Hurricane Mitch: Effects on Mangrove Soil Characteristics and Root Contributions to Soil Stabilization

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USGS Open File Report
OFR 03-178

U.S. Department of the Interior
U.S. Geological Survey

Suggested citation:

McKee, K.L. and T. E. McGinnis, II, 2002, Hurricane Mitch: Effects on mangrove soil characteristics and root contributions to soil stabilization: USGS Open File Report 03-178, x p.

USGS Activity B6 and B7

Hurricane Mitch: Effects on Mangrove Soil Characteristics and Root Contributions to Soil Stabilization

By

Karen L. McKee[1] and Thomas E. McGinnis, II[2]

[1]Principal Investigator, USGS-National Wetlands Research Center, 700 Cajundome Blvd, Lafayette, LA 70506, www.nwrc.usgs.gov; [2]General Biologist, National Wetlands Research Center, Johnson Controls Inc., Lafayette, LA 70506

October, 2002

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Introduction

Although numerous descriptions of hurricane damage to mangrove forests exist (e.g., Davis, 1940; Egler, 1952; Craighead and Gilbert, 1962; Sauer, 1962; Stoddart, 1963), there is little information about ecological effects (Roth, 1992; Smith and others, 1994; Baldwin and others, 1995) and even less understanding of effects on soils and belowground processes. Most quantitative work has concentrated on aboveground damage to mangrove forests caused by hurricane passage (Roth, 1992; Smith and others, 1994; Baldwin and others, 1995). Although aboveground recovery of mangroves has been studied in a few cases (Roth, 1992; Baldwin and others, 1995), information on belowground recovery of hurricane-damaged vegetation is limited (Parotta and Lodge, 1991). There are no quantitative observations of hurricane effects on mangrove root production or mangrove root stabilization of soils and sediments after hurricane passage.

The deposition of sediment during hurricanes may directly alter chemical and physical characteristics of mangrove soils, which will in turn affect health and productivity of surviving mangrove stands as well as reestablishment of mangroves in areas of high mortality. The rapid stabilization of this newly deposited sediment by mangrove roots is also important to prevent remobilization and future damage to adjacent, sensitive areas such as seagrass beds and coral reefs. Cahoon and others (1995) quantified the effects of Hurricane Andrew on areal extent and temporal patterns of sediment deposition in delta marshes and shallow water bodies in Louisiana’s coastal zone. However, no published information exists that quantifies hurricane-induced changes in mangrove soil properties such as soil texture, shear strength, bulk density, redox potential, sulfide concentrations (potential plant toxin), and other physicochemical characteristics.

Habitat stability of mangrove forests is also dependent on a feedback relationship between sediment chemistry and plant growth. Physicochemical conditions (e.g., salinity, oxidation status, nutrient availability) directly and indirectly influence mangrove growth and reproduction (McKee, 1993; McKee, 1995). Mangroves in turn influence soil physical and chemical characteristics (McKee and others, 1988; McKee, 1993). Thus, changes in soil chemistry, whether directly due to storm deposits of sediment or indirectly due to hurricane effects on mangrove root systems, may have long-term effects on forest productivity and recovery.

Preliminary observations conducted shortly after hurricane passage indicated that causes of mangrove mortality differed between Caribbean and Pacific coasts (Proffitt, and others, 1999). These differences have implications for both aboveground and belowground vegetative recovery and soil stabilization in high impact areas. In areas where the vegetation survived mostly intact, soil conditions may have changed sufficiently to alter primary production, which could ultimately influence secondary production (e.g., food sources or nursery habitat). The objectives of this study, therefore, were to investigate changes in soil conditions and belowground recovery of mangrove forests affected by Hurricane Mitch. This effort was closely coordinated with investigations of aboveground damage and recovery of mangroves and hurricane effects on soil elevation change and vertical accretion rates described in separate reports in this series. Mangrove forests in three different areas, which were differentially impacted by storm deposits and wind, were examined. On the Pacific coast of Honduras, mangroves in the Gulf of Fonseca were primarily damaged by debris flows and terrigenous sediment burial. On the Caribbean coast of Honduras, mangroves in the Bay Islands were damaged by wind and submergence by storm tides, whereas mangroves at Punta Manabique, Guatemala were affected by both wind and burial by sediment. The results provide insights into how these different disturbance types and severity affect mangrove soil physical and chemical characteristics and mangrove root production and consequences for soil stabilization.

Methodology

Experimental Design

On each coast, areas with three levels of damage (high, intermediate, and low/none) were identified, and sample plots were established at two spatial positions (shoreline and interior). *Rhizophora mangle* was the dominant mangrove species along the shoreline, while the interior forest had mixed stands with *R. mangle*, *Avicennia germinans,* and *Laguncularia racemosa*. At each sample site, we randomly established three plots for a total of 36 plots in which sediment stratigraphy, soil physicochemistry, and mangrove root production were assessed. At the Guatemala site, only the shoreline zone was assessed at each of two impact levels (high and low/none) for a total of six plots. In general, field and laboratory procedures followed the guidelines for quality control (Association of Official Analytical Chemists International, 1990; American Society for Testing and Materials, 1991). A single, deep core from each plot to a depth of up to 2 m (Honduras) or 0.4 m (Guatemala) was collected for visual description of strata and determination of selected physicochemical characteristics. Duplicate surface soil samples were collected from each plot for determination of bulk density, water content, and organic matter content. Duplicate samples of interstitial water were also collected from each plot for analysis of salinity, pH, sulfide, and soluble NH_4^+ and PO_4^{3-}. Soil redox potential (E_h) and soil shear strength were measured in situ in duplicate within each plot. Mangrove root production was determined in duplicate in each plot at Honduras sites only.

Soil Stratigraphy

A single, deep core was collected from each plot to the point of refusal (up to 2 m in Honduras) or to 0.4 m (Guatemala) for visual description of strata and determination of selected physicochemical characteristics. The core was extracted in 50 cm sections with a manual Russian peat corer (plate 1). Where the soil was impenetrable with the Russian corer, a shallower core (30 cm) was taken with an aluminum cylinder coring device (7.3 cm diameter x 50 cm depth). After extraction of each core section, the stratification was described by noting visual changes in color and texture (peat, mineral, or calcareous deposits) and their depths. A photograph was taken with a digital camera (Nikon Coolpix 950, Nikon Inc., Torrance, CA) to provide a visual record of each core section. The soil core was then divided into 10 cm increments, and each section was stored in plastic bags for further analysis.

Color classification of all increments was made with a Munsell Color Chart (Macbeth Division of Kallmorgen Instruments Corporation, New Windsor, NY). The

Plate 1. Russian peat corer used to collect deep cores of soil for characterization of soil stratigraphy. See text (Methodology - Soil Stratigraphy) for detailed description of method.

first 10 cm section and a subsample from each strata in a core were selected for analysis of moisture, mineral and organic matter content, total C and N (CHN analyzer, CE440 Elemental Analyzer, Leeman Labs, Inc.), and particle size distribution (Gulf of Fonseca only). At the lab, the soil was weighed, dried at 80°C to constant mass, and reweighed to determine moisture content (percent water in soil sample). The dried soil was ground with a mortar and pestle and a subsample was ashed at 550°C for 6 h to determine mineral mass after organic loss on ignition. Particle size distribution analysis (PSDA) was performed using a micro-pipette method for water dispersible clay (see Burt and others, 1993). The PSDA was modified by a series of ashing (moisture sample and sand fraction) to correct for high organic content.

Surface Physicochemical Conditions

Shallow, duplicate soil cores were collected from each plot with a piston corer (54.3 cm^3, 12 cm long x 1.2 cm radius) and stored in water-tight plastic bags until analysis of bulk density, water content, and mineral and organic content. At the lab, the soil was weighed, dried at 80°C to constant mass, and reweighed to determine bulk density (mass of dry soil per volume) and relative saturation (%) The dried soil was ground with a mortar and pestle and a subsample was ashed at 550°C for 6 h to determine mineral mass after organic loss on ignition.

Soil Shear Strength

Soil shear strength was determined with a Torvane device (H-4212 1, Humbolt Manufacturing Company, Durham Geo-Enterprises, Inc.) that measures the torque required to shear or deform the soil (see McGinnis, 1997) (plate 2A). Soil strength was measured at the soil surface and along a vertical depth profile to 30 cm. The only selective criterion was flatness, because the torvane required a flat or nearly flat surface for accurate measurements. On the soil surface, six replicate measurements were made to account for microtopologic variation. Depth profile measurements (5, 15, and 25 cm) were taken from duplicate soil cores (12.5 cm diameter) that were divided in half vertically, thus leaving a smooth surface.

Pore water

Pore water samples were collected in duplicate from each plot and processed according to McKee and others (1988). A sipper apparatus consisting of a rigid plastic tube connected to a 60 ml syringe was used to extract interstitial water from the soil. The first 5 ml of each extraction was discarded to remove debris, sediment, and gas. An aliquot of water for sulfide determination was added to an equal volume of antioxidant buffer (electrode operating instructions) upon collection, and all samples were analyzed with a sulfide electrode (Lazar Model IS-146 sulfide electrode, Lazar Research Laboratories, Los Angeles, CA, USA). A second aliquot was filtered through a 0.45 μm filter into an acid-washed vial and frozen until nutrient analysis. The remainder was stored at room temperature for analysis of salinity (refractometer, Vista Model A366 ATC) and pH (pH/mV meter, model 5938-00, Cole-Parmer, Chicago, IL, USA).

Pore water was analyzed for NH_4^+ and PO_4^{3-} with a LACHAT system (QuikChem 8000 Series FIA, Zellweger Analytics, Milwaukee, WI, USA) (Parsons and others, 1984. Analytical procedures were checked by use of external standards and blanks as specified by instrument manufacturer.

Plate 2. A) Measurement of soil shear strength with a Torvane soil test device that measures the torque required to cause soil failure, or shearing. See text (Methodology - Soil Shear Strength) for detailed description of method. B) Example of low soil integrity at the high impact interior site on the Caribbean Coast (Guanaja, Bay Islands) of Honduras.

Soil Redox Potential

Redox potential (E_h) measurements were made in situ at three soil depths (1, 15, and 30 cm) to characterize reducing conditions in the soils (McKee and others, 1988). Brightened platinum electrodes were inserted to the desired depth and allowed to equilibrate for a minimum of 15 min before measurement. Voltage (mV) between the platinum electrode and a calomel reference electrode was measured with a hand-held pH/mV meter (Cole-Parmer, model 5938-00, Chicago, IL, USA) and corrected for the calomel potential by adding 244 mV.

Root Production

Root production to a 30 cm depth was assessed using the implanted mass technique (Gallagher and others, 1984) (Plate 3). Duplicate soil cores (7.3 cm diameter x 30 cm depth) were removed near a mangrove tree inside the plot with a coring device, and in-growth bags containing root-free substrate were inserted. The in-growth bags were constructed of loose nylon mesh (3 mm^2, J&M Industries, Ponchatoula, LA). Bags placed in the Pacific Coast plots were filled with native sediment collected from adjacent mud flats, whereas bags placed in the Caribbean Coast plots were filled with root-free, milled peat (sphagnum) because the native peat at the experimental sites was composed primarily of mangrove roots. The in-growth bags were exhumed after 12 months with a larger diameter corer (10.3 cm). Soil surrounding the excavated bags was carefully removed using scissors and razor blades, and all in-grown roots were severed at the bag surface while taking care not to pull roots from the bag. The bag was opened lengthwise and the contents divided into three 10 cm sections. In-grown root material was washed over a sieve (1 mm^2) with freshwater to remove sediment. Large, non-root particles were separated by hand, and roots and root fragments were separated from small debris by flotation. Roots were separated into two size categories (coarse, >2 mm diameter; fine, = 2 mm diameter), dried at 70°C, and weighed.

Plate 3. Sequence of steps for determination of root production: A) removal of soil core, B) insertion of in-growth bag containing root-free substrate, C) retrieval of in-growth bag with in-grown roots and sectioning by depth, and D) washing of roots to be separated into size classes, dried, and weighed. See text (Methodology - Root Production) for detailed description of method.

The samples from the Pacific sites were readily washed and separated from the silty substrate, which passed easily through the mesh screen. However, fine (= 2 mm diameter) roots from Caribbean sites could not be easily separated from the peat substrate, which was also trapped on the mesh screen. Complete recovery of fine roots from a subsample required on average 2 to 3 h and was not feasible at the field site. After initial processing, a set time period (10 min) was spent to remove visible fine roots from the peat substrate. The peat with fine roots was resuspended in water against a dark background, and visible roots were collected with tweezers. To quantify the proportion of fine roots that were not recovered, a subset of material from nine cores was fully processed under magnification in the laboratory to completely separate all fine roots and root fragments. When compared to the total, additional fine roots recovered were about 12% of the total fine root mass. However, not all of this unrecovered material represented in-grown roots. Two core samples from the high impact Caribbean site (where there was no living vegetation) were similarly examined under magnification and were also found to contain fine roots and root fragments. Since examination of the milled sphagnum peat (unused) under magnification revealed no roots, the presence of roots in in-growth cores from dead forest sites could only be due to physical transport of root material from the surrounding soil into the in-growth cores. Thus, no attempt was made to correct samples for “unrecovered roots.”

Statistical Analyses

Each of the three locations (Bay Islands, Gulf of Fonseca, and Guatemala) was analyzed separately due to differences in experimental design and human interference.

The Bay Islands data were analyzed as a 3 x 2 factorial, where impact level and spatial position were grouping factors (two-way ANOVA). Although the Pacific sites were established in the same design as for the Bay Islands, human interference necessitated an alternative analysis procedure. The high impact interior site was altered by local shrimp farmers during the study and is designated hereafter as “shrimp pond”. The shrimp pond area initially received huge amounts of sediment and debris, but during the course of the study this deposit was removed and the area was graded in preparation for reestablishment of a shrimp pond. Thus, the measurements conducted at this site reflect both hurricane and human influences, whereas the other sites were primarily affected by the hurricane or were undisturbed. Because a two-way ANOVA would not be appropriate, we treated each site on the Pacific coast as a separate location and analyzed the data with a one-way ANOVA, with zone/impact combination as the grouping factor. The Guatemala sites were analyzed with a t-test, with two impact levels. Although Gulf of Fonseca, Bay Islands, and Punta Manabique sites were not compared statistically, the patterns observed at these sites were compared qualitatively.

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. Post-test comparisons among treatments were described with a Tukey HSD test and one degree of freedom contrasts for single comparisons of interest between two levels. In the Pacific, a priori contrasts were constructed to make impact (low impact shoreline and interior versus high impact shoreline and medium impact interior) and zone (low and high impact shorelines versus low and medium impact interiors) comparisons.

Results

Soil Stratigraphy

Soil stratigraphy and textural characteristics of strata differed between zones and among impact levels on each coast (fig. 1A, table 1). In the Bay Islands, the predominant pattern found was fibrous peat (> 40% organic matter) overlying marine inorganic sediment (calcareous chips, sand, shells, and/or marl), and there was no evidence of mineral sedimentation of marine or terrigenous origin on or near the soil surface at low and high impact sites (plate 4A). This finding supported initial observations that sediment plumes from the mainland rivers did not reach the Bay Islands of Roatán or Guanaja. Storm surge did not deposit marine sediment at the high impact site on Guanaja but did create a narrow ridge of material landward of the medium impact shoreline at Roatán. A core collected on this ridge showed a surface layer of marine sediment about 70 cm thick. The deposition of this layer clearly occurred during Hurricane Mitch, since existing tree bases and aerial roots were partially buried. Below this layer were peat deposits interspersed with lenses of marine sediment 20-50 cm thick. Peat deposits at the low impact site on Roatán extended to about 50 cm depth in the forest interior and to 150 cm along the shoreline. A stratum of marine sediment with some mangrove roots occurred below the peat deposit. At the high impact site on Guanaja, peat strata were thinner (20-60 cm depth) and overlay marine sediment deposits that extended to a 2 m depth. As on Roatán, the peat deposits at Guanaja were thicker along the shoreline. Soil cores collected in Guatemala showed deep deposits (> 30 cm) of quartz sand at high impact sites, whereas low impact sites exhibited varying layers of sandy loam and peat (fig. 1B).

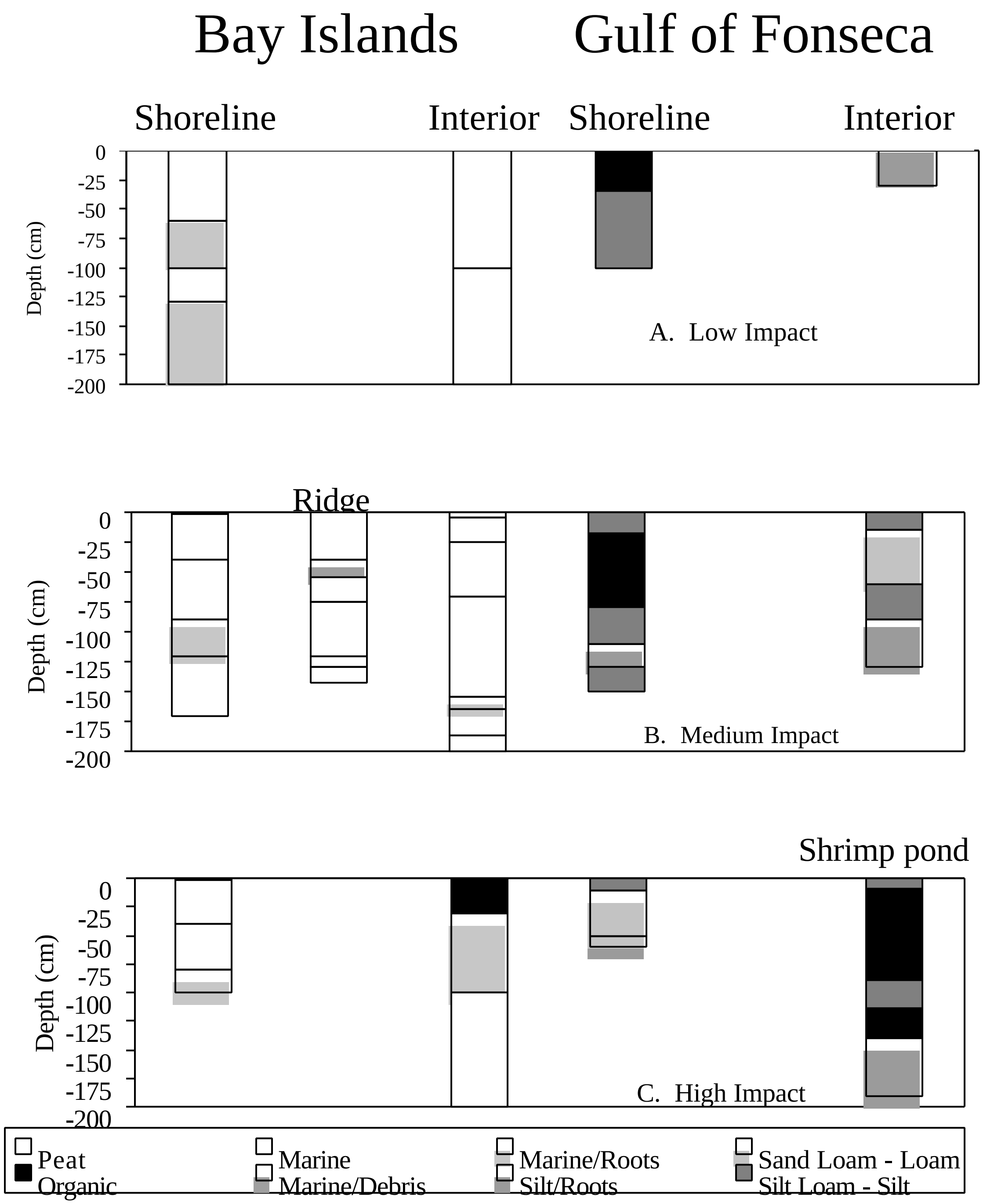

Figure 1A. Selected soil stratigraphy profiles from January 2000 at shoreline and interior plots established at three impacts on the Caribbean and Pacific coasts of Honduras. There was a "ridge" of marine sediment in the Caribbean Medium Impact site, and the Pacific High Impact Interior site was a shrimp pond (S P). See Table 1 for quantitative characterizations of the strata.

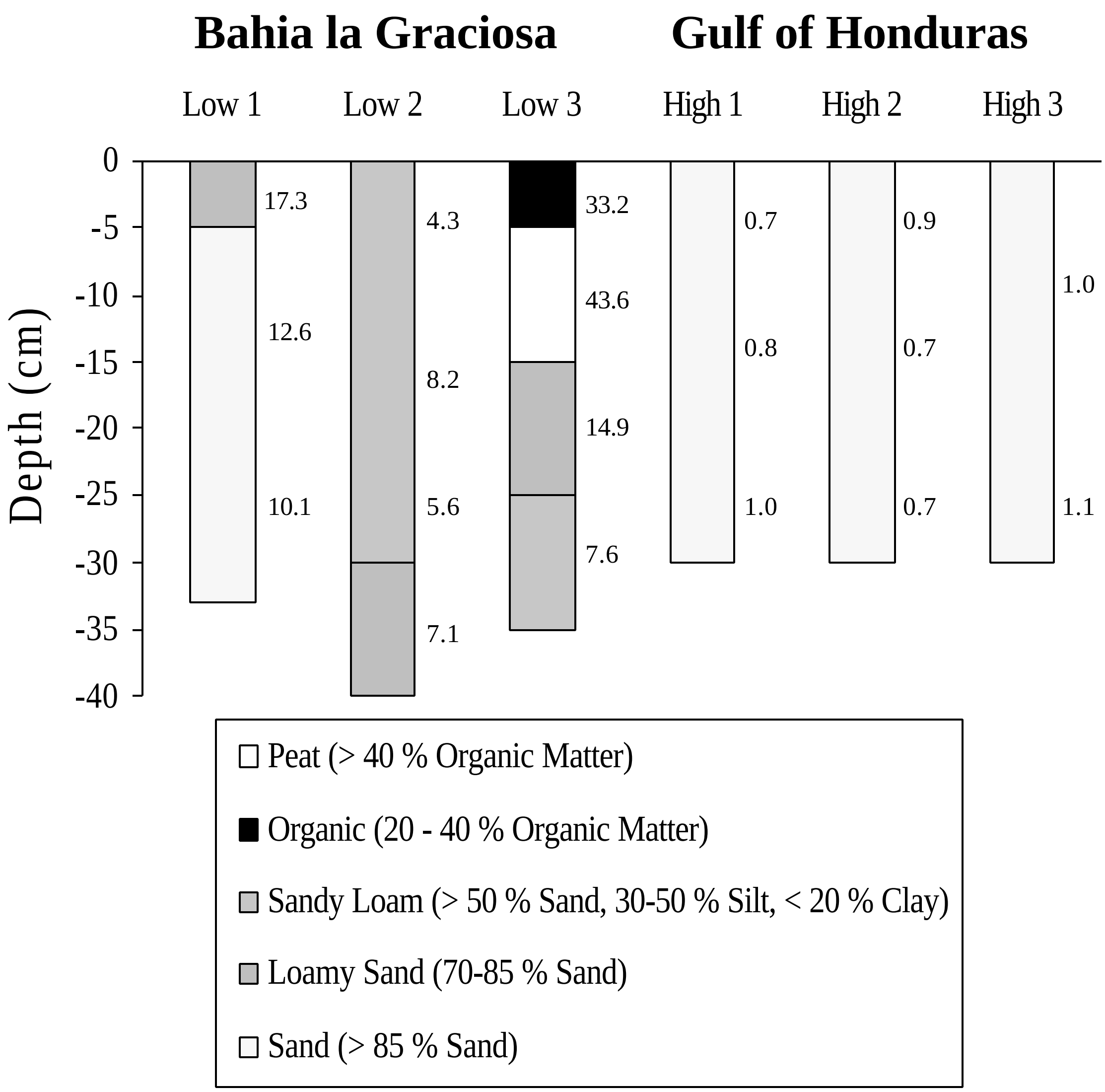

Figure 1B. Soil stratigraphy profiles characterized in August 2000 at mangrove plots established at low and high impact levels on either side of Punta Monabique, Guatemala, which is a penninsula that separates Bahia la Graciosa (low impact) and the Gulf of Honduras (high impact). Values are % organic matter. Note higher % organic matter in Bahia la Graciosa; this is indicative of mangrove roots and detritus.

Table 1. Physicochemical characteristics of soil strata at different hurricane impact sites (see fig. 1 for visual reference of stratifications). Strata type: peat (> 40% organic matter); organic (20-40% organic matter); marine (shell, calcareous algal chips, sand, and marl, shells deposits); marine/roots (marine deposits with roots); marine/debris (marine deposits with recently live plant parts); sand loam - loam (sand loam: < 7% clay/< 50% silt/ 43-52% sand to loam: 7-27% clay/28-50% silt/< 52% sand); silt loam - silt (silt loam: >50% silt/12-27% clay or 50-80% silt/<12% clay to silt:>80% silt/<12% clay); silt/roots (silt with roots). Soil characteristics: Munsell color designation(hue = hue; v/c = value/chroma); number of samples per strata (n); moisture content; organic matter content (% OM); organic carbon content (OC, mg C/g soil); total nitrogen (TN, mg N/g soil); and organic carbon to total nitrogen ratio (C:N). Values are the mean ± 1 standard deviation; strata with 1[a] or 2[b] replicates.

Impact	Zone	Strata	Munsell Hue	Munsell V/C	n	Moisture %	O M %	O C (mg C/g soil)	T N (mg N/gsoil)	C:N
Caribbean Coast										
Low	Shoreline	Peat	7.5r	2.5/1	12	86.9 ± 2.5	67.8 ± 3.7	484 ± 20	15.0 ± 1.1	32.5 ± 2.2
		Marine/roots	5yr	4/1	2	79.0 ± 6.2	31.6 ± 1.1	176 ± 40	10.1 ± 2.8	17.6 ± 0.9
		Marine	10yr	6/2	3	59.9 ± 7.2	12.9 ± 3.2	105 ± 3	3.4 ± 1.1	32.8 ± 11.4
		Marine/roots	10yr	4/2	3	62.8 ± 7.6	15.4 ± 6.3	109 ± 7	5.4 ± 2.9	22.3 ± 5.7
	Interior	Peat	7.5r	2.5/1	11	86.7 ± 1.9	72.8 ± 14.1	487 ± 11	16.8 ± 3.4	29.9 ± 5.6
		Marine	10yr	5/2	8	60.7 ± 10.4	16.9 ± 7.3	124 ± 35	4.4 ± 2.1	30.6 ± 8.0
Medium	Shoreline	Peat	2.5yr	3/1	7	89.7 ± 4.7	60.2 ± 10.1	433 ± 116	14.0 ± 2.7	30.9 ± 6.0
		Marine	10yr	5/2	5	51.0 ± 9.1	7.2 ± 1.1	84.8 ± 5.0	1.8 ± 0.4	48.5 ± 12.4
		Marine/roots	10yr	4/2	2	54.0 ± 12.0	13.3 ± 11.2	114 ± 43	3.6 ± 2.9	40.7 ± 21.0
		Peat	10yr	2/2	2	78.8 ± 10.0	59.5 ± 11.4	479 [a]	15.5 [a]	30.9 [a]
	Ridge	Marine	10yr	6/2	2	43.5 ± 1.2	9.9 ± 0.2	107 ± 3	2.7 ± 0.2	40.4 ± 2.2
		Marine/debris	10yr	5/2	1	44.6	10.1	115	2.6	44.4
		Marine	10yr	4/2	1	47.6	11.0	114	2.9	39.4
		Marine/roots	10yr	3/2	1	62.7	24.6	178	6.4	27.9
		Peat	10yr	2/2	3	80.0 ± 2.2	57.5 ± 6.7	496 [a]	10.5 [a]	47.3 [a]
	Interior	Peat	7.5r	2.5/1	5	81.5 ± 6.1	61.2 ± 10.8	401 ± 109	18.4 ± 2.8	21.6 ± 3.9
		Marine	10yr	5/2	4	62.1 ± 3.4	17.0 ± 1.9	109 ± 9	4.8 ± 0.4	22.7 ± 0.9
		Marine/roots	10r	2.5/1	2	74.8 ± 4.6	38.5 ± 0.7	182 ± 14	10.4 ± 1.3	17.7 ± 0.9
		Peat	10yr	2.5/1	5	84.1 ± 0.9	60.2 ± 4.9	453 ± 52	11.4 ± 1.2	39.8 ± 3.7

Table 1 cont'd

Impact	Zone	Strata	Munsell Hue	Munsell V/C	n	Moisture %	O M %	O C (mg C/g soil)	T N (mg N/gsoil)	C:N
Caribbean Coast										
		Marine/roots	10yr	4/2	1	83.2	45.7	284	9.7	29.3
		Peat	10yr	2/2	3	89.3 ± 3.3	52.6 ± 0.5	480 ± 31 [b]	9.6 ± 1.8 [b]	51.4 ± 12.7 [b]
		Marine	10yr	3/2	2	62.2 ± 0.5	10.9 ± 1.1	93.3 ± 7.8	3.6 ± 0.8	26.9 ± 8.5
High	Shoreline	Peat	2.5yr	2.5/1	7	83.3 ± 6.2	52.3 ± 16.2	348 ± 146	14.3 ± 4.5	23.5 ± 4.7
		Marine	10yr	6/2	3	53.0 ± 8.6	10.0 ± 0.9	110 ± 6	2.3 ± 0.6	50.5 ± 11.4
		Marine/roots	7.5yr	7/1	4	44.1 ± 6.1	7.2 ± 1.0	100 ± 5	1.5 ± 0.4	71.6 ± 19.7
	Interior	Organic	7.5yr	2.5/2	5	70.4 ± 4.6	31.7 ± 8.1	188 ± 25	10.3 ± 2.2	18.5 ± 2.7
		Marine/roots	10yr	4/2	6	57.1 ± 9.3	15.5 ± 5.8	130 ± 19	4.8 ± 2.0	32.6 ±18.5
		Marine	10yr	7/2	9	40.2 ± 2.5	6.5 ± 0.4	96.5 ± 4.5	1.1 ± 0.3	97.5 ± 40.1
Pacific Coast										
Low	Shoreline	Organic	7.5yr	2.5/2	4	59.6 ± 2.4	18.6 ± 3.5	73.7 ± 13.3	2.3 ± 0.3	32.0 ± 4.3
		Silt loam - silt	gley2	4/5b	9	49.6 ± 5.5	9.9 ± 2.7	31.4 ± 14.5	1.1 ± 0.5	27.5 ± 3.3
	Interior	Silt/roots	7.5y	3/2	8	33.6 ± 2.1	6.7 ± 0.7	7.1 ± 1.9	0.4 ± 0.1	17.7 ± 3.4
Medium	Shoreline	Silt loam - silt	7.5yr	3/2	5	41.0 ± 5.6	8.8 ± 2.8	19.4 ± 9.8	1.7 ± 1.2	13.0 ± 5.0
		Organic	2.5yr	3/1	7	69.4 ± 5.1	23.7 ± 6.8	94.3 ± 30.7	4.1 ± 1.7	24.8 ± 8.4
		Silt/roots	7.5yr	2.5/1	2	69.2 ± 1.1	19.4 ± 0.4	74.5 ± 5.9	4.9 ± 0.1	15.3 ± 1.0
	Interior	Silt loam - silt	7.5yr	3/2	3	27.7 ± 2.8	5.2 ± 1.0	5.0 ± 2.0	0.5 ± 0.2	10.7 ± 2.8
		Sand loam - loam	10yr	3/2	4	28.8 ± 1.6	4.7 ± 0.9	4.7 ± 1.6	0.3 ± 0.1	15.5 ± 6.0
		Silt loam - silt	7.5r	3/1	3	29.8 ± 3.1	5.4 ± 0.6	6.9 ± 2.6	0.7 ± 0.2	10.5 ± 1.7
		Silt/roots	5y	2.5/1	4	46.9 ± 3.7	11.8 ± 3.1	40.0 ± 26.1	1.9 ± 1.8	24.5 ± 5.7
High	Shoreline	Silt loam - silt	7.5yr	3/2	2	29.9 ± 0.6	5.2 ± 0.1	9.5 ± 2.6	0.6 ± 0.0	15.8 ± 4.4
		Sand loam - loam	10yr	3/2	3	27.3 ± 1.2	4.6 ± 0.8	6.1 ± 2.5	0.5 ± 0.2	13.8 ± 8.2
		Silt/roots	7.5yr	3/2	3	33.1 ± 13.8	6.7 ± 5.3	16.6 ± 22.7	1.1 ± 1.2	12.3 ± 4.1
	Shrimp	Silt loam - silt	7.5yr	3-4/1	2	34.7 ± 1.0	6.1 ± 0.2	8.7 ± 2.7	0.8 ± 0.1	11.5 ± 2.5
	Pond	Organic	2.5yr	2.5/1	6	65.0 ± 18.1	25.1 ± 6.2	103 ± 45	3.2 ± 1.3	33.8 ± 9.5
		Silt loam - silt	5y	2.5/1	1	62.8	16.3	58.8	1.8	32.7
		Silt/roots	2.5yr	2.5/2	2	57.3 ± 4.2	13.4 ± 2.3	40.3 ± 8.4	1.3 ± 0.1	30.8 ± 3.1

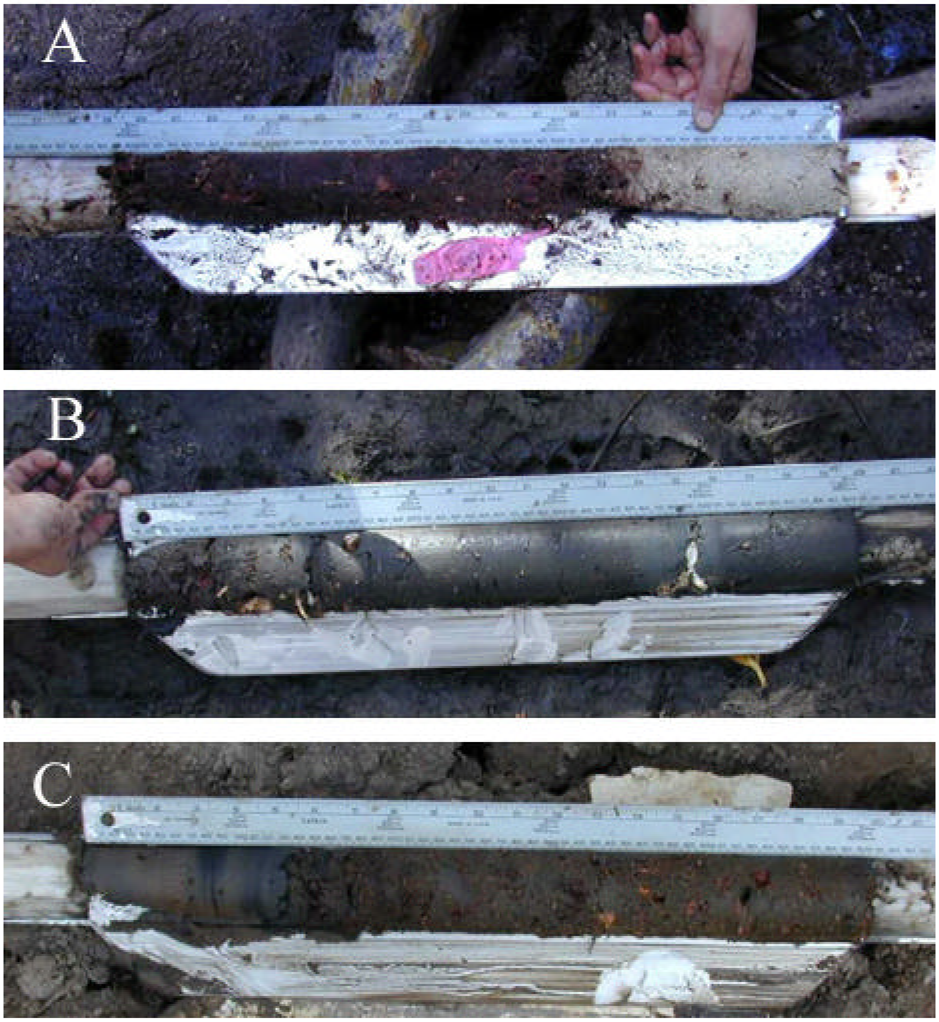

Plate 4. Examples of cores extracted from sites on the Caribbean and Pacific coasts of Honduras in January 2000. A) Core from the Caribbean high impact site (Guanaja, Bay Islands) shows sub-surface red mangrove peat overlying calcareous sediment. B) Core from the Pacific low impact shoreline site (Gulf of Fonseca) shows a surface organic layer over silt layer. C) Core from the Pacific medium impact shoreline site (Gulf of Fonseca) shows a surface silt loam deposit over an organic stratum.

On the Pacific coast, full cores could not be collected in several instances due to the harder, dryer soil encountered at this location. However, sampling was sufficient to allow description of general patterns of deposition as well as identification of sediment deposits resulting from the hurricane. At the low impact site, the shoreline cores had an upper layer of organic soil (20-40 % organic matter) about 30 cm thick above a silt layer but with no overlying sediment deposit (plate 4B). In the interior, the soil was composed of hard-packed silt and interspersed mangrove roots, and coring could extend to only 30 cm below the soil surface. At the medium, high, and shrimp pond impact sites, organic deposits were overlain by silt or silty loam of varying depths, depending on impact level, zone, and human disturbance. Sediment thickness over root-containing strata was almost 1 m at the medium impact interior site and consisted of grading strata of silt or silty loam and sandy loam. The high impact shoreline also showed a thick loam to silty loam deposit (40-50 cm) over organic layers. Sediment and debris were initially deposited in the high impact interior (shrimp pond) to a depth of about 1 m (McKee, personal observation in August 1999), but most of this sediment was removed by shrimp farmers prior to coring in January 2000. Thus, the sediment thickness overlying organic layers was about 10 cm deep when cores were taken.

Total soil N in the Bay Islands showed little effect of hurricane impact and ranged from 14 to 18 mg/g in the upper 10 cm across sites (table 1). Total N generally decreased with depth and with transition from peat to marine sediment (table 1). At Pacific sites, total soil N was considerably lower than at Bay Island sites and exhibited different depth profiles across impact levels (table 1). Total N was highest in the upper organic layer at the low impact shoreline and was lower at depth. At medium and high impact sites, the upper soil strata had low total N (< 1 mg/g), which generally reflected the storm deposition of mineral sediment; deeper organic strata had higher total N (1.1 to 5 mg/g).

Physical Characteristics of Surface Soils and Sediments

Soil bulk density, percent organic matter, relative saturation, and shear strength were measured to assess hurricane impacts on soil physical characteristics. In Honduras, soil bulk density was low on the Caribbean coast (0.15 ± 0.04 g cm^{-3}), compared to the Pacific coast (0.86 ± 0.17 g cm^{-3}), and generally reflected the difference in soil texture (organic vs. mineral). Bulk density did not differ significantly among the Bay Island sites, although the high impact sites tended to have a higher bulk density than the other sites (fig. 2A, table 2a). In the Gulf of Fonseca, the low impact sites had lower bulk density than the medium and high impact sites, and bulk density increased from shoreline to interior (fig. 2B, table 2b). The low impact site in Guatemala exhibited a bulk density intermediate to the sites in Honduras; the high impact site had a higher bulk density due primarily to sand deposition (table 3). Organic matter content averaged $7.1 \pm 3.8\%$ on the Pacific coast and $62.2 \pm 14.6\%$ in the Bay Islands (fig. 2). Although bulk density did not differ significantly among Bay Island sites, percent organic matter varied among impact levels (low impact > medium and high impact), and was greater in shoreline versus interior zones (fig. 2A, table 2a). Percent organic matter in the Pacific was highest along the low impact shoreline while all other sites were similar (fig. 2B, (table 2b). In Guatemala, soil organic matter content was highest at the low impact site (table 3).

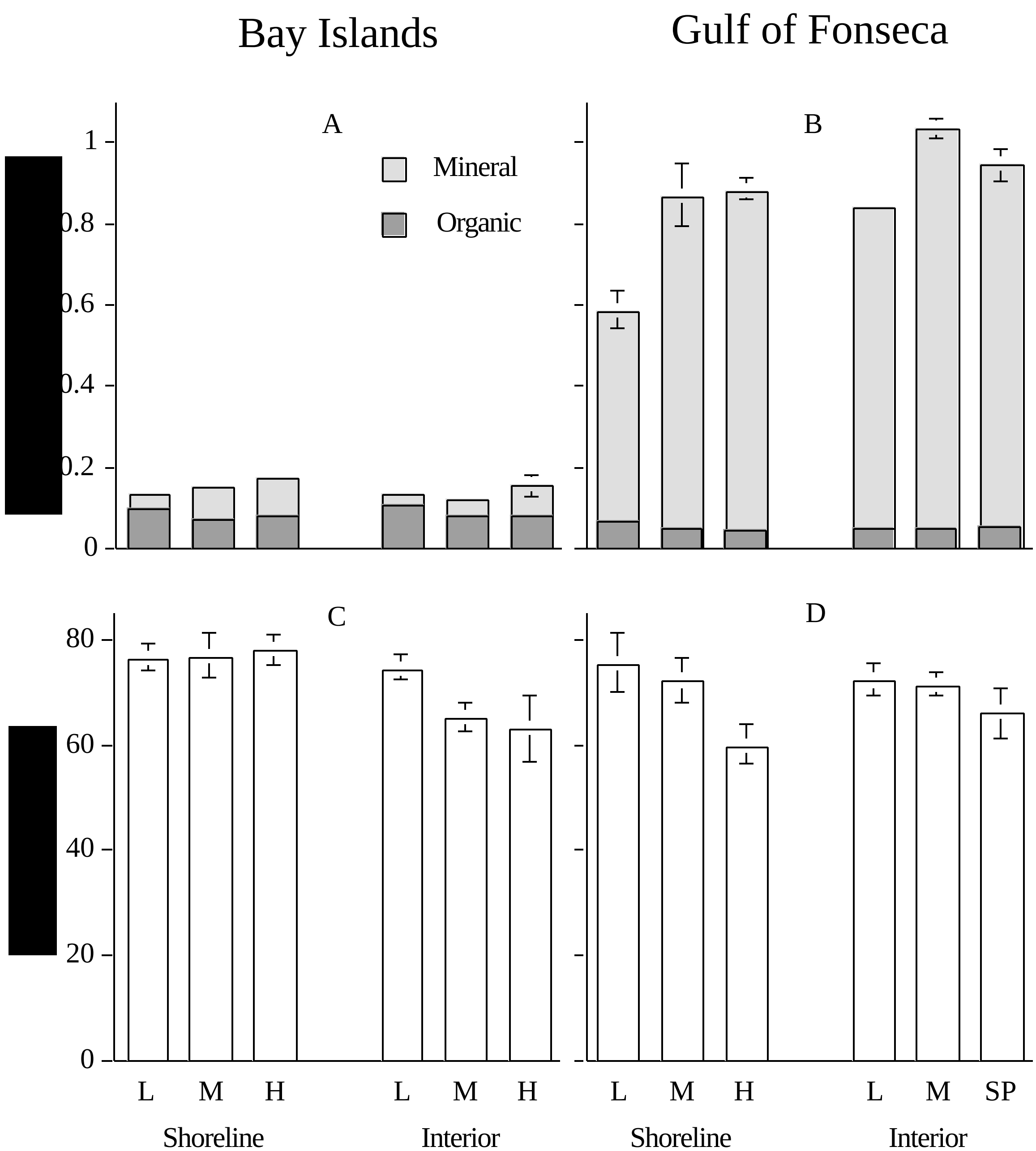

Figure 2. Bulk density (with mineral and organic components) and relative saturation of soil measured in January 2000 at shoreline and interior plots established at different impact levels (L = low impact; M = medium impact; H = high impact) on the Caribbean (Bay Islands) and Pacific (Gulf of Fonseca) Coasts; SP = shrimp pond. Values are the mean and 1 standard error (n = 6).

Table 2a. ANOVA results for physical characteristics of surface soils on the Caribbean (Bay Islands) Coast of Honduras in January 2000. Data were analyzed as a 3 x 2 factorial with Impact (I) and Zone (Z) as main effects. Repeated measures ANOVA was used to analyze depth effects (D). Values are F-ratios with significant differences indicated by ****$p < 0.0001$, ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and $^{ns}p > 0.05$ (not significant); n = 6.

Source:	I	Z	I x Z	D	D x I	D x Z	D x I x Z
Variables	$F_{2,30}$	$F_{1,30}$	$F_{2,30}$				
Bulk Density	2.867^{ns}	1.203^{ns}	0.780^{ns}				
Organic Matter	20.77^{****}	9.087^{**}	0.535^{ns}				
Relative Saturation	1.038^{ns}	9.351^{**}	1.605^{ns}				
Shear Strength at:	$F_{2,30}$	$F_{1,30}$	$F_{2,30}$	$F_{2,29}$	$F_{4,60}$	$F_{2,29}$	$F_{4,60}$
Surface	45.23^{****}	123.7^{****}	22.34^{****}				
5 – 25 cm	26.09^{****}	112.6^{****}	5.312^{**}	0.676^{ns}	1.596^{ns}	1.059^{ns}	1.367^{ns}

Table 2b. ANOVA results for physical characteristics of surface soil on the Pacific (Gulf of Fonseca) Coast of Honduras in January 2000. Data was analyzed as a one-way, 6 level ANOVA grouped by Impact (I) by Zone (Z) combinations. *A priori* 1 df contrasts were used to examine impact and zone effects. Repeated measures ANOVA was used to analyze depth effects (D). Values are F- and T- ratios with significant differences indicated by ****$p < 0.0001$, ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and $^{ns}p > 0.05$ (not significant); n = 6.

Source:	IZ	I	Z	D	D x IZ	D x I	D x Z
Variables	$F_{5,30}$	$T_{1,20}$	$T_{1,20}$				
Bulk Density	12.00****	5.615****	4.653****				
Organic Matter	5.903***	3.400**	2.609*				
Relative Saturation	1.960^{ns}	2.025^{ns}	0.052^{ns}				
Shear Strength at:	$F_{5,30}$	$T_{1,20}$	$T_{1,20}$				
Surface	55.71****	14.24****	2.052*				
	$F_{5,30}$	$F_{1,30}$	$F_{1,30}$	$F_{2,29}$	$F_{10,60}$	$F_{2,29}$	$F_{2,29}$
5 – 25 cm	16.50****	59.93****	4.998*	0.146^{ns}	2.061*	1.279^{ns}	2.229^{ns}

Table 3. Physicochemical characteristics of soils and sediments at high and low hurricane impact sites in Guatemala. Values are the mean ± 1 standard error. Significant difference between impact levels was determined with a t-test and indicated by * (p = 0.05), ** (p = 0.01), ***(p = 0.001), **** (p = 0.0001), and ns (not significant); n = 3.

Variable	Impact Level		Student's t-value
	High	Low	
Soil			
Bulk Density (g/cm^3)	0.76 ± 0.04	0.47 ± 0.08	3.18**
% Organic Matter	0.71 ± 0.03	15.3 ± 3.3	-4.48**
Moisture Content (g/cm^3)	0.07 ± 0.01	0.60 ± 0.02	-24.30****
Eh (mV) at depth:			
1 cm	336 ± 24	-106 ± 18	14.70****
15 cm	468 ± 34	-110 ± 3	16.99***
30 cm	307 ± 149	-110 ± 9	2.80*
Pore water			
Salinity (‰)	0.00 ± 0.00	13.0 ± 3.0	3.98*
pH	7.95 ± 0.13	6.29 ± 0.07	-11.4***
Sulfide (mM)	0.02 ± 0.003	0.64 ± 0.30	2.11^{ns}
NH_4-N (µM)	11.04 ± 2.99	11.30 ± 4.46	0.05^{ns}
PO_4-P (µM)	6.57 ± 0.70	1.79 ± 1.01	3.87**

At Caribbean sites, the shoreline soils were relatively more saturated with water than the interior soils, which held less water as the impact level increased (low impact > high impact) (fig. 2C, tables 2a and 3). This pattern may be caused by the decrease in soil organic matter along the same gradient. Relative saturation of the soil varied across Pacific Coast sites (table 2b). The Pacific shoreline sites tended to be relatively drier due to the elevation increase caused by the imported sediment as well as lower organic matter content (fig. 2D).

Shear strength at the soil surface ranged from 0 (not detectable) to 0.55 kg cm^{-2} over both coasts (fig. 3). In the Bay Islands, shoreline soils were much stronger, due primarily to prolific surface root production by mangroves, compared to interior soils (plate 5). Soil strength at both medium and low impact interior sites was about four times lower than in respective shoreline sites (fig. 3A, table 2). However, high impact sites had the lowest shear strength among impact levels in both zones. In the Pacific, shear strength did not vary significantly with zone, but medium and high impact soil surfaces, regardless of spatial position, were about three times weaker than low impact soils (fig. 3B, table 2b). At these sites, surface shear strength reflected differences in soil moisture content in addition to root density.

Overall, subsurface shear strength also showed a wide range across sites and significant differences with hurricane impact (fig. 3C and D). The differences among impact levels and position were most pronounced in the Bay Islands where the highest soil strength was measured in the medium and low shoreline sites, while medium and high impact interior sites showed low subsurface soil strength. However, there were no significant changes over depth (fig. 3C, table 2a). At Pacific sites, changes in shear strength over depth were significant in three sites; soil strength increased with depth in the shrimp pond and medium impact shoreline, whereas it decreased with depth in the low impact shoreline (fig. 3D, table 2b).

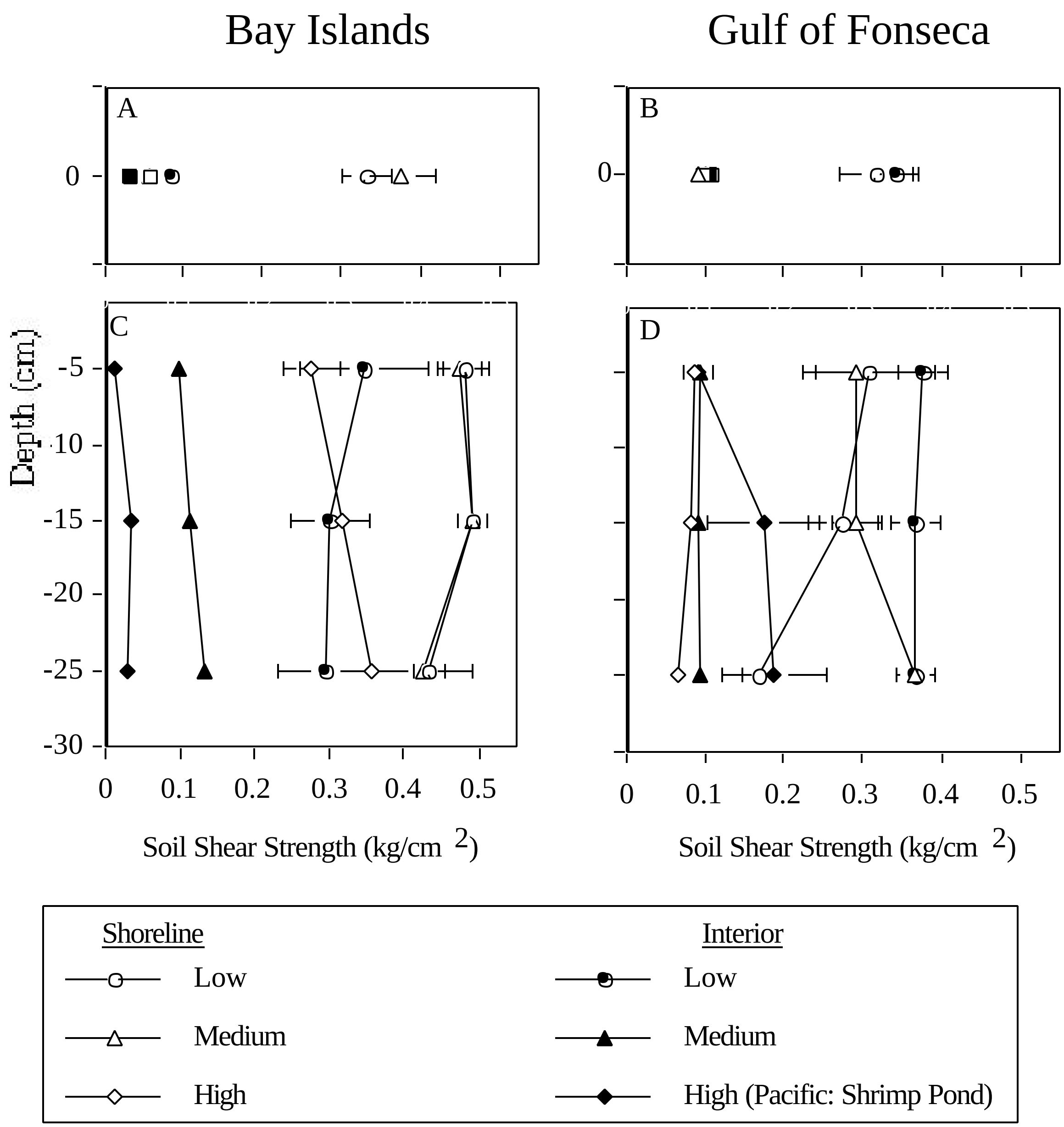

Figure 3. Soil shear strength measured in January 2001 at the soil surface and at depth at shoreline and interior plots established at different impact levels on the Caribbean (Bay Islands) and Pacific (Gulf of Fonseca) coasts of Honduras. Values are the mean and 1 standard error (n = 18 at the soil surface; n = 6 over depth).

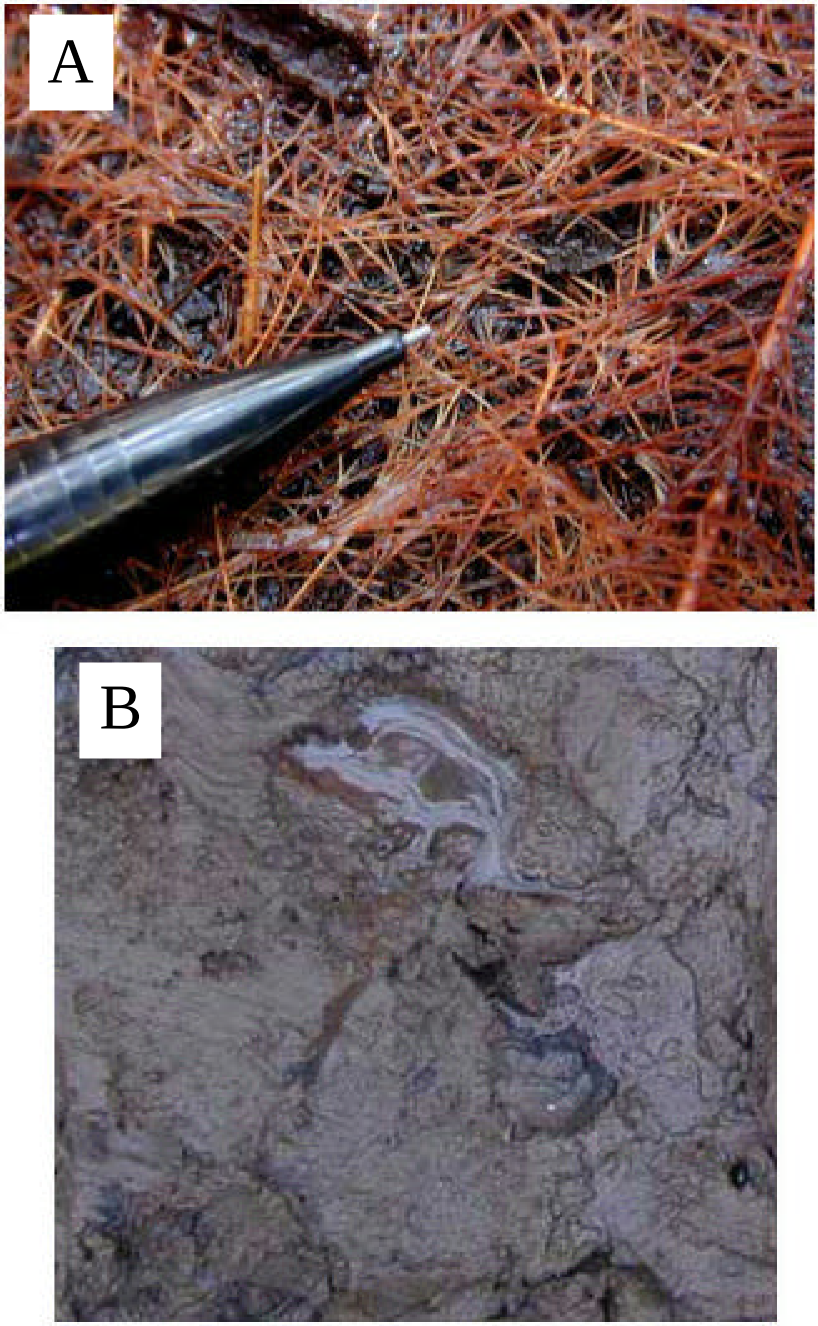

Plate 6. Close-up view of soil surface at A) the Caribbean low impact site (Roatán, Bay Islands) versus B) that on the Pacific coast (Gulf of Fonseca). Note the prolific production of fine roots at the soil surface on Roatán, which contributes significantly to soil strength and soil formation in this low-sediment environment.

Chemical Characteristics of Soils and Sediments

Pore Water Salinity

Overall, pore water salinity varied across sites from 0 to 56 ppt but exceeded 10 ppt at most sites (fig. 4). In Honduras, interior sites showed the most variation across impact levels (table 4), but the patterns were different on the two coasts. In the Bay Islands, salinity increased over time across impact level and was greatest in the interior zone. The high impact site at Guanaja exhibited hypersaline conditions in January 2000 and 2001, and the medium impact site at Roatán was slightly hypersaline in 2001 but not 2000 (fig. 4A). In the Gulf of Fonseca, the interior low impact site showed higher salinity than the medium and high impact sites in January 2000. Pore water could not be acquired from low and medium impact interior sites in January 2001 due to soil dryness, but the high impact (shrimp pond) site showed an increase in pore water salinity from 2000 to 2001 ($t = 5.66$, $p = 0.0109$; fig. 4B). Salinity in Guatemalan mangrove forests ranged from 0 to 19 ppt; the high impact sites were less saline than the low impact sites (table 3).

Pore Water pH

In Honduras, pore water pH ranged from 6-7.2, and there were no consistent patterns across impact levels, between zones, or between coasts (fig. 4, table 4). Averaged over all sites in the Bay Islands, pH increased slightly (0.28 pH unit) from January 2000 to 2001.

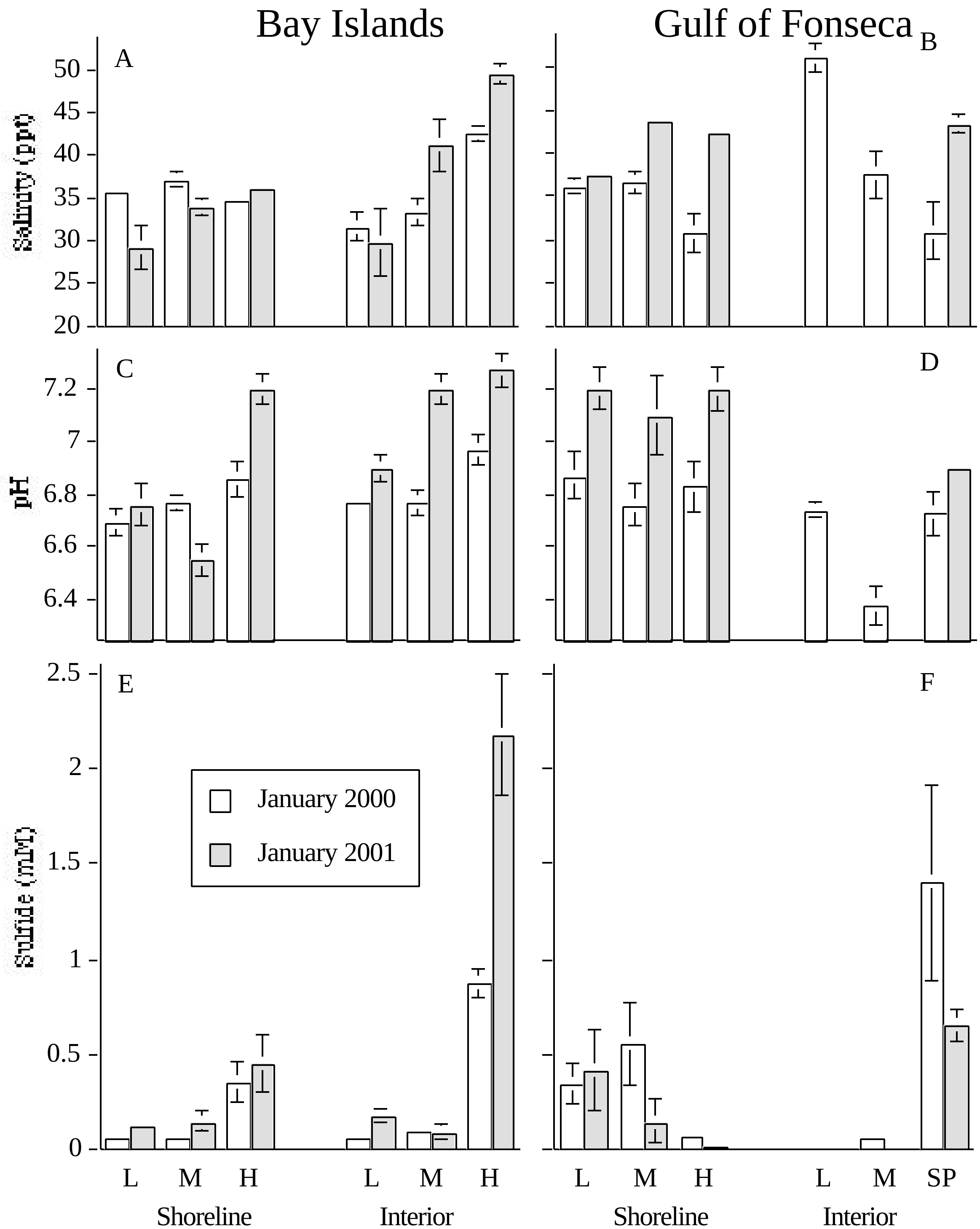

Figure 4. Pore water salinity, pH, and sulfide concentrations measured in January 2000 and January 2001 at shoreline and interior plots established at impact levels (L = low impact; M = medium impact; H = high impact; SP = shrimp pond) on the Caribbean (Bay Islands) and Pacific (Gulf of Fonseca) coasts of Honduras. Samples were not collected at the Pacific low and medium impact interior plots in January 2001. Values are the mean and 1 standard error (n = 6).

Table 4a. ANOVA results for physicochemical characteristics of surface soil collected January 2000 and 2001 from the Bay Islands, Honduras (Caribbean). Data was analyzed as a 3 x 2 factorial with Impact (I) and Zone (Z) as main effects and Time (T) as the repeated measure. Some values were transformed (nutrients, ln(x+1); sulfide, (1/(x+1)) to correct uneven variance. Values are F-ratio with significant differences indicated by ****p < 0.0001, ***p < 0.001, **p < 0.01, *p < 0.05, and ^{ns}p > 0.05 (not significant), n = 6.

Source:	I	Z	I x Z	T	T x I	T x Z	T x I x Z
Variables	$F_{2,30}$	$F_{1,30}$	$F_{2,30}$	$F_{1,30}$	$F_{2,30}$	$F_{1,30}$	$F_{2,30}$
Pore Water							
Salinity	15.78^{****}	6.907^{*}	7.884^{**}	0.821^{ns}	10.88^{***}	21.18^{****}	1.581^{ns}
pH	22.51^{****}	3.239^{ns}	1.000^{ns}	74.14^{****}	8.058^{**}	0.067^{ns}	0.362^{ns}
Sulfide	85.75^{****}	38.21^{****}	35.91^{****}	16.57^{***}	9.807^{***}	8.436^{**}	9.270^{***}
$NH_4 – N$	26.13	1.179	1.424				
PO_4 - P	30.98^{****}	26.06^{****}	3.897^{*}				
Soil E_h at:							
1 cm	14.57^{****}	1.136^{ns}	10.33^{***}	295.9^{****}	1.324^{ns}	2.696^{ns}	3.635^{*}
15 cm	15.75^{****}	0.101^{ns}	4.390^{ns}	122.5^{****}	1.273^{ns}	0.421^{ns}	2.326^{ns}
30 cm	22.38^{****}	2.382^{ns}	0.830^{ns}	150.4^{****}	0.723^{ns}	2.487^{ns}	2.581^{ns}

Table 4b. ANOVA results for physicochemical characteristics of surface soil collected January 2000 and 2001 from the Gulf of Fonseca, Honduras (Pacific). Data were analyzed as a one-way ANOVA with six impact by zone combinations as levels; repeated measures ANOVA was conducted on variables measured in both 2000 and 2001; a priori 1 df contrasts were used to make impact and zone comparisons--see text for further statistical details. Some values were transformed (nutrients, ln(x+1); sulfide, (1/(x+1)) to correct uneven variance. Values are F- and T- (1 df contrasts) ratios with significant differences indicated by ****$p < 0.0001$, ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and $^{ns}p > 0.05$ (not significant), n = 6.

Source:	IZ	I	**Z**	T	T x IZ	T x I	T x Z
Variable	$F_{5,30}$	$T_{1,20}$	$T_{1,20}$	$F_{1,14}$	$F_{3,14}$	$F_{2,11}$	
Pore water							
Salinity	11.32****	4.311***	4.910****	57.25****	5.746**	6.577*	NA
pH	4.953**	2.567*	3.691***	14.74**	2.052^{ns}	0.072^{ns}	NA
Sulfide	6.177***	0.811^{ns}	1.804	18.23***	8.900**	2.538^{ns}	NA
NH_4 – N	5.951**	2.277*	0.617				
PO_4 - P	9.066***	1.310	1.227				
Soil E_h at:	$F_{5,30}$	$F_{1,30}$	$F_{1,30}$	$F_{1,30}$	$F_{5,30}$	$F_{1,30}$	$F_{1,30}$
1 cm	9.763****	13.12**	29.25****	0.026^{ns}	4.898**	5.942*	0.171^{ns}
15 cm	12.65****	2.504^{ns}	46.02****	4.891*	8.678****	9.828**	8.058**
30 cm	14.97****	4.247*	48.78****	2.059^{ns}	4.041**	7.520*	1.459^{ns}

Pore Water Sulfide

Sulfide concentrations in pore water ranged from below detection limits to ~3 mM in Honduras and were generally higher in interior forest zones (fig. 4E and F). In the Bay Islands, the most consistent pattern was elevated sulfide at both shoreline and interior zones at high impact sites(Guanaja). Sulfide increased significantly from January 2000 to 2001, especially at the high impact interior site (fig. 4E, table 4a). In the Gulf of Fonseca, sulfide was low in the low and medium impact interior sites but elevated at the shrimp pond site (fig. 4F, table 4b). In contrast to the Bay Islands, sulfide in the Gulf of Fonseca decreased from January 2000 to 2001 at medium impact shoreline (df = 2, t-ratio = -3.28, $p = 0.0818$) and high impact interior (df = 5, t-ratio = -3.22, $p = 0.0235$) locations. In Guatemala, the high impact sites had lower sulfide concentrations (table 3). At both Gulf of Fonseca and Guatemala locations, sites with high mineral sediment deposition (fig. 1) had low sulfide concentrations.

Soil Redox Potential

In Honduras, soil redox potential (E_h) varied across sites and dates from strongly reducing (-224 ± 13 mV, 30 cm depth) to oxidized (+515 ± 88 mV, 15 cm depth). In general, Bay Island soils were more reducing and less variable than Pacific soils (fig. 5). In the Bay Islands, soils were more reducing in 2001 than in 2000, and E_h was lowest overall in the high impact interior and highest in the low impact sites (fig. 5A and C, table 4a). In the Gulf of Fonseca, the shoreline zones were more reducing than the interior zones (fig. 5B and D, table 4b). The shrimp pond site was consistently more reducing at depth than the low and medium

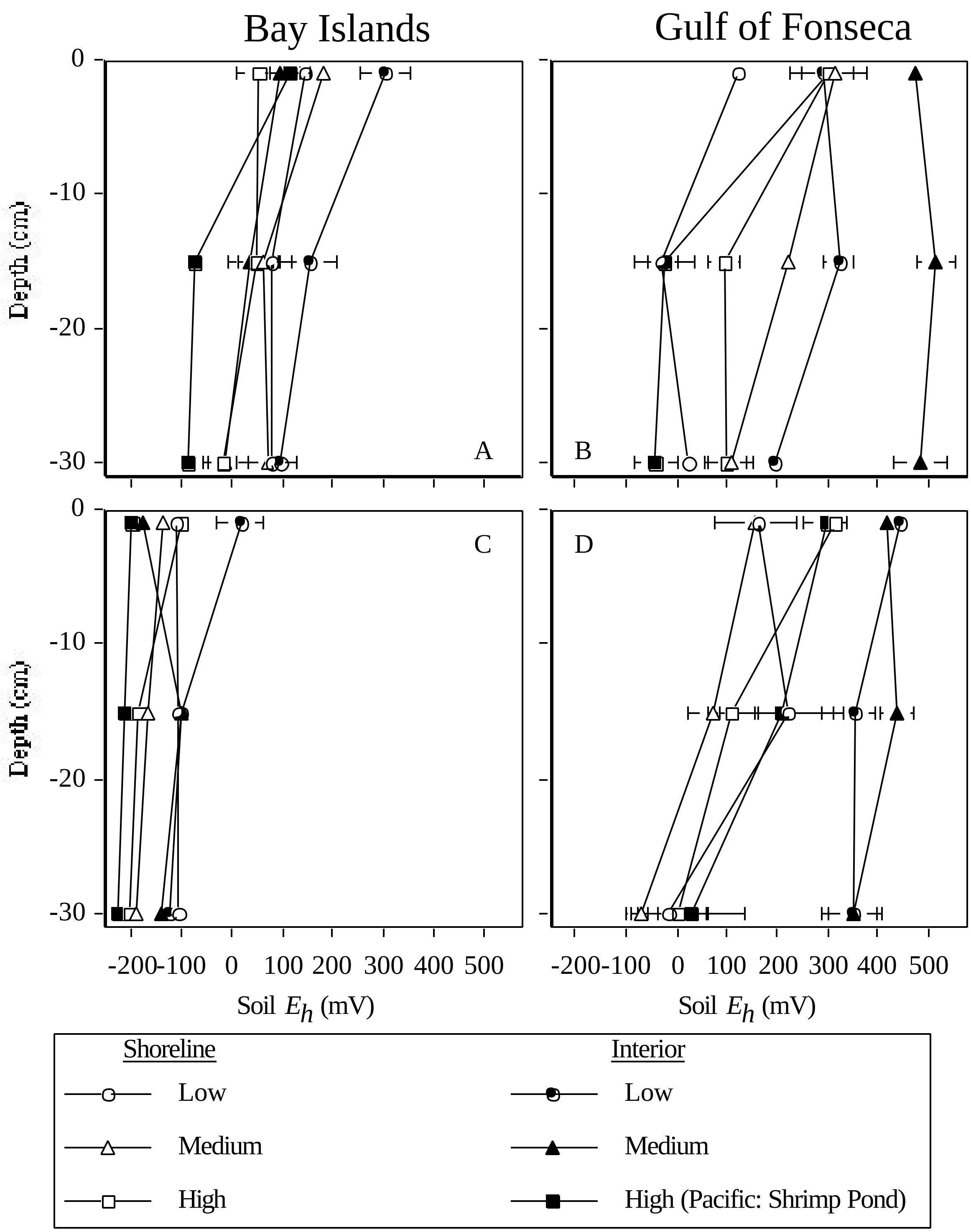

Figure 5. Soil REDOX potentials (E_h) measured in January 2000 (A, B) and 2001 (C, D) at shoreline and interior plots established at different impact levels on the Caribbean (Bay Islands) and Pacific (Gulf of Fonseca) coasts of Honduras. Measurements were made in situ at 1, 15, and 30 cm depths after equilibration for 15 minutes. Values are the mean and standard error (n = 6).

impact interior sites (table 4b). In Guatemala, soil E_h was higher at high impact sites, compared to low impact sites, a pattern that reflected elevation differences (table 3).

Nutrients

Pore water NH_4-N and PO_4-P concentrations, which were determined in 2000 only, varied from 5 to 138 µM and 0.15 to 32 µM, respectively, in Honduras (fig. 6). In the Bay Islands, NH_4-N and PO_4-P concentrations were elevated along high impact shorelines and in the interior zone at medium and high impact sites (fig. 6, table 4a). On the Pacific coast, NH_4-N and PO_4-P concentrations were elevated in the shrimp pond plots, and NH_4-N was elevated in the high impact shoreline (fig. 6B and D, table 4b). In Guatemala, there was no difference in NH_4-N, but PO_4-P was higher at the high impact site (table 3).

Root Production

Total mangrove root production (to a 30 cm depth) ranged from 0 to 1,523 g m^{-2} y^{-1} across zones and impact levels on the two coasts of Honduras (fig. 7). Root production generally decreased over depth at all sites, but the difference between upper and lower depths was most pronounced at high impact sites. In the Bay Islands, total root production did not differ between interior (308 ± 62 g m^{-2} y^{-1}) and shoreline (265 ± 56 g m^{-2} y^{-1}) zones, but did vary by impact level (table 5). At Guanaja, where mangroves experienced near total mortality, no root growth into bags occurred at either shoreline or interior positions. Both fine and coarse root production at medium impact sites did not differ by zone and was not significantly different from that at low impact sites. Fine roots accounted for 76% of the total production along the shoreline and 50%

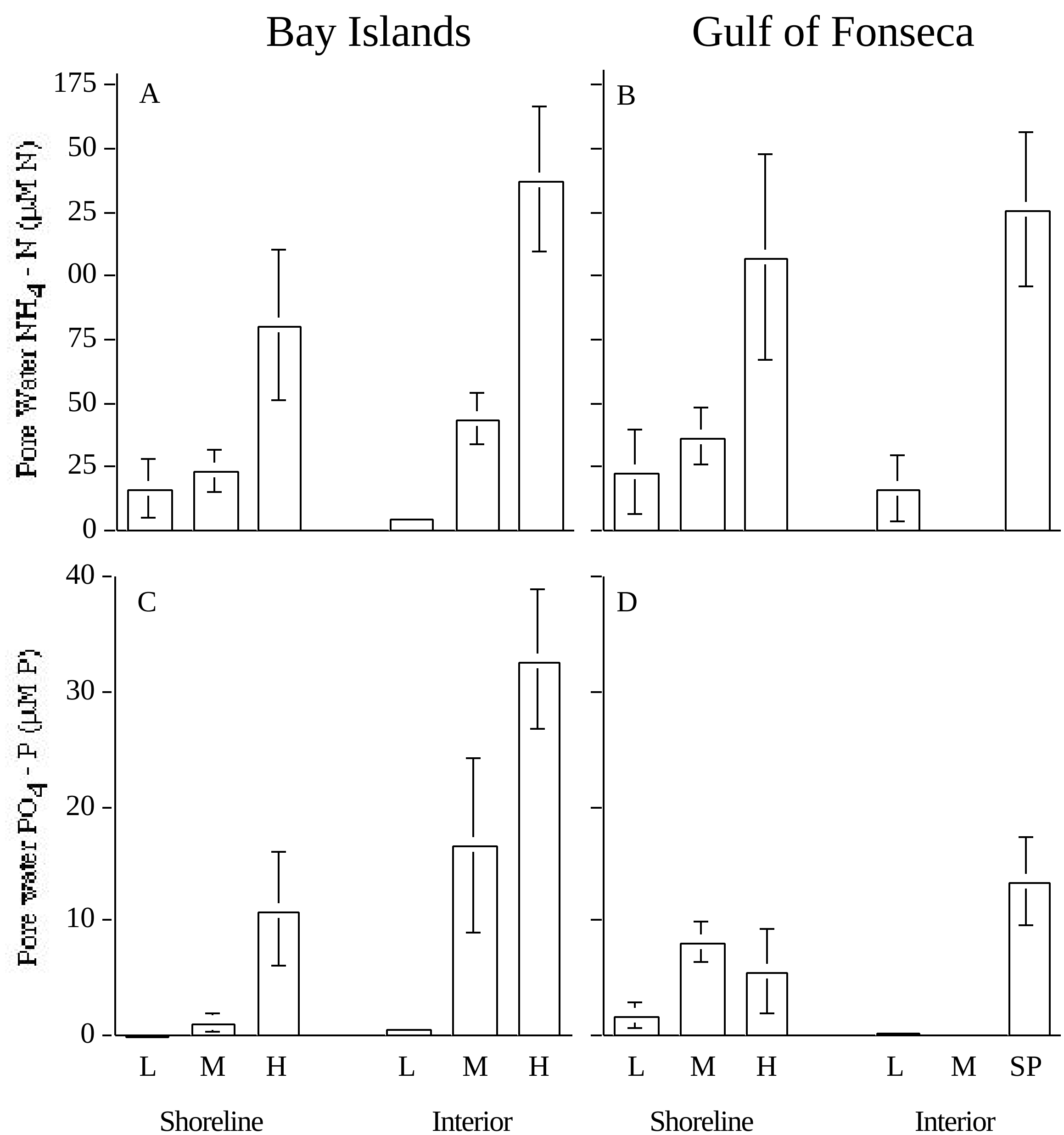

Figure 6. Pore water NH_4 - N, and PO_4 - P concentrations measured in January 2000 at shoreline and interior plots established at different impact levels (L = low; M = medium; H = high; SP=shrimp pond) on the Caribbean (Bay Islands) and Pacific (Gulf of Fonseca) coasts of Honduras. Samples were not collected at the Pacific medium impact interior site, and only three samples were collected at the Pacific high impact shoreline site. Values are the mean and standard error (n = 6).

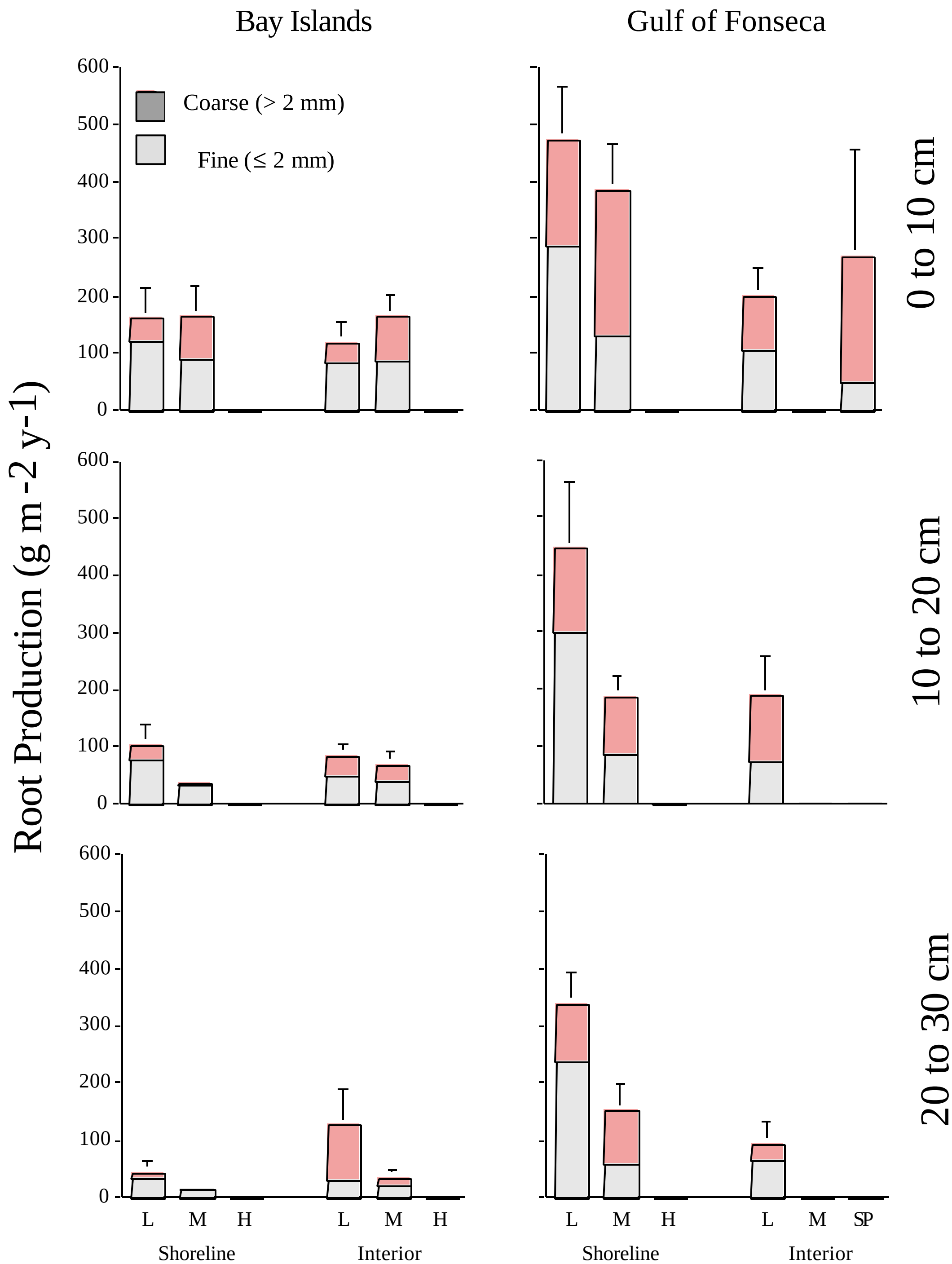

Figure 7. Belowground root production (to a 30 cm depth) by size class (fine and coarse) at shoreline and interior plots established at different impact levels (L = low impact; M = medium impact; H = high impact; SP = shrimp pond) on the Caribbean (Bay Islands) and Pacific (Gulf of Fonseca) Coasts of Honduras. Values are the mean and 1 standard error (n = 6).

Table 5. ANOVA results for root production by size class (fine and coarse) measured on the Caribbean (Bay Islands) and Pacific (Gulf of Fonseca) Coasts of Honduras. Data were analyzed as a two-way ANOVA (Caribbean) or a one-way, 6 level ANOVA (Pacific) grouped by Impact (I) by Zone (Z) combinations. *A priori* 1 df contrasts were used to examine impact and zone effects at Pacific sites—see text for statistical details. Repeated measures ANOVA was used to analyze depth effects (D). Values are F- and T- ratios with significant differences indicated by ****$\underline{p} < 0.0001$, ***$\underline{p} < 0.001$, **$\underline{p} < 0.01$, *$\underline{p} < 0.05$, and $^{ns}\underline{p} > 0.05$ (not significant); n = 6.

Source	I	Z	I x Z	D	D x I	D x Z	D x I x Z
Caribbean Coast	$F_{2,28}$	$F_{1,28}$	$F_{2,28}$	$F_{2,29}$	$F_{4,60}$	$F_{2,29}$	$F_{4,60}$
Total Root Production	149.2^{****}	1.724^{ns}	0.491^{ns}	37.03^{****}	9.26^{****}	4.28^{*}	1.21^{ns}
Fine Root Production	13.42^{****}	0.384^{ns}	0.592^{ns}	27.80^{****}	6.41^{***}	1.32^{ns}	1.03^{ns}
Coarse Root Production	5.03^{*}	1.87^{ns}	0.712^{ns}	3.39^{*}	2.81^{*}	1.00^{ns}	0.855^{ns}
	IZ	I	Z	D	D x IZ	D x I	D x Z
Pacific Coast	$F_{5,21}$	$F_{1,21}$	$F_{1,21}$	$F_{2,20}$	$F_{10,40}$	$F_{2,42}$	$F_{2,20}$
Total Root Production	78.21^{***}	137.7^{***}	26.33^{****}	19.29^{****}	4.39^{*}	2.08^{ns}	7.17^{**}
Fine Root Production	61.00^{****}	219.4^{****}	99.23^{****}	3.59^{*}	1.29^{ns}	1.58^{ns}	1.89^{ns}
Coarse Root Production	7.34^{***}	7.52^{*}	8.33^{**}	4.96^{*}	1.73^{ns}	1.91^{ns}	0.677^{ns}

in the interior at the low impact site. Impact level had no significant effect on the proportion of fine versus coarse roots.

Pacific sites (375 ± 84 g m^{-2} y^{-1}) exhibited higher root production overall than the Bay Islands sites (184 ± 35 g m^{-2} y^{-1}). Also in contrast to the Bay Islands, there was a dramatic difference in total root production between shoreline (861 ± 125 g m^{-2} y^{-1}) and interior (295 ± 106 g m^{-2} y^{-1}) sites. At the low impact site in the Gulf of Fonseca, fine roots accounted for 66% of total root biomass at shoreline plots and 51% at interior plots. No roots were produced at the high impact shoreline, which was consistent with observations of aboveground mortality. Few or no roots grew into bags at the medium and high impact interiors, despite the presence of scattered trees. Although coarse root production at the medium impact shoreline site was similar to that at the low impact shoreline, the production of fine roots was lower (1 df contrast: t-ratio = -2.61, $p = 0.016$).

Discussion

Hurricane Effects on Physicochemical Characteristics of Soils and Sediments

Hurricanes may directly alter physicochemical attributes of mangrove soils by deposition of sediment or organic debris or indirectly by alteration of hydrology or biotic processes affecting soil structure and chemistry. All study sites in Honduras and Guatemala experienced localized impacts from sediment deposition, although the sediment type and amount of deposition differed. However, highest mangrove mortality occurred in the Bay Islands where little or no sediment burial occurred. Thus, it is important to consider indirect hurricane effects on soil physical and chemical properties that, in turn, may have contributed to mortality and influenced subsequent recovery.

Inorganic sediment deposition may alter soil texture, nutrient concentrations, and permeability, which have feedback effects on mangrove productivity. The most obvious alteration in mangrove soil properties was a consequence of sediment deposition. The storm deposits in the Gulf of Fonseca were distinguishable from prestorm soils by changes in particle size distribution and organic matter content and by the visible lack of mangrove roots. The coarser sediment with low organic content increased bulk density of surface strata in these locations. Cahoon and others (1995) also found that sediment deposited by Hurricane Andrew in Louisiana marshes was coarse silt with a higher bulk density (>0.8 g/cm^3) than soils at prestorm depths. Sediment deposition in the Bay Islands was easily recognized since the deposited material consisted of shells, calcareous algal chips, sand, or marl, and this light-colored material contrasted sharply with the darker peat substrate (plate 5). The greatest impact of sediment deposition on the Caribbean coast occurred in Guatemala, where over 1 m of quartz sand (terrestrial origin) was deposited on mangroves. Localized deep deposits (marine origin) were also observed at the medium impact site on Roatán and directly affected a narrow zone just landward of the shoreline plots (ridge; fig. 3; table 1).

Mangrove soils are normally saturated, but deposition of sediment raised elevations and resulted in dryer soils relative to low impact sites. Effects of sediment deposition on soil moisture were evident at both Pacific and Caribbean sites even though the storm deposit differed in composition. Dryer soil conditions may slow regrowth and/or alter the species composition of recolonizing vegetation from that of the original forest. Since there was little sediment deposition at the high impact site on Guanaja and in shoreline and interior plots on Roatán, changes in soil texture, bulk density and moisture content were comparatively less.

One important feature of soils that determines resistance to erosion and other disturbances is shear strength (McGinnis, 1997). However, little is known about how resistant mangrove soils are to impacts of hurricanes or what soil components contributing to soil shear strength might be altered. At Pacific sites, changes in soil texture and moisture content, along with a lower root density, decreased soil strength but did not substantially alter soil integrity. At Bay Island sites, death of the root system decreased soil strength substantially at the medium and high impact sites and caused a loss of soil integrity in interior forest plots at Guanaja (plate 2B). Despite total mortality of trees, the high impact shoreline on Guanaja surprisingly maintained shear strength, which appeared to be due to a higher density of fine roots produced by *R. mangle* prior to the hurricane. The fine roots form a strong matrix that can apparently persist for some time and may prevent soil slumping and/or erosion in this zone, thereby protecting the interior soils. Interior forests on Roatán produced proportionately less fine roots than along the shoreline (fig. 7), and this difference may explain this soil strength pattern. The slow decay of fine mangrove roots (15% in 270 d) has been reported previously (van der Valk and Attiwill, 1984), and their refractory nature may also explain maintenance of soil strength after root mortality.

Information about hurricane effects on other soil factors known to affect mangrove growth is also limited. Smith and others (1994) proposed that large-scale disturbances such as hurricanes would alter soil salinity, temperature, redox potential and sulfide concentrations, which are important factors that influence mangrove seedling establishment and subsequent growth (McKee, 1993; 1995). Pore water salinity was elevated at high and medium impact sites in Honduras, due to changes in hydrology as well as to loss of canopy, which increased soil temperature and evapotranspiration. High impact interior soils were also more reducing with elevated sulfide concentrations. Release of simple carbon compounds and nutrients from dead mangrove tissues may stimulate sulfate-reducing bacteria with a consequent increase in sulfide production.

The pattern was different at Pacific sites in Honduras and in Guatemala where sediment deposition raised soil elevations and decreased exposure to tidal inundation. Higher redox potentials and lower salinity and sulfide concentrations generally reflected reduced tidal inundation and better soil aeration. The shrimp pond, which had a lower elevation and was open to tidal flooding, had elevated salinity and sulfide and lower redox potentials compared to other sites. However, the values were within the typical range reported for other mangrove forests (McKee and others, 1988; McKee, 1993;1995) and likely reflected the lack of vegetation (McKee, 1993). The salinity differences between impact sites in Guatemala, however, appear to be a consequence of site differences rather than hurricane impacts.

Defoliation during hurricane passage may result in enormous inputs of litter to the soil and cause changes in microbial activity, carbon accumulation, soil texture, and nutrient cycles (Tanner and others, 1991). Nutrient inputs as a result of hurricane defoliation may be higher than normal because the trees have no opportunity to retranslocate nutrients prior to leaf abscission (Lodge and others, 1991). Released nutrients may be taken up by surviving plants, algae, or soil bacteria; remain in the soil; or be leached. Although there is no data on changes in nutrient cycling and nutrient pools in mangrove forests as a consequence of hurricane impacts, information exists for other habitats. Hurricane Hugo altered soil and stream nutrient cycling in Puerto Rico rainforests due to a massive pulse of litterfall (Lodge and others, 1991). In contrast, Hurricane Andrew had minimal impact on NH_4-N and soluble reactive P in freshwater aquatic habitats of the Everglades National Park (Roman, and others, 1994). Although our study was not designed to capture nutrient pulses soon after hurricane passage, the results indicate changes in soluble pools of N and P but not total pools. The lack of hurricane impact on total N indicates that there were no substantial inputs of N via litter deposition. The major differences in total N were between organic and inorganic strata and between the Bay Island (peat-based soil), Guatemala (sand deposits), and Pacific (mineral soils) sites. The higher porewater concentrations of NH_4-N and PO_4-P at medium and high impact sites in Honduras could be due to reduced plant uptake in damaged forests but also to increased mineralization or decreased volatilization. Boto and Wellington (1984) found that extractable ammonium varied with growth cycles of mangroves in Australia and likely reflected variation in plant uptake.

Comparison of Damage Types and Effects on Mangroves: Sediment Burial, Prolonged Submergence, and Defoliation

Sediment Burial

Mangroves typically experience rates of sedimentation ranging from <1 mm/yr (Florida) to 10 mm/yr (Australia) (Cahoon and Lynch, 1997; Ellison, 1998). Highest rates of deposition occur along muddy coasts with high tide ranges and fluvial inputs. Mangroves are adapted to and even thrive in depositional environments, such as that found in the Gulf of Fonseca, Honduras. However, massive inputs of sediment that cover aerial roots and block aeration pathways can cause mangrove mortality (Ellison, 1998). The impacts of sediment or sand burial on mangrove mortality were evident in the Gulf of Fonseca, Honduras and Punta Manabique, Guatemala.

Ellison (1998) reviewed effects of sediment burial on mangroves. Mortality of mangroves due to sediment burial from fluvial processes has been reported in Colombia (West, 1956), Mexico (Thom, 1967), Puerto Rico (Lugo and Cintron, 1975), and elsewhere (see Ellison, 1998). Storm deposits have also caused widespread mortality of mangroves in Florida by Hurricane Donna (Craighead and Gilbert, 1962), in American Samoa by Cyclone Ofa (Ellison, 1998), and in Florida by Hurricane Andrew (Smith and others, 1994). Ellison also reviewed mangrove mortality resulting from excessive sedimentation as a result of human disturbance. Such disturbances have been reported as a result of dredge deposition, road construction, siltation from mining activities, coastal infilling, and dam construction (reviewed in Ellison, 1998).

Depths of sudden sediment deposits from natural and human causes range from 5 to 200 cm (Ellison, 1998). The storm deposits observed in Honduras and Guatemala during our study (50-100 cm) are comparable to that reported to kill mangroves (Ellison, 1998). When sediment deposits completely cover the pneumatophores of *Avicennia* spp. or stilt roots of *Rhizophora* spp. as they did in some locations in Honduras and Guatemala, death typically occurs. Stress or death can even occur when aerial roots are only partially buried, if sufficient interruption of oxygen transport occurs. Burial by sand appears to be less damaging in general than burial by silt or clay (Ellison, 1998). The reason is not known, but could be due to more rapid diffusion of oxygen through sand. At the medium impact site on Roatán, the deposition of sand to a depth of about 70 cm in a ridge between shoreline and interior plots caused dieback of mangroves that were buried, but some survived and were resprouting by January 2000. Also, new mangroves were colonizing this zone by January 2001.

Prolonged Submergence

Mangroves are adapted to periodic submergence by tides. However, if aerial root systems are covered by water for an extended period of time sufficient for depletion of internal oxygen stores, then the roots will die. The mechanism causing mortality is the same as for sediment burial: lack of oxygen to support root respiration. Plant root meristems are particularly sensitive to oxygen deprivation and begin dying within 24 h of onset of anoxia (Xia and Saglio, 1992). Mangrove roots are similarly sensitive, but are able to survive and grow in an anoxic soil environment due to an internal aeration system whereby atmospheric oxygen diffuses through air space tissue in roots (Scholander and others, 1955; McKee and Mendelssohn, 1987; McKee, 1996). However, if this aeration pathway is blocked, oxygen levels in mangrove roots decline within 6 h from 16 to less than 2 % (Scholander and others, 1955) and the plant must switch to anaerobic pathways of respiration (McKee and Mendelssohn, 1987). The rate of root oxygen depletion depends on two factors: root respiration rate and external oxygen demand in the surrounding soil. Soil temperature also affects mangrove root respiration (McKee, 1996). If loss of canopy via defoliation promotes soil warming because of increased radiant energy, increased soil temperatures may exacerbate effects of submergence by increasing root respiration rates and oxygen depletion rates.

The elevated water levels at Guanaja during hurricane passage likely blocked aeration of mangrove roots and contributed to massive tree mortality at this site. However, it is not known how long the trees were inundated above normal levels. This site exhibited strongly reducing soils with sulfide accumulation in the interior forest two years after the hurricane, in part due to restricted drainage and impoundment. The medium impact forest on Roatán also experienced stress and mortality partly from submergence and blockage of aeration. The sand ridge that was deposited between the shoreline and interior plots blocked water flow and caused an impounded area landward of the ridge. The trees within the impounded area experienced high mortality.

Standing water 50-75 cm deep, which was still present two years after Hurricane Mitch, had prevented revegetation of this area.

Defoliation

Loss of leaves temporarily suspends ability of a mangrove tree to photosynthesize. If apical buds survive and sufficient carbohydrate reserves exist to support refoliation, then the trees may survive. Coppicing by mangroves may be prolific following massive defoliation as reported in Florida after Hurricane Andrew (Baldwin and others, 1995). However, ability to resprout varies with species. *Rhizophora* spp. are less able to recover because the trees have few reserve meristems once maturity is reached. Other genera such as *Avicennia* and *Laguncularia* can readily sprout from surviving trunks and after severe damage that removes all leaves and most branches (Roth, 1992; Baldwin and others, 1995). However, if defoliation occurs simultaneously with burial or prolonged flooding from storm tides, then mangroves will almost certainly not recover vegetatively. This was apparently the case at Guanaja where the trees were defoliated, and aerial root systems were submerged for at least 24 h.

Effects of Sediment Burial, Defoliation, and Extended Submergence on Mangrove Root Systems and Consequences for Habitat Stability

Mangrove roots not only bind newly deposited sediment, but directly contribute to soil formation by adding organic matter (McKee and Faulkner, 2000a; 2000b; Middleton and McKee, 2001). The resultant soil conditions influence root growth rates and patterns. This feed-back process allows the mangrove forest to self-adjust to prevailing water levels and is particularly important in allowing coastal areas to keep pace with rising sea level (Cahoon and Lynch, 1997).

Hurricane Mitch caused death of both aboveground and belowground parts of mangroves. What are the consequences of root death for habitat stability and the potential for sediment erosion? If sedimentation, hydrology or other factors (e.g., defoliation) affecting root growth are altered by hurricane disturbance, then the ability of the plant community to stabilize the soil and maintain surface elevations relative to water levels will be altered. Mangrove mortality may render coastal areas more vulnerable to soil erosion and loss of elevation because root death could lead to loss of soil stability as well as a decrease in direct contribution of roots to soil volume. Mangrove roots also contribute to sediment trapping (Cahoon and Lynch, 1997) and to peat formation in habitats deficient in terrigenous sediment (e.g., in the Caribbean Region) (McKee and Faulkner, 2000a; Middleton and McKee, 2001). Death of the vegetation may also indirectly affect soil conditions through sudden mortality of roots and release of simple carbon compounds and nutrients that stimulate microbial activity and decomposition of soil organic matter. Death of the root system would also affect soil aeration, since transport of oxygen through living roots to soil has a substantial effect on soil redox potential and sulfide concentrations (McKee and others, 1988). Other long-term effects are reduced mineral uptake and consequent changes in nutrient dynamics.

What happens to the root systems of mangroves as a consequence of sediment burial, defoliation, or extended submergence? Obviously, total death of the root system may occur, as it did at Guanaja and high impact shoreline in the Gulf of Fonseca. An immediate effect of root mortality would be on soil aeration via leakage of oxygen from roots. Oxygen is lost rapidly from fine roots, which have a large surface area relative to coarse roots (Sorrell, 1994).

Decreased soil aeration due to root oxygen leakage would promote accumulation of sulfide (McKee and others, 1988). The complete death of mangrove root systems and loss of oxidized rhizospheres at Guanaja likely contributed to the higher sulfide concentrations there.

Although total root production at medium impact sites was similar to that at low impact sites, fine root production in the Gulf of Fonseca decreased at impacted sites. In a lowland tropical forest (Luquillo Experimental Forest) damaged by Hurricane Hugo, fine root biomass in the top 10 cm of soil dropped to almost zero within 1-3 months following Hurricane Hugo, but subsequently increased (Parrotta and Lodge, 1991). Death of fine roots can be caused by diversion of carbohydrate reserves to refoliation, drought, elevated soil temperature, and/or mechanical damage (Parrotta and Lodge, 1991). Consequences of loss of fine roots include reduced mineral uptake and increased leaching losses for mobile ions (nitrate), but not for immobile ions such as ammonium and phosphate.

Would death of the mangrove root system have greater effects on habitat stability in Caribbean settings compared to areas with high mineral sediment input such as the Gulf of Fonseca, Honduras? High sedimentary environments promote mangrove root growth, as long as sediment accretion rates do not exceed the ability of the trees to aerate belowground parts. Mangrove root growth contributed to soil stabilization in the Gulf of Fonseca by providing a matrix for inorganic particles. Soil strength was clearly enhanced by the presence of roots, since the high impact shoreline devoid of root growth had the lowest shear strength of all sites in the Gulf of Fonseca. However, vertical accretion and soil integrity were primarily controlled by mineral sediment inputs. Thus, roots are mainly important to stabilization of soils and inhibition of erosion in the Gulf of Fonseca.

The peat-based soils in Caribbean mangrove forests are clearly more dependent upon root inputs for soil formation and vertical accretion (McKee and Faulkner, 2000a; Middleton and McKee, 2001). Mangrove roots account for up to 95% of peat mass in Belizean island forests (McKee and Faulkner, 2000a), and mangrove root production may be as high as 60% of leaf inputs to the forest floor (McKee and Faulkner, 2000b). In addition, a recent study of mangrove degradation rates concluded that roots make a much greater contribution to peat formation in Belizean island forests than either leaves or wood (Middleton and McKee, 2001). Thus, mortality of mangroves or dieback of the root systems would have serious consequences for maintenance of soil surface elevations in the Bay Islands and in mainland forests with low mineral sediment inputs. The loss of soil strength in the interior plots, but not shoreline plots at Guanaja illustrates the importance of mangrove roots in these sediment-poor habitats.

Conclusions

Mangrove forests are dynamic ecosystems that change over geological time scales in response to sea-level fluctuations as well as over shorter time scales in response to natural disturbances such as hurricanes or to human-induced alterations. Although mangroves are adapted to periodic disturbance, forest structure and productivity may be disrupted temporarily by catastrophic storms or floods. Human disturbances, particularly those that involve alteration of hydrology, are damaging to wetland systems and can lead to permanent losses, because the effects are generally outside the capacity of the component species to adapt (McKee and Baldwin, 2000). A variety of factors may determine resilience of mangroves to hurricane impacts and subsequent recovery rates and patterns. Mangrove structure and function are strongly related to the environmental setting, particularly sedimentary processes. Thus, sediment type and origin may play a key role in mangrove vulnerability and ability to recover from hurricane disturbance. Vulnerability of coastal wetlands to hurricane disturbance is also affected by prior disturbance regimes and general health of the system (Guntenspergen and others, 1995). Thus, an evaluation of the impact of Hurricane Mitch on mangrove ecosystems in Central America must be conducted with the environmental setting and prior disturbance regimes in mind.

Mangroves may develop in a variety of sedimentary environments, including (1) muddy shorelines where terrigenous sediment originates outside the system (i.e., allochthonous), (2) systems lacking terrestrial sediments but where mangroves are underlain by calcareous substrate, (3) or peat-forming systems where sediments are derived from organic material (primarily roots) produced by mangroves themselves (Woodroffe, 1992; McKee and Faulkner, 2000a). The latter two types are considered to have autochthonous sediments (i.e., produced in situ). The calcareous sediments may arise from reef development, skeletal remains of calcareous organisms such as macroalgae, or precipitated carbonate, which are produced and deposited within the system (Woodroffe, 1992). The organic or peat sediments in carbonate settings are also produced in situ by deposition and slow decay of mangrove roots (Middleton and McKee, 2001). Along with sedimentary processes, other environmental features such as tides, drainage patterns, geomorphology, nutrient availability, freshwater inflows, and relative sea-level rise determine the environmental setting for mangrove development. The three mangrove areas examined in this study represent distinct environmental settings as described by Woodroffe (1992): river or tide dominated (Gulf of Fonseca, Honduras), composite river and wave dominated (Punta Manabique, Guatemala), and carbonate setting (Bay Islands, Honduras). An understanding of the functional classification of mangrove forests (sensu Lugo and Snedaker, 1974) is also important to an evaluation of hurricane effects and potential for recovery. Mangroves may be classified as riverine, fringe, basin, scrub/dwarf, and overwash, which are categories that reflect hydrologic energy and are characterized by differences in mangrove physiognomy and primary production. Forest types found in the Gulf of Fonseca included riverine and scrub/dwarf categories, whereas those in the Caribbean included fringe, basin, and riverine mangroves.

Hurricane impacts on soils and belowground recovery observed in Honduras and Guatemala thus differed within and among study sites. The following points summarize the findings of this project relevant to restoration and/or future management of mangrove forests in these areas:

- Direct impacts of Hurricane Mitch (sediment burial, prolonged submergence, and/or defoliation) contributed most to mangrove root mortality and potential for soil stabilization and erosion control. Changes in elevation, moisture availability, and soil strength, which were directly altered by sediment burial and disruption of root aeration, limited recovery more than indirect effects on soil chemistry (e.g., salinity, pH, redox potential, and sulfide and nutrient concentrations). *Thus, in areas where soil surface elevation, flood depth/duration, and soil integrity have not been substantially altered (all low impact sites and medium impact shorelines), soil conditions will not likely prevent natural recovery of mangroves.*

- Mangrove forests in settings that normally receive high inputs of terrigenous sediment (e.g., Gulf of Fonseca) may be better buffered against land loss subsequent to hurricane damage compared to peat-forming systems (e.g., Bay Islands). However, changes in physicochemical conditions may alter plant community composition in both settings. Where soil formation is primarily dependent upon biogenic processes of mangrove root production for maintenance of soil elevations, mangrove mortality may lead to high subsidence rates after a hurricane. Stabilization of storm-deposited sediments along muddy shorelines (e.g., Gulf of Fonseca), however, may also be important to prevent soil erosion and slumping with consequent siltation of navigable waterways. *Belowground recovery of Caribbean mangrove forests is critical not only for restoration of ecosystem productivity but for maintenance of habitat stability and protection against further disturbance. Rapid mangrove reestablishment is thus most needed in areas dependent upon organic matter accumulation to maintain soil elevations (e.g., Guanaja). However, soil conditions need to be reevaluated in high impact areas before any restoration efforts take place. If adverse conditions have escalated, then restoration plans should be tailored to the situation.*

- Relative vulnerability of interior versus shoreline mangrove zones to post-hurricane erosion or loss of soil integrity differed between Caribbean and Pacific sites. At Caribbean sites, interior forest soils where total mortality occurred (Guanaja) lost shear strength due to root death, but shoreline zones maintained shear strength up to two years after hurricane passage. At Pacific sites, vulnerability to sediment erosion was higher along shorelines regularly inundated by tides than in interior forests, primarily because the latter were more isolated from tidal currents. *Thus, interior forest stands in the Bay Islands may change more rapidly and recover more slowly from hurricane impacts than shoreline zones. Loss of soil strength (interior zone on Guanaja) may also hamper restoration efforts, since the soil will no longer support human weight (making walking difficult) and also may not provide a stable substrate* *for planted propagules or transplanted seedlings. In the Gulf of Fonseca, shorelines may change more quickly due to erosion and slumping, but recovery of interior stands may also be delayed due to dryer soils and other negative conditions preventing vegetative reestablishment.*

- Examination of soil stratigraphy revealed that recent storm deposits were a meter or more in depth at some locations, particularly in interior forest stands (e.g., Gulf of Fonseca). *Interior forest stands may thus be important sinks for storm sediments, a finding that has implications for future management of scrub or dwarf mangrove forests.* Alternation of strata composed of various sediment types was typical on both Caribbean and Pacific coasts. Strata containing mangrove roots were interspersed with inorganic sediment deposits lacking roots. *This historical record shows that these sites are characterized by cycles of mangrove development, deterioration or elimination by disturbance events, and reestablishment. Thus, damaged areas will likely recover given sufficient time and absence of further alterations (natural or human-caused) that inhibit mangrove establishment and growth.*

Acknowledgments

Patti Faulkner participated in field work and supervised laboratory analyses of soil and pore water chemistry and root production measurements. David Jaen and Adrian Oviedo also provided field assistance. Andrea Anteau assisted with nutrient analyses. Rebecca Burt from the USDA-NRCS-NSSC provided valuable guidance with the particle size distribution analyses.

References Cited

American Society for Testing and Materials (ASTM), 1991, Annual Book of ASTM Standards: Philadelphia, Pa., USA, ASTM.

Association of Official Analytical Chemists-International (AOAC), 1990, Official Methods of Analysis (15th edition): Arlington, Va., USA, AOAC-International, 1298 p.

Baldwin, A.H., Platt, W.J., Gathen, K.L. , Lessmann, J.M., and Rauch, T.J., 1995, Hurricane damage and regeneration in fringe mangrove forests of Southeast Florida, USA: Journal of Coastal Research Special Issue, v. 21, p.169-183.

Boto, K.G., and Wellington, J.T., 1984, Soil characteristics and nutrient status in a northern Australian mangrove forest: Estuaries, v. 7, p. 61-69.

Burt, R., Reinsch, T.G., and Miller, W.P., 1993, A micro-pipette method for water dispersible clay: Communications in Soil Science and Plant Analysis, v. 24, p.2531-2544.

Cahoon, D.R., and Lynch, J.C., 1997, Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, USA: Mangroves and Salt Marshes, v. 1, p. 173-186.

Cahoon, D.R., Reed, D.J. , Day, Jr., J.W., Steyer, G.D., Boumans, R.M., Lynch, J.C., McNally, D., and Latif, N, 1995, The influence of Hurricane Andrew on sediment distribution in Louisiana coastal marshes: Journal of Coastal Research Special Issue, v. 21, p. 280-294.

Craighead, F.C., and Gilbert, V.C., 1962, The effects of Hurricane Donna on the vegetation of southern Florida: Quarterly Journal of the Florida Academy of Sciences, v. 25, p. 1-28.

Davis, J.H., Jr., 1940, The ecology and geologic role of mangroves in Florida, Paper from Tortugas Lab 32, Washington, D.C., Carnegie Institute Washington Publication, v. 517, p. 305-412.

Egler, F.E., 1952, Southeast saline everglades vegetation, Florida, and its management: Vegetatio, v. 3, p. 213-265.

Ellison, J.C., 1998, Impacts of sediment burial on mangroves: Marine Pollution Bulletin, v. 37, p. 420-426.

Gallagher, J.L., Wolf, L., and Pfeiffer, W.J., 1984, Rhizome and root growth rates and cycles in protein and carbohydrate concentrations in Georgia *Spartina alterniflora* Loisel. plants: American Journal of Botany, v. 71, p. 165-169.

Guntenspergen, G.R., Cahoon, D.R., Grace, J., Steyer, G.D., Fournet, S., Townson, M.A., and Foote, A.L., 1995, Disturbance and recovery of the Louisiana coastal marsh landscape from the impacts of Hurricane Andrew: Journal of Coastal Research Special Issue, v. 21, p. 324-339.

Lodge, D.J., Scatena, F.N., Asbury, C.E., and Sánchez, M.J., 1991, Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico: Biotropica, v. 23, p. 373-378.

Lugo, A.E., and Cintron, G.,1975, The mangrove forests of Puerto Rico and their management, *in* Walsh, G., Snedaker, S., Teas, H., eds., Proceedings of the International Symposium on Biology and Management of Mangroves: Gainsville, Fla., University of Florida, p. 825-846.

Lugo, A.E., and Snedaker, S.C., 1974, The ecology of mangroves: Annual Review of Ecology and Systematics, v. 5, p. 39-64.

McGinnis, T.E., II., 1997, Shoreline movement and soil strength in a Louisiana coastal marsh: Lafayette, La.,University of Southwestern Louisiana, M.S. Thesis.

McKee, K.L., 1993, Soil physicochemical patterns and mangrove species distribution: reciprocal effects?: Journal of Ecology, v. 81, p. 477-487.

McKee, K.L., 1995, Seedling recruitment patterns in a Belizean mangrove forest: effects of establishment ability and physicochemical factors: Oecologia, v. 101, p. 448-460.

McKee, K.L., 1996, Growth and physiological responses of mangrove seedlings to root zone anoxia: Tree Physiology, v. 16, p. 883-889.

McKee, K.L., and Baldwin, A.H., 1999, Disturbance regimes in North American wetlands. *in* Walker, L.R., ed., Ecosystems of Disturbed Ground, Ecosystems of the World 16: Amsterdam, Elsevier, p.331-363.

McKee, K.L., and Faulkner, P.L., 2000a, Mangrove peat analysis and reconstruction of vegetation history at the Pelican Cays, Belize: Atoll Research Bulletin, v. 468, p. 46-58.

McKee, K.L., and Faulkner, P.L., 2000b, Restoration of biogeochemical function in mangrove forests: Restoration Ecology, v. 8, p. 247-259.

McKee, K.L., and Mendelssohn, I.A., 1987, Root metabolism in the black mangrove, *Avicennia germinans* (L.) L.: Response to hypoxia: Environmental and Experimental Botany, v. 27, p.147-156.

McKee, K.L., Mendelssohn, I.A., and Hester, M.W., 1988, Reexamination of pore water sulfide concentrations and redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*: American Journal of Botany, v. 75, p. 1352-1359.

Middleton, B.A., and McKee, K.L., 2001, Degradation of mangrove tissues and implications for peat formation in Belizean island forests: Journal of Ecology, v. 89, p. 818-828.

Parrotta, J.A., and Lodge, D.J., 1991, Fine root dynamics in a subtropical wet forest following hurricane disturbance in Puerto Rico: Biotropica, v. 23, p. 343-347.

Parsons, T.R., Maita, Y., and Lalli, C.M., 1984, A Manual of Chemical and Biological Methods for Seawater Analysis (1st ed.): New York, Ny., Pergamon, 173 p.

Proffitt, E., McKee, K.L., and Cahoon, D.R., 1999, Preliminary reconnaissance of Hurricane Mitch impacts on coastal systems of Honduras-August 8-18, 1999. Final Report submitted to US-AID.

Roman, C.T., Aumen, N.G., Trexler, J.C., Fennema, R.J., Loftus, W.F., and Soukup, M.A., 1994, Hurricane Andrew's impact on freshwater resources: water quality, so important to defining the Everglades' unique ecological composition, appears little affected: Bioscience, v. 44, p. 247-255.

Roth, L.C., 1992, Hurricanes and mangrove regeneration: effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua: Biotropica, v. 24, p. 375-384.

Sauer, J.D., 1962, Effects of recent tropical cyclones on the coastal vegetation of Mauritius: Journal of Ecology, v. 50, p. 275-290.

Scholander, P.F., van Dam, L., and Scholander, S.I., 1955, Gas exchange in the roots of mangroves: American Journal of Botany, v. 42, p. 92-98.

Smith, T.J., Jr., Robblee, M.B., Wanless, H.R., and Doyle, T.W., 1994, Mangroves, hurricanes, and lightning strikes: BioScience, v. 44, p. 256-262.

Sorrell, B.K., 1994, Airspace structure and mathematical modelling of oxygen diffusion, aeration and anoxia in *Eleocharis sphacelata* R. Br. roots: Australian Journal of Marine and Freshwater Research, v. 45, p. 1529-1541.

Stoddart, D.R., 1963, Effects of Hurricane Hattie on the British Honduras reefs and cays, Oct. 30-31, 1961: Atoll Research Bulletin, v. 95.

Tanner, E.V.J., Kapos, V., Healy, J.R., 1991, Hurricane effects on forest ecosystems in the Caribbean: Biotropica, v. 23, p. 513-521.

Thom, B.G., 1967, Mangrove ecology and deltaic geomorphology, Tabasco, Mexico: Journal of Ecolology, v. 55, p. 301-343.

van der Valk, A.G., and Attiwill, P.M., 1984, Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia: Aquatic Botany, v. 18, p. 205-221.

West, R.C, 1956, Mangrove swamps of the Pacific coast of Colombia: Annals of the American Association of Geographers, v. 46, p. 98-121.

Woodroffe, C.D., 1992, Mangrove sediments and geomorphology, *in* Alongi, D. and Robertson, A., eds., Tropical Mangrove Ecosystems: Washington, D.C., American Geophysical Union, p. 7-41.

Xia, J., and Saglio, P.H., 1992, Lactic acid efflux as a mechanism of hypoxic acclimation of maize root tips to anoxia: Plant Physiology, v. 100, p. 40-46.