additionally, the labile organic matter decomposition rate for the surface cohort is separate from that for the rest of the cohorts (allowing for a distinction from leaf and root labile organic matter). Finally, there is a separate, depth-dependent decomposition rate for deep refractory material. A simple negative exponential (–*k*) model describes decomposition for each organic matter state variable in each cohort. Required decomposition constants include *kdeep*, *klab*, *kref*, *leaf_lab_frac*, *rlab%* and *klabsurf* (Table 1).

Mineral inputs

Previous models have simulated mineral inputs as a function of wetland elevation (French 1993; Callaway *et al*. 1996). A similar approach is used here where mineral inputs are a simple linear function of elevation.

Root distribution

Although root production is simulated in the productivity submodel, root biomass is distributed to the sediment cohorts in the sediment submodel. We used an adaptation of the distribution algorithm originally developed by Morris & Bowden (1986), where root biomass is assumed to be greatest near the surface and decreases exponentially with depth. A complete description of this function is provided in Rybczyk *et al*. (1998).

Sediment compaction

Soil compaction is a function of organic matter decomposition and the reduction of sediment pore space (primary consolidation; Penland & Ramsey 1990). Callaway *et al*. (1996) simulated the compaction of pore space as an asymptotic decrease with depth, bounded by preset minimum and maximum pore space values. We used a modified version of Callaway's algorithm, where the decrease in pore space for a given cohort is a function of the mass of material above it. Again, a complete description of this function is provided in Rybczyk *et al*. (1998).

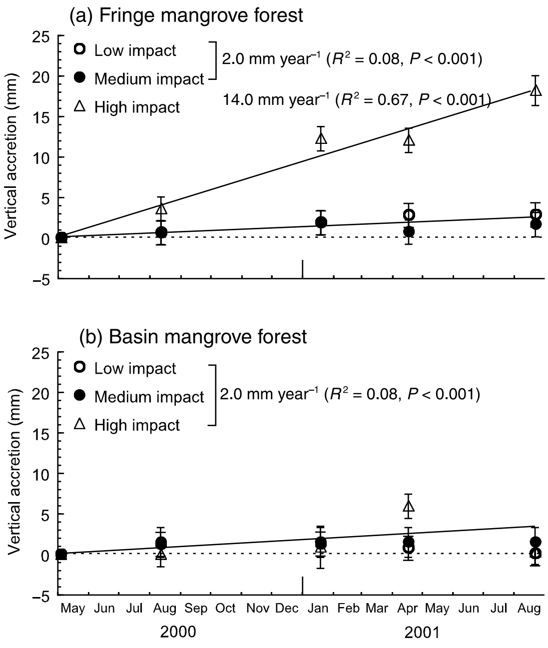

Fig. 4 Cumulative vertical accretion above sand marker horizons in the (a) fringe and (b) basin mangrove forests of the Bay Islands (Honduras), over the period May 2000–August 2001.

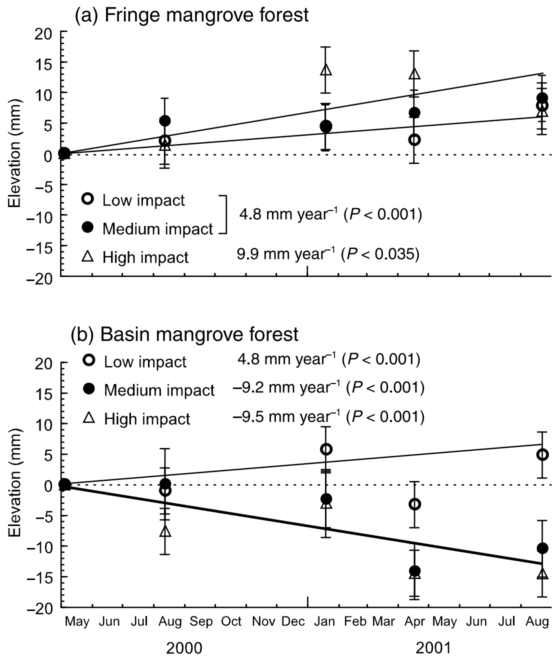

Fig. 5 Cumulative surface elevation change in the (a) fringe and (b) basin mangrove forests of the Bay Islands (Honduras), over the period May 2000–August 2001. The regression lines for the medium and high impact basin forests appear as a single line because they are so similar.

Results

POST-STORM SEDIMENTATION

Surface sediment accretion rates for 18–33 months after the storm were uniformly low in all forests except the high impact fringe forest (14.0 mm year^{-1} vs. 2.0 mm year^{-1} Fig. 4). The high accretion rate in the dead fringe forest is related to the accumulation of encrusting algae rather than inorganic sediment deposition. In the basin mangrove forests on both Guanaja and Roatan, the source of accreted material is likely reworked sediments from within the degraded substrate.

POST-STORM SEDIMENT ELEVATION DYNAMICS

Despite positive accretion, significant elevation losses were measured for the medium and high impact basin forests (Fig. 5b), indicating that peat collapse occurred in these damaged and dead mangrove forests. The rate of shallow subsidence (accretion minus elevation change) was 11 mm year^{-1}. Interestingly, elevation alternately declines and increases between sample dates (Fig. 5), indicating that a seasonally varying below-ground process, such as water storage, influenced elevation, in addition to peat collapse driven by decomposition and compaction.

Sediment compaction also played an important role in the high impact fringe forest. Elevation change was positive and, during the first 12 months of measurements, matched accretion very closely (Figs 4 and 5), demonstrating the importance of algal mat development in controlling sediment elevation. However, during the last sampling interval, elevation declined substantially while accretion continued to increase, so that the annual rate of elevation change lagged behind vertical accretion suggesting shallow subsidence of 4.1 mm year^{-1} ($P = 0.052$). By 2.5 years after the storm, the dead fringe forest appears to be undergoing peat collapse similar to the dead basin forest.

The importance of subsurface processes in controlling sediment elevation is further indicated by elevation gain in the low and medium impact fringe forests and in the low impact basin forest being twice as great as vertical accretion (Figs 4 and 5). Despite high variability in the data, this suggests that below-ground processes such as root growth contributed to sediment surface elevation in these low mortality sites.

GUANAJA SEDIMENT ELEVATION MODEL

The simulated sediment columns were in agreement with observed characteristics at the high impact basin forest, although the model did not simulate the very abrupt transition between high and low organic matter found at all forests with depth (Fig. 6). Simulations revealed a rapid sediment collapse of 37 mm year^{-1} in the first 2 years after the hurricane (Table 2; Fig. 7), caused by the rapid decomposition of the labile root fraction, followed by a decrease to 7.4 mm year^{-1}. Because field measurements of sediment elevation did not begin until 18 months after the storm, we cannot verify the simulated collapse rates during the first 2 years. However, the rate measured in the field from

Table 2 Simulated effects of Hurricane Mitch on sediment dynamics and overall wetland elevation at the high impact basin forest on Guanaja

Parameter	*Value*
Initial elevation relative to MLLW	37.5 cm
Elevation relative to MLLW 10 year after Mitch	21.0 cm
Loss in elevation relative to MLLW	16.5 cm
Loss in elevation due to sediment collapse alone	13.3 cm
Rate of sediment collapse in the first 2 years	3.7 cm year^{-1}
Rate of sediment collapse over the next 8 years	0.74 cm year^{-1}

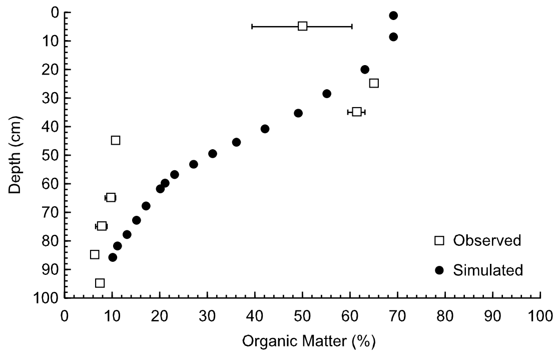

Fig. 6 Simulated vs. observed sediment organic matter in the high impact basin mangrove forest on Guanaja (Bay Islands, Honduras).

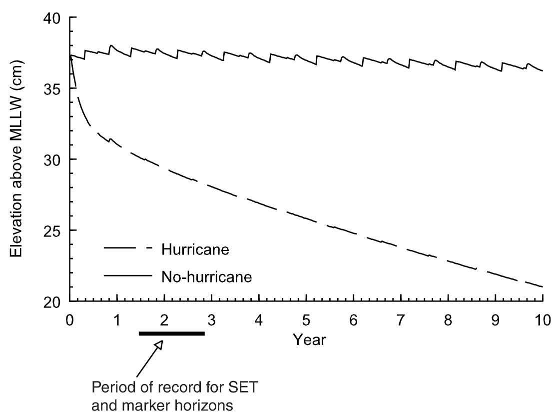

Fig. 7 Simulated change in sediment elevation relative to mean low low water (MLLW) in the high impact basin mangrove forest beginning in October 1998 with (dashed line) and without (solid line) Hurricane Mitch impacts.

18 months to 33 months after the storm (11 mm year^{-1}), was similar to the simulated value (7.4 mm year^{-1}). The simulated total loss in relative elevation in the basin forest is higher than the simulated sediment collapse (Table 2) because simulated elevation loss is a function of both sediment collapse and relative sea-level rise (3.2 mm year^{-1}; Emery & Aubrey 1991).

MANGROVE FOREST STRUCTURE

The acute impact of Hurricane Mitch in Mangrove Bight caused virtually complete mortality across all diameter size classes: no live mangroves were encountered within either fringe or basin study plots in 2000, 15 months after the storm (total area 300 m^2; Table 3). The trunks of adult red mangroves were broken, while adult black mangrove trunks were uprooted. Only 3 live mangrove trees, all saplings, were observed in the entire forest, all located outside the study plots and within the fringe forest. As expected, the percentage of dead mangroves decreased along the gradient from high to low impact levels in 2000 ($P < 0.0001$; Table 3) and was significantly less at the low than at the medium level ($P < 0.0001$). Basin forests had higher mortality in the adult size classes than the fringe, although the difference was barely significant ($P = 0.053$). An important characteristic of the medium impact fringe was that the mature canopy had remained intact. There was no major blow down of canopy trees, and high mortality was confined to the smaller size classes (saplings within the class < 2 cm; Table 3). In contrast, the adjacent basin forest suffered higher mortality in canopy trees (50% in the largest size class; Table 3).

Table 3 Percentage mortality of mangroves in experimental plots in the Bay Islands, Honduras. Data from January 2000

	High impact		Medium impact		Low impact	
Diameter/size class	Fringe	Basin	Fringe	Basin	Fringe	Basin
Seedling	N/A	100	0	0	0	0
< 2 cm	100	100	94	0	5	15
2–4.9 cm	100	100	35	50	0	9
5–9.9 cm	100	100	19	20	0	0
10–19.9 cm	100	100	17	17	0	10
20+ cm	100	100	0	50	0	0
Total*	100	100	36	10	2	7

*Total does not include contribution from seedlings.

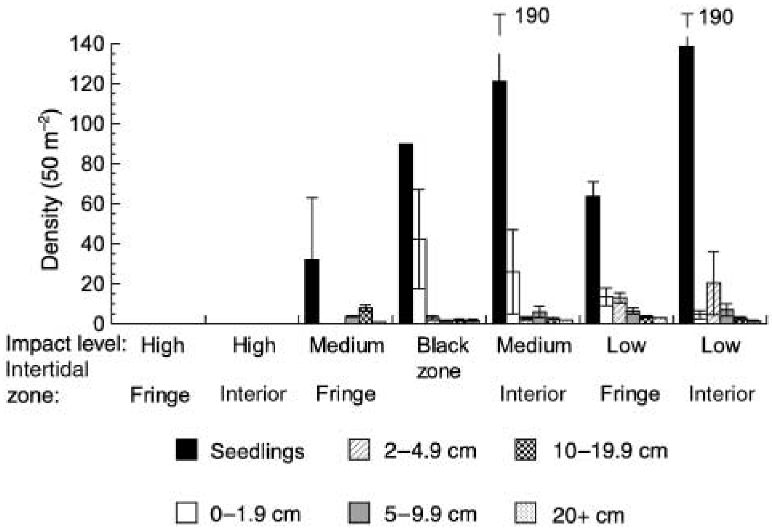

Fig. 8 Density of live mangrove trees in the Bay Islands, Honduras, 27 months after Hurricane Mitch (data from January 2001).

Continued severe impact in Mangrove Bight was indicated by a complete lack of recovery (i.e. no regrowth) within the high impact area in 2001, 27 months after the storm. Lack of recolonization was also indicated by a complete absence of propagules, live or dead. In contrast, a strong recovery was seen in the medium and low impact forests, where high recruitment into the seedling size class was observed in 2001 (Fig. 8). High recovery was also recorded in the edge of the dead black mangrove zone along the north shore of Roatan in 2001 ('Black Zone', Fig. 8).

ROOT PRODUCTION

Total root production (range: 0–656 g m^2 year^{-1}) did not differ between fringe and basin forest zones or between low and medium impact sites (1 d.f. contrast: $P > 0.05$; Table 4). However, no roots were produced in either zone at the high impact site. Although the proportion of fine roots produced was higher in the fringe than the basin zone, there was no significant effect of impact level, nor was there an interaction (Table 4).

SOIL SHEAR STRENGTH

Soil strength differed with both zone and impact level, but the patterns varied between surface and subsurface positions (Table 4). At the surface, soil strength was significantly lower at the high than the low impact site in both the fringe (1 d.f. contrast: t-ratio = −4.39, $P < 0.0001$) and basin (1 d.f. contrast: t-ratio = −11.0, $P < 0.0001$) zones. Subsurface soil strength in the basin zone was significantly lower overall compared to the fringe and decreased with increasing hurricane impact level (Table 4). Subsurface soil strength in the basin zone at medium and high impact sites was significantly lower than at the low impact site (1 d.f. contrast: t-ratio = 4.81 and –13.44, respectively, $P < 0.0001$). The

Table 4 Comparison of total root production (to 30 cm depth), percentage fine (≤ 2 mm) roots produced, and soil shear strength (surface and average of three depths: 5, 15 and 25 cm) in fringe and basin forest zones and three hurricane impact levels (low, medium and high) in the Bay Islands, Honduras. Values are the mean ± SE (n = 6)

	Low impact		Medium impact		High impact	
	Fringe	Basin	Fringe	Basin	Fringe	Basin
Total root production (g m^{-2} year^{-1})	311 ± 101	333 ± 98	218 ± 52	271 ± 61	0 ± 0	0 ± 0
Percentage fine foots	75 ± 3	62 ± 10	75 ± 11	50 ± 11	–	–
Soil strength (kg cm^{-2}):						
Surface	0.31 ± 0.02	0.08 ± 0.01	0.34 ± 0.02	0.05 ± 0.01	0.05 ± 0.01	0.03 ± 0.004
5–25 cm	0.47 ± 0.02	0.30 ± 0.06	0.46 ± 0.03	0.11 ± 0.004	0.32 ± 0.02	0.025 ± 0.003

ANOVA source	Impact level	Zone	Impact level × Zone
Total root production	$P < 0.0001$	$P > 0.05$	$P > 0.05$
Percentage fine foots	$P > 0.05$	$P < 0.05$	$P > 0.05$
Soil strength			
Surface	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$
5–25 cm	$P < 0.0001$	$P < 0.0001$	$P < 0.0001$

extremely low values of subsurface soil strength found in the basin forest on Guanaja agreed with qualitative observations that the soil structure would often not support the weight of a person. However, subsurface strength in the fringe zone remained relatively high at all impact levels (Table 4). Although subsurface soil strength in the fringe zone was significantly lower at the high compared to the low impact site (1 d.f. contrast: *t*-ratio = –2.254, $P = 0.0317$), it was significantly higher than in the basin zone (1 d.f. contrast: *t*-ratio = 14.25, $P < 0.0001$) where peat collapse was occurring.

Discussion

PEAT COLLAPSE

Nearly 3 years after the passage of Hurricane Mitch, there remained a ghost forest of dead trees at Mangrove Bight, Guanaja. There had been essentially no mangrove recovery, no re-colonization by mangrove propagules (Fig. 8), no root growth (Table 4) and no inorganic sediment deposition. Consequently, the substrate collapsed in the basin forest as the mangrove peat decomposed (Fig. 5). H.R. Wanless (pers. comm.) measured an elevation loss (20–30 mm year^{-1}) during the 2 years immediately following the death of a mangrove forest in south-west Florida caused by Hurricane Andrew. Similarly, Sherman *et al*. (2000) observed a reduction in soil elevation 2 years after lightning gap formation, and Lugo (1997) attributed increased water depths in the vicinity of dead trees to peat oxidation. Model simulation results indicate that sediment elevation in the Guanaja basin forest will collapse for at least 10 years after the storm in the absence of inorganic sediment input or renewed root production (Fig. 7). Empirical evidence of the initiation of sediment collapse in the fringe forest, combined with the model simulation results from the basin forest, suggest that sediment elevation in the fringe forest could decline for the next several years. Predicted increases in sea level (Church *et al*. 2001) would be expected to increase the rate of sediment elevation loss simulated by the model, in which we used only the current rate of eustatic sea-level rise (1.5 mm year^{-1}; Church *et al*. 2001).

The difference in collapse rates between the basin and fringe forests on Guanaja implies that sediment elevation in the basin forests responded more quickly to mass tree mortality, probably related to differences in soil structure. Subsurface soil strength was greater in fringe than basin forests and remained surprisingly high in the fringe forest on Guanaja even 15 months after forest mortality (Table 4). The greater strength of the fringe soils can be attributed to prolific production and higher density of fine roots of the dominant red mangrove, compared to those of the black mangrove found in basin forests (Table 4). Soil strength may have been maintained longer in the fringe forest after root mortality because it was higher initially (based on values observed in the low impact site; Table 4) and/or because mangrove roots decay slowly (Middleton & McKee 2001), particularly fine roots (15% in 270 days; van der Valk & Attiwill 1984). The encrusting algal mats observed on the sediment surface in the fringe zone did not contribute to greater soil strength because values were low at the sediment surface and comparable to that in the basin forest where peat collapse occurred (Table 4).

IMPLICATIONS FOR MANGROVE SUSTAINABILITY

Recovery of mangrove forests from hurricane impacts has been reported to rely on mangrove survival, generally among the smallest size classes (Smith *et al*. 1994; Imbert *et al*. 1998). The paucity of such survival at Mangrove Bight suggests that recovery will depend primarily on seedling recruitment. Given the high rate of peat collapse and the current paucity of propagules, it is unclear if colonization will occur quickly enough to stabilize sediment elevation before it becomes too low within the tidal range for seedling establishment to occur, as suggested by Lugo (1997). Continued elevation loss could also lead to the development of unfavourable soil conditions (e.g. low redox potential, increased salinity and sulphides), which may further limit the potential for seedling establishment. Wanless *et al*. (1995) reported that, as of 1992, natural recolonization had not occurred in most of the mudflats created by the 1935 and 1960 hurricanes in south Florida, despite a plentiful source of propagules in the immediate vicinity. They hypothesized that high concentrations of sulphides and low oxygen levels combined with lower elevations in the poorly drained, decomposing soils inhibited seedling establishment. Such conditions may already exist in the basin ghost forest of Mangrove Bight, which had the lowest redox potential, highest concentration of sulphides and highest interstitial salinity 18 months after the storm of all the mangrove forests studied by McKee & McGinnis (2003). The combined effects of limited mangrove survivorship, lack of propagules, rapid elevation loss, and development of inimical soil conditions for plant growth could limit the potential for recovery of damaged forests on Guanaja.

The potential for long-term recovery is greater for the forests on Roatan. The fringe forest on the north shore (medium impact site) survived the passage of Hurricane Mitch despite 36% overall mortality. Our data indicate that sediment elevation of this forest remained stable 3 years after the storm and patterns of change were identical to those of the reference (low impact) fringe forest on the south shore. The survivorship of this zone may be related to the high soil strength associated with the development of a red mangrove forest. Parts of the basin forest on the north shore, especially areas dominated by black mangrove, suffered severe mortality, and sediment collapsed at the same rate as in the basin forest on Guanaja, but recolonization is occurring throughout the medium impact forest (Fig. 8).

The occurrence of peat collapse on Guanaja, where the substrate consisted of 52% organic matter on average (range = 32–73%), suggests that on a broader geographical scale (e.g. the wider Caribbean and other tropical regions of the world), the potential for peat collapse following mass mortality (regardless of cause) is high for any mangrove system with a peat (> 40% organic matter) or organic (20–40%) substrate. Mangrove peat can consist of as much as 90% organic matter (Cameron & Palmer 1995; McKee & Faulkner 2000). What role hurricane-induced mass tree mortality and subsequent peat collapse play in the formation of dieback areas and unvegetated flats, and the perpetuation of gaps in mangrove forests is not known, but other investigators have suggested a possible connection (Wanless *et al*. 1995; Woodroffe 1995; Lugo 1997; Sherman *et al*. 2000). Our study provides the first direct evidence that mangrove mortality caused by hurricanes leads to collapse of peat substrates, particularly in interior stands where dieback flats are often observed. The recognition that mass mortality of mangrove forests affects sediment elevation dynamics will improve models used to predict the potential for mangrove recovery and patterns of mangrove forest succession, and help to develop better mangrove restoration guidelines.

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