VEGETATION AND SEA-LEVEL HISTORY

OF A MANGROVE SWAMP AT LEVERA POND, GRENADA

by

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A Thesis submitted in conformity with the requirements
for the Degree of Masters of Science,
Graduate Department of Botany,
in the University of Toronto

There roles the deep where grew the tree.

O earth, what changes hast thou seen!

Alfred Lord Tennyson,

In Memorium

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ABSTRACT

Grenada is a tropical, mountainous island in the Caribbean (12°1'N, 61°4'W). Levera, a national park on the northeast coast, has a brackish pond (3 m deep, 0.5 km^2) and mangrove swamp, sheltered by a beach barrier. *Rhizophora* fringes the pond and tidal inlet, followed by an *Avicennia* zone, mixed mangrove zone, and *Hippomane* zone. Surface pollen samples reflect local vegetation, but *Rhizophora* and *Conocarpus* are over-represented, while *Avicennia* and *Laguncularia* are under-represented. Sediment lithology, pollen, and macrofossil analysis indicate that the mangrove swamp was formerly a bay. Two sediment cores (445 cm long) have a basal horizon of marine shelly sand, overlain by *Rhizophora* peat, mixed mangrove peat, and then clay. A sharp contact between shelly sand and *Rhizophora* peat indicates a sudden decrease in energy of deposition. Approximately 2300 years ago, formation of a beach barrier and accumulation of sediments caused the mangrove swamp to prograde into the bay. The succession from *Rhizophora* peat to mixed mangrove peat indicates a progressive drying of the swamp. In historic times, forest clearance and agriculture have increased erosion, causing deposition of clay. Pollen from weeds and *Hippomane* increase, while *Conocarpus* declines.

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Finally, I'd like to thank my parents for their encouragement, and Rory for keeping me sane and happy in times of stress.

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INTRODUCTION

Mangroves are facultative halophytes which grow on sheltered coasts in the tropics and subtropics. Recent studies reviewed by Grindrod (1988) have shown that the history of mangrove swamps can be reconstructed using pollen analysis. Mangrove species are zoned according to distance from source of tidal inundation, as described below. Coastlines vary over time, prograding or receding in response to movements of land and sea. Coastal evolution impacts mangrove swamps, causing vegetation zones to migrate with the coastline. Thus, pollen analysis of mangrove sediments provides a precise record of coastal evolution.

The objective of my study is to determine the vegetation and sea-level history of a mangrove swamp at Levera Pond, Grenada, during the last 2500 years. Pollen, macrofossils, and sediment lithology indicate that the mangrove swamp was formerly a bay. Approximately 2300 years ago, sediment accumulation and possibly tectonic uplift caused the mangrove swamp to begin prograding into the bay. In historic times, forest clearance and agriculture have increased upland erosion, causing deposition of clay.

Mangrove zonation

Levera Swamp has three mangrove species: *Rhizophora mangle, Avicennia germinans,* and *Laguncularia racemosa,* and two mangrove associates: *Conocarpus erectus* and *Hippomane mancinella* (all botanical names follow Howard,

1974-89). The latter are considered "mangrove associates", rather than "true" mangroves, because they lack the morphological and biological features (such as pneumatophores and vivipary) that characterize true mangroves (Tomlinson, 1986).

These species show consistent patterns of zonation throughout the New World (Ellison and Farnsworth, 1993). *Rhizophora* occupies areas subject to almost constant inundation with brackish to saline water. It occurs as a monospecific fringe along sheltered coasts, tidal inlets, and brackish ponds (Harris, 1965; Bacon, 1972; Morrow and Nickerson, 1973; Onuf *et al.*, 1977; Pool *et al.*, 1977; Woodroffe, 1983; Heatwole, 1985; McKee *et al.*, 1988; Pezeshki *et al.*, 1989; Rada *et al.*, 1989; Ellison and Farnsworth, 1993; McKee, 1993). Somewhat further inland, *Rhizophora* may occur in mixed stands with *Avicennia* and/or *Laguncularia* (Thom, 1967; Pool *et al.*, 1977; Woodroffe, 1983; McKee, 1993) and occasionally with *Conocarpus* (Ellison and Farnsworth, 1993).

Avicennia usually forms the next vegetation zone in areas subject to intermittent inundation (Bacon, 1972; Onuf *et al.*, 1977; Pool *et al.*, 1977; Ellison and Farnsworth, 1993). It is also common in depressions within the mangrove swamp, where sea water remains behind in pools after the tide goes out (Morrow and Nickerson, 1973). *Avicennia* may form pure stands or occur in association with other mangrove species. Greenhouse experiments show that *Avicennia* propagules can root in salinities ranging from 0 ppt (distilled water) to at least 75 ppt (twice the salinity of seawater) (McMillan, 1971). Seedling establishment is inhibited in water depths greater than 5 cm and in turbulent water.

Conocarpus occurs at the transition from mangrove to upland vegetation in areas subject to occasional tidal flooding (Bacon, 1972; Pool *et al.*, 1977; Woodroffe, 1983; Ellison and Farnsworth, 1993). It may form pure stands or occur with mangrove species.

Laguncularia may occur as a minor constituent in any zone (Pezeshki *et al.*, 1989), but it is most common in landward mangrove zones (Tomlinson, 1986). It rarely forms pure stands except in recently disturbed areas (Thom, 1967; Tomlinson, 1986).

Hippomane has received relatively little study (Tomlinson, 1986). It occurs on drier sand or clay substrates, landward of mangrove vegetation or in adjacent beach communities (Harris, 1965; Tomlinson, 1986).

The underlying causes of mangrove zonation are still in dispute (see Smith, 1992, for review). Explanations for zonation in New World mangrove swamps include succession due to land building (Davis, 1940), geomorphic processes (Thom, 1967), interspecific competition (Ball, 1980), tidal sorting of propagules (Rabinowitz, 1978), predation on propagules (Smith *et al.*, 1989), and physiological tolerance of salinity (Morrow and Nickerson, 1973) and waterlogging (Pesezshki *et al.*, 1989; McKee, 1993).

Davis (1940) suggested that the zonation of a Florida mangrove swamp reflected a successional sequence from pioneer colonizers (seagrass and *Rhizophora*) to a tropical forest climax. However, Thom (1967) demonstrated that the zonation of a deltaic mangrove swamp in Tabasco, Mexico, was a response to

external forces rather than a temporal sequence induced by the plants themselves. External forces included changes in sea-level, subsidence, and shifting river paths and consequent shifts in the centres of active fluvial sedimentation. Once mangroves are established, stilt roots and pneumatophores may encourage sediment accumulation by slowing water velocity and reduce erosion by consolidating sediments. However, mangroves appear to follow siltation rather than cause it (Thom, 1967).

Few studies have examined the role of competition in mangrove species zonation (Smith, 1992). Ball (1980) used historical aerial photographs and site descriptions to trace the expansion of a Florida mangrove swamp between 1928 and 1977, after urban development had reduced the height of the freshwater table and increased saline intrusion into the coastal swamp. *Laguncularia* and *Rhizophora* colonized all intertidal zones of the new site, but by 1977, *Rhizophora* dominated the lower intertidal zone and *Laguncularia* dominated the higher intertidal zone. Ball suggests the zonation pattern was due to competitive exclusion, but other possible explanations, such as changing environmental conditions, were not examined (Smith, 1992).

Rabinowitz (1978) suggests that tidal sorting of propagules caused species with small, light-weight propagules to grow higher in the intertidal zone of a Panama mangrove swamp than species with large, heavy propagules. Rabinowitz used transplant experiments to demonstrate that all mangrove species are capable of growing in any of the zones. However, these results are confounded because

Rabinowitz weeded other seedlings from the experimental plots, thus eliminating interspecific seedling competition. Observations of species distributions in other locations indicate that there are many exceptions to the size-sorting pattern observed in Panama (Smith, 1987). Therefore, tidal sorting of propagules is not the controlling factor in mangrove zonation.

Using transplant experiments, Ellison and Farnsworth (1993) demonstrated that seedlings of *A. germinans* and *R. mangle* are both capable of growing in the mid-intertidal zone of a mangrove swamp in Belize. They suggest (but do not prove) that interspecific competition determines the relative abundance of the two species in this zone. In the low-intertidal zone, (subject to almost constant tidal inundation), transplanted *Avicennia* seedlings had a 0% survival rate (cause of death unknown). In contrast, *Rhizophora* seedlings showed highest growth rates and lowest levels of insect herbivory in the low-intertidal zone. This experiment suggests that several factors may influence species zonation.

Smith *et al.* (1989) observed predation levels of tethered mangrove propagules to determine whether there was a relationship between predation and species dominance. *Avicennia germinans* propagules were consumed in greatest quantity where *Avicennia* was rarest in the forest canopy, suggesting that predators may prevent *Avicennia* from becoming established in this zone. However, this pattern was not observed for *Rhizophora*. In Panama, more propagules were consumed in the low intertidal, *Rhizophora*-dominated forest than the high intertidal, *Avicennia*-dominated forest. In Florida, (which lacks the predator grapsid crab), no

Rhizophora propagules were consumed in any mangrove zone. Thus predation may influence zonation in some mangrove swamps but not others.

Morrow and Nickerson (1973) correlated the salinity of ground water with the distribution of *R. mangle* and *A. germinans* in the Bahamas. *Rhizophora* dominated where salinity was similar to seawater, *Avicennia* dominated in hypersaline locations, and mixed stands occurred at intermediate salinity levels. This study is not conclusive as other environmental factors may have varied with salinity. McMillan (1975) demonstrated that salinity tolerances of *A. germinans* and *L. racemosa* were modified by soil texture. Seedlings grown in hypersaline conditions in 100% sand all died whereas seedlings grown in 75% sand and 25% clay had 100% survival.

Waterlogging can lead to root oxygen deprivation and the accumulation of soil phytotoxins such as H_2S. McKee (1993) demonstrated that *R. mangle* is more tolerant of waterlogging than *A. germinans*. While both species were flood tolerant (at a salinity similar to seawater), *Avicennia* showed a 20-40% decrease in biomass compared to drained controls, while *Rhizophora* showed a 9-24% increase relative to drained controls. In contrast, Pesezshki *et al.* (1989) observed an increase in biomass of flooded *A. germinans* relative to drained controls. The latter experiment used a lower salinity level (50% that of seawater), a different potting medium, and lower soil sulphide levels than McKee (1993). The different experimental results suggest that other environmental factors may influence tolerance of waterlogging.

The above experiments suggest that mangrove zonation is influenced by a combination of physical and biotic factors, which tend to vary with distance from the

sea and tidal inlets. If geomorphic processes cause these factors to vary, then mangrove zones are expected to change accordingly.

Gauge Sea-level

Sea-level fluctuations are one of the most important factors in coastal evolution. "Gauge" sea-level refers to the absolute level of the water relative to some stable datum, such as the centre of the earth, while "relative" sea-level refers to the position of the sea relative to the land. Several factors cause gauge sea-levels to fluctuate with time. Over millions of years, sea-floor spreading and tectonic movement change the volume of ocean-basins, causing sea-levels to fluctuate by hundreds of metres (Williams *et al.*, 1993). Over thousands of years, climate-driven fluctuations in the volume of fresh-water stored as lakes, groundwater, and ice, alter sea-levels by up to 200 m (Meier, 1990; Hallam, 1992; Jacobs and Sahagian, 1993).

Gauge sea-level varies over space, as well as time. The surface of the sea lies horizontally with respect to the local net gravity field. The field is modified by water depth and properties of nearby rock or ice masses, causing the elevation of the sea surface to vary by about 180 m (Williams *et al.*, 1993). The three-dimensional form of this surface is known as the "geoid". The geoid changes over time (e.g. with the growth and retreat of glaciers), but the extent and pattern of this change is largely unknown (Dawson, 1992). Because of geoidal variations, no single sea-level curve can be globally valid.

Relative sea-level

Relative sea-levels are affected by the above factors, as well as by local uplift or subsidence of the land, caused by isostatic rebound, tectonic movement, and sediment compaction, accumulation, and erosion.

Isostatic movement refers to a rise or fall of the land as it adjusts to a change in load. Isostasy plays a relatively minor role in the Holocene sea-level history of tropical regions, as they were not directly affected by ice loading. However, tropical coasts may have undergone minor isostatic adjustment during deglaciation, as a result of increased loading by water (Woodroffe, 1990) and sediment (Emery and Aubrey, 1991).

Movement of tectonic plates may cause folding, faulting, or tilting of the land (Bird, 1984). Nunn (1994) distinguishes two broad types of tectonic uplift. Aseismic uplift occurs slowly (in the order of mm/year), over thousands of years. In contrast, coseismic uplift occurs abruptly, in association with earthquakes. Seismic activity is concentrated along tectonic plate boundaries.

Sediment compaction is caused by decay and oxidation of organic matter (Gable, 1988), draining of fluid from interstitial spaces, and reduction of air spaces between sediment particles due to loading (Greensmith and Tucker, 1986). Most compaction probably occurs within the first few thousand years after deposition, and may be accelerated due to human activities, such as the extraction of water, gas, and oil from underground reservoirs (Greensmith and Tucker, 1986). There is local variation in degree of subsidence, reflecting differences in sediment type (Bartlett

and Barghoorn, 1973). Peat has the highest compactibility, followed by clay and then sand.

Sediment deposition and erosion may also cause shoreline migration. In mangrove swamps, sediment deposition is determined by autochthonous (local) peat production and allochthonous (non-local) sediment supply from upland and sea. The sea is the primary erosive agent (Bird, 1984). Destructive waves are usually associated with storms and high wind velocities (King, 1972) and may cause rapid shoreline retreat (Hopley, 1974). These factors contribute to local- and regional-scale variations in sea-level history and coastal evolution. Because of these variations, no single sea-level curve can be globally valid.

Sea-level Curves

Gauge sea-level has risen by about 120 m during the last 18,000 years due to glacier melt (Fairbanks, 1989) and thermal expansion of near-surface water (Leatherman, 1989). Rate of rise was rapid at first, slowing with the rate of ice melt (John, 1977). Sea-level curves from the West Indies and Florida (Fig. 1) all show a decelerating rate of sea-level rise over the Holocene (last 10,000 years). There is some disagreement over absolute rate, depending on geographical location and/or methodology. During the last 2500 years, sea-level rose between 0.5 m (Jamaica) and 2 m (Florida).
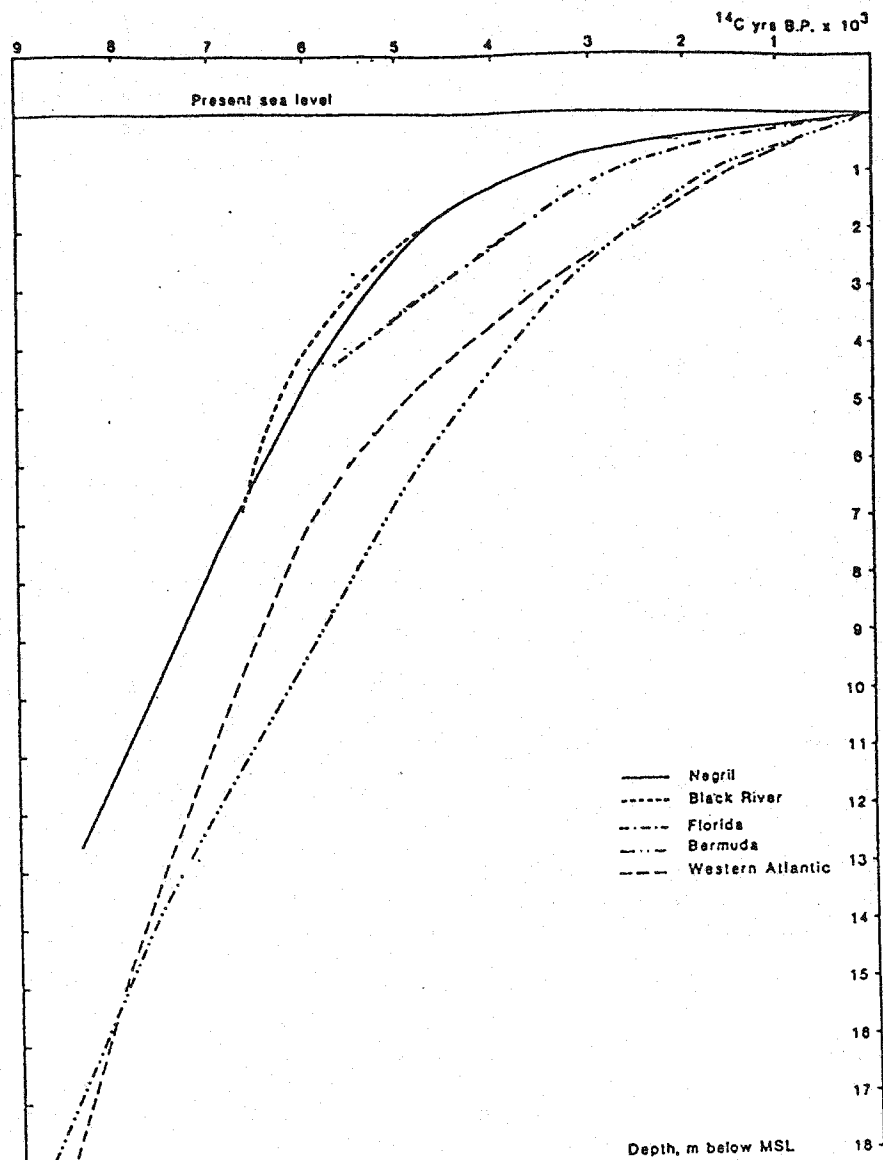
Figure 1. Sea-level curves for Negril and Black River, Jamaica (Digerfeldt and Enell, 1984), Florida (Scholl *et al.*, 1969), and Bermuda (Neumann, 1971) were constructed using radiocarbon dates of freshwater and mangrove peat. A "minimum" sea-level curve for the tropical Western Atlantic was constructed using radiocarbon dates of *Acropora palmata* reefs (Lighty *et al.*, 1982). Figure modified from Digerfeldt and Hendry (1987).

Mangrove Studies (Western Atlantic)

Studies of mangrove sediments in the Western Atlantic indicate a decelerating rate of sea-level rise over the Holocene. A comparison of these studies reveals regional variations in the pattern of coastal evolution.

Cores taken from the Ten Thousand Islands in southwest Florida show a transgressive/regressive sediment sequence (Parkinson, 1984, 1988). The transgressive sequence, in which mangrove peat is overlain by shelly sand, indicates that the coastline receded between 7000 and 3500 yr B.P. The regressive sequence, in which shelly sand is overlain by oyster or vermetid reef deposits, followed by mangrove peat, indicates that the coastline prograded from 3500 yr B.P. to present. The presence of a continuous quartz sand supply and reef building organisms influenced the relative sea-level of this region. After 3390 ± 140 yr B.P., growth of vermetid reefs and oyster bars outpaced gauge sea-level rise, providing substrates for mangrove colonization. The mangrove islands reduced current energy, providing a protected setting for the accumulation of quartz sediments.

A core taken near Georgetown, Guyana, also shows a transgressive/regressive sediment sequence (Van der Hammen, 1974). The transgressive sequence, in which grass savanna is succeeded by *Avicennia/Rhizophora*, and then *Rhizophora*, indicates that the coastline began receding before 8590 yr B.P. The regressive sequence, in which *Rhizophora* is gradually succeeded by *Avicennia/Rhizophora*, and then fresh-water swamp,

indicates coastline progradation. No radiocarbon dates were made on the regressive sequence. A core from Surinam has a similar sedimentary sequence, but no radiocarbon dates were made (Wijmstra, 1969). A core from French Guiana corresponds to the regressional sequence of the Guyana and Surinam cores (Tissot and Marius, 1992). *Rhizophora* pollen dominates from 9000 to 5000 yr B.P., followed by freshwater swamp pollen from 5000 yr B.P. to present. All three locations receive abundant sediment from a humid, mountainous upland. Sediment accumulation rate for Guyana and French Guiana was approximately 25 cm/100 yrs during the Holocene. The Surinam core consists of gray clay, with little organic matter, indicating that it also had a rapid rate of sediment accumulation.

In contrast, cores taken from Grand Cayman, in the Greater Antilles, show a transgressive sediment sequence during the late Holocene (Woodroffe, 1980, 1981, 1983). Grand Cayman is a low-lying coralline island which lacks a terrestrial drainage system, and accumulates little marine sediment within the mangrove swamp. Therefore, most sediments on the island are of autochthonous origin. Cores contain a basal unit of orange or green mud, characteristic of seasonally flooded herbaceous cover now growing at elevations above the mangrove swamp. Mud is overlain by mangrove peat, indicating marine transgression. Mangrove encroachment occurred between 2160 ± 75 yr B.P. in the lower elevation areas, and 567 ± 55 yr B.P. in the higher elevation areas. The continuous nature of mangrove encroachment across an elevational gradient suggests gradual

submergence. Pollen analysis was not performed and the succession of mangrove species was not identified.

Baja California Sur, Mexico, is located in a geologically active zone, along the boundary of the Pacific and North American tectonic plates, and therefore has a more complicated sea-level history. Sudden shifts in pollen and sediment sequences suggest several episodes of tectonic uplift during the Holocene (Sirkin *et al.*, 1984).

These studies illustrate the role of sediment supply and tectonic activity in coastal evolution. Sediment supply varies with physiographic setting. Low coralline islands, such as Grand Cayman, usually receive less allochthonous sediment than high islands and continental coasts (Ellison and Stoddart, 1990). Sediment loss also varies among locations. Growth of reefs in southwest Florida reduced wave energy, thus enabling sediments to accumulate. If the rate of accumulation of allochthonous sediment plus autochthonous peat exceeds rate of gauge sea-level rise, then the shore will prograde, as observed during the late Holocene in southwest Florida, Guyana, Surinam, and French Guiana. If accumulation of allochthonous sediment plus autochthonous peat is less than gauge sea-level rise, then the shore will recede, as observed in Grand Cayman. The magnitude of the difference will control the rate of shoreline migration. Tectonic activity also influences coastal evolution, especially near tectonic plate boundaries.

Study Site

Grenada is a small, mountainous island located at the southern end of the Lesser Antillean island chain (Fig. 2). It is south of the storm belt and is rarely affected by hurricanes. Trade winds come from the east-southeast to east-northeast. The Levera area, on the north-east coast (12°12'N, 61°37'W) receives about 1270 mm of rain per year, with a dryer season from January to May and a wetter season from June to December (Caribbean Conservation Association, CCA, 1991). Grenada's location near the Caribbean Tectonic Plate margin makes it vulnerable to tectonic activity. A submarine volcano called "Kick 'em Jenny", located 7 km north of Grenada, has erupted at least eight times this century. Earthquakes of magnitude 3.2 to 3.9 on the Richter scale have been recorded with epicenters less than 80 km from Grenada (CCA, 1991). A fault line runs northeast across Grenada and through the Levera area (Mann *et al.*, 1990). There are several explosion craters near the fault line, including St. George's Harbour, Grand Etang, and Lake Antoine (Mann *et al.*, 1990). Levera Pond may have originated as a collapse along the fault line. The north end of Grenada appears to have risen relative to the south end, which has an irregular coastline from drowned river valleys (Fig. 2). The northeast coast of Grenada, near Levera Pond, has a raised shore platform approximately 3 m above mean sea-level (Fig. 3a). Levera Island (Fig. 3b), Green Island, and Sandy Island (Fig. 4a), which are located to the northeast and east of Levera Pond, have raised shore platforms at a similar elevation.
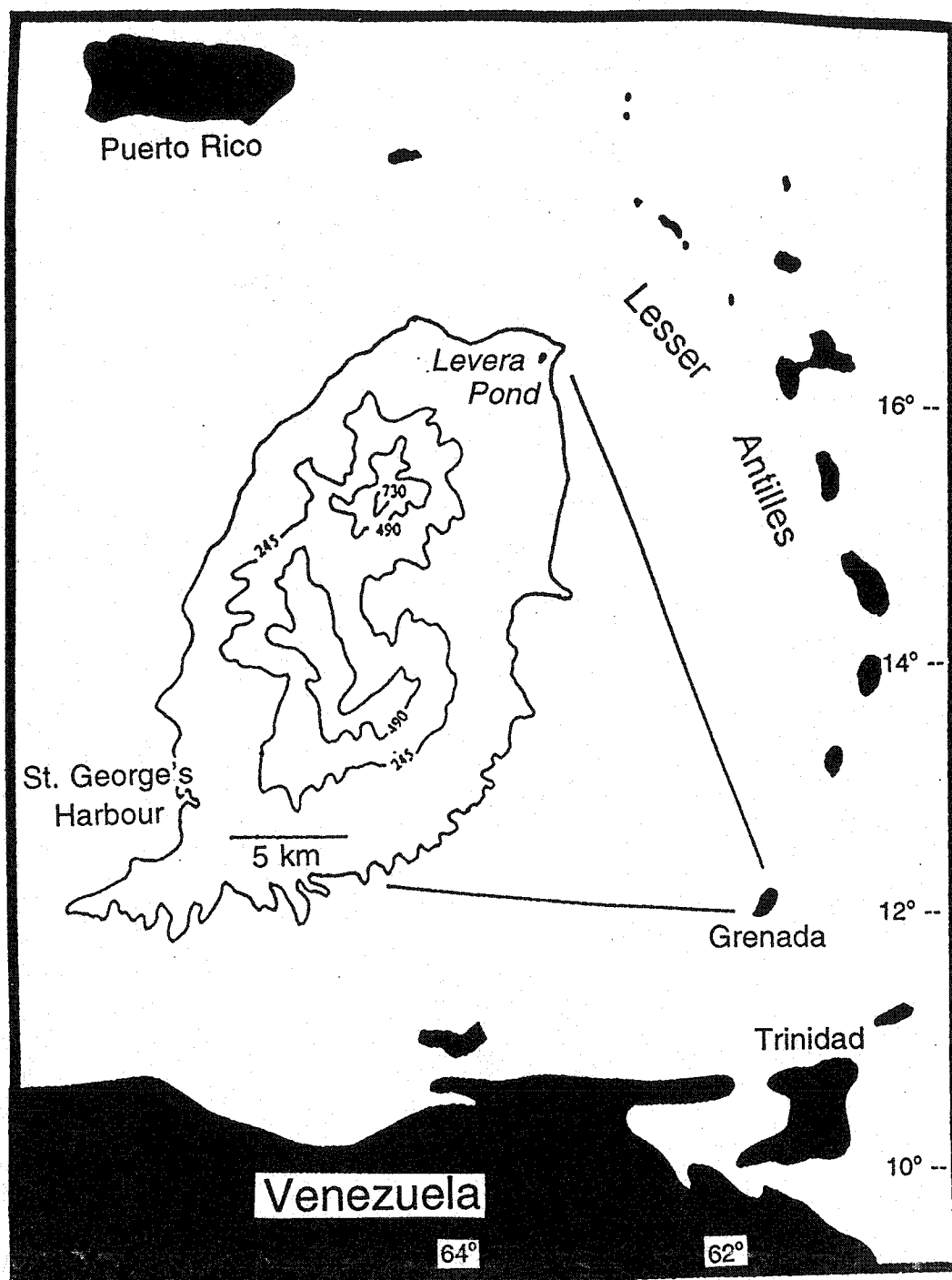
Figure 2. Grenada is a small, mountainous island located at the southern end of the Lesser Antilles island chain. Levera Pond is on the northeast coast (12°12'N, 61°37'W). Contours in metres.
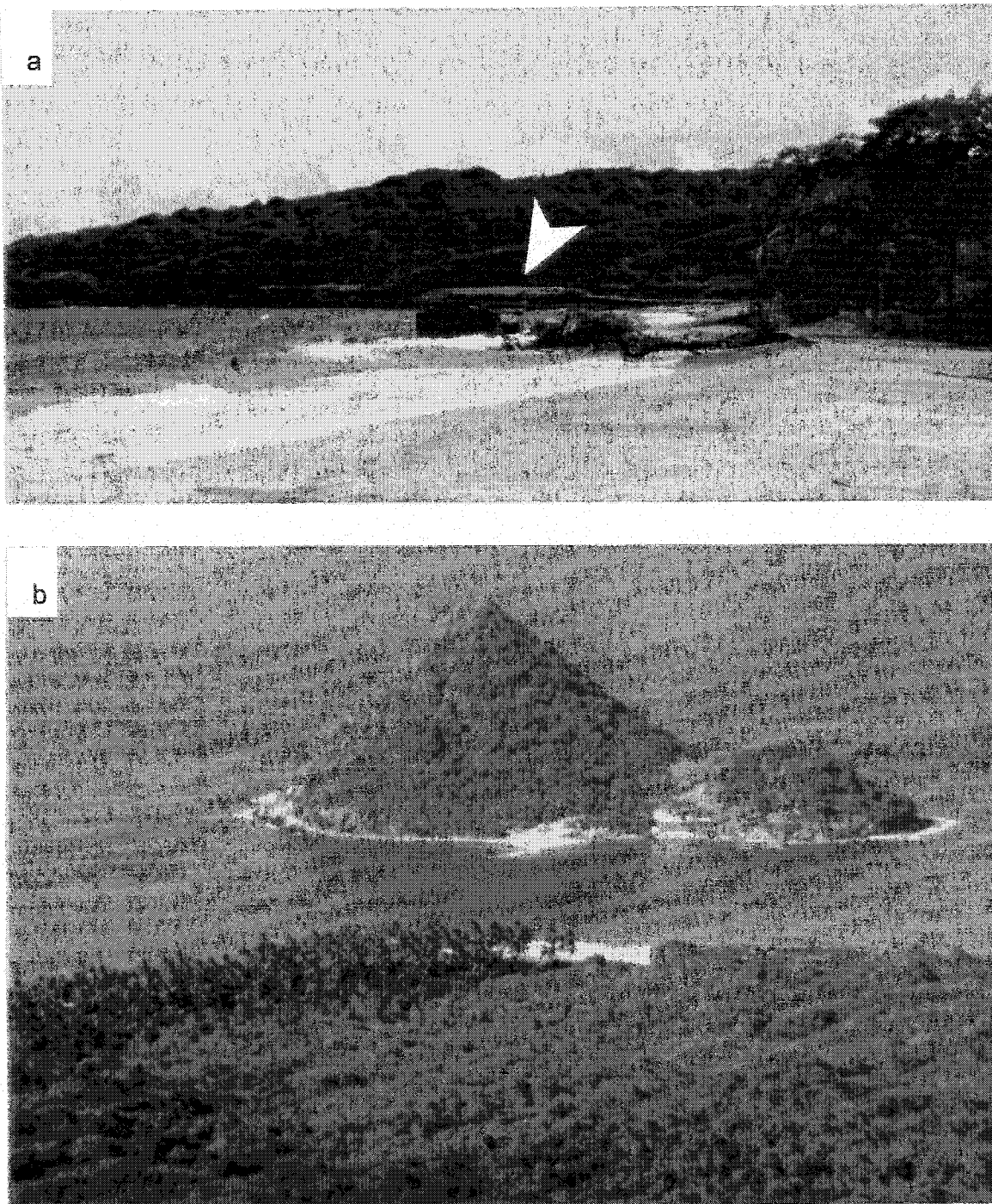
Figure 3. a) Levera Beach, looking eastward. The arrow indicates a raised shore platform, about

3 m above mean sea-level. Also note the washed out bridge.

b) Raised shore platforms of Levera Island, located northeast of Levera Pond. The white house

can be used for scale. Also note the coconut plantation, by Levera Beach.

Figure 4. a) Levera Island, Green Island, and Sandy Island (from left to right), have raised shore platforms about 3 m above mean sea-level. Levera Pond is in the foreground, Levera Beach to the left, and Bathway Beach to the right. Also visible is a footpath to Bathway Beach and a pasture at the extreme right. b) Sand barrier at the tidal inlet of Levera Pond. The inlet is fringed with a pure stand of *Rhizophora mangle*. Littoral vegetation is visible in the foreground, but absent infront of the tidal inlet.

No tide data are available for Levera Beach, but maximal tidal range at St. George's Harbour on the southwest coast is 42 cm. There are some coral patches near Levera and the adjacent islands, however, their extent is limited by turbulence and the scouring action of strong currents (CCA, 1991). The tidal inlet to Levera Pond is blocked by a sand barrier (Fig. 4b), which is breached twice a month, during spring tide (local fisherman, personal communication, 1992). Levera Island refracts waves, focussing sediments onto Levera Beach (Fig. 5a). Levera Beach was linked to Levera Island by a tombolo (sand spit) until the 1970's, when erosion reduced it to a cuspate spit on Levera Beach and on the lee side of Levera Island. Between 1951 and 1971 the tombolo was stable, a road ran along the beach, and a bridge crossed the tidal inlet to Levera Pond. From 1971 to 1984, erosion rates of 3.6 m per year washed out the tombolo and bridge (Fig. 5b). Increased beach erosion was reported elsewhere on Grenada and other Eastern Caribbean islands during this period (CCA, 1991). This coastal erosion may be caused by sea-level rise, increased storm activity and wave energy, and land subsidence. These processes may be accelerated by man, through removal of coastal vegetation, sand-mining, and destruction of coral reefs (CCA, 1991).

Levera Pond is a shallow, brackish body of water (3 m deep, 0.5 km^2), located in a coastal lowland. It is fed by two intermittent streams, from the south-west and west. In November, 1992, (rainy season) the stream beds contained isolated puddles of standing water. The stream beds, which are about 2 m wide and 2 m deep, contained boulders, suggesting episodic high-energy flow. The east,
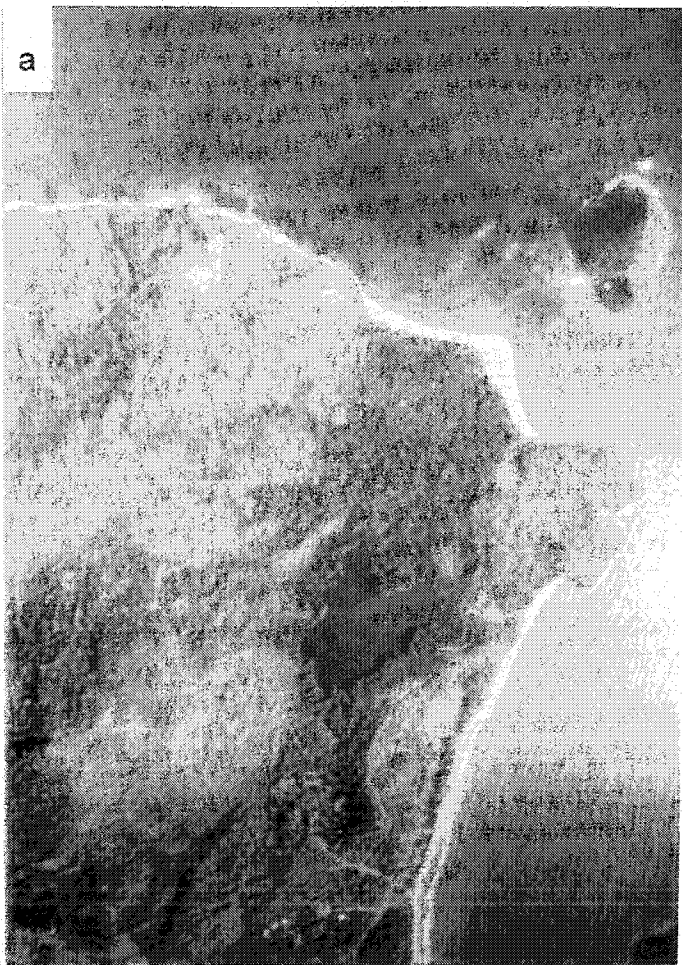
Figure 5. a) Aerial photograph of Levera Pond and Levera Island. Swamp vegetation appears darker green than surrounding dry vegetation. Levera Island refracts waves, focussing sediments onto Levera Beach. Both Levera Island and Levera Pond have cuspate beaches, which were linked as a tombolo until the 1970s.

b) A bridge at Levera Beach was washed out in the 1970s, due to increased erosion.

south, and west side of Levera Pond is surrounded by a thin strip (5 to 15 m wide)

of low-lying land, followed by an abrupt rise in elevation. The low, flat land between

Levera Pond and Levera Beach is covered with mangrove swamp. Zonation of

Levera Swamp (Fig. 6) is similar to that of other New World mangrove swamps.

Levera Pond and its tidal inlet are bordered by a pure *Rhizophora* zone, followed by

an *Avicennia* zone, and then a mixed mangrove zone with *Conocarpus*, *Avicennia*,

and *Laguncularia* (Table 1). The mixed mangrove zone occurs at altitudes of about

0.5 m, where sediments are drier. Where elevation rises steeply on the east side of

Levera Pond, the *Rhizophora* zone is followed immediately by a mixed mangrove

zone. *Hippomane* occurs along the periphery of the mangrove, where soils are

dryer. It forms a thin band to the east of the coring sites, and a pure zone south of

the coconut plantation. Levera Swamp has a few localized patches of

Amaranthaceae, Cyperaceae, and Poaceae but, like most mangrove swamps, lacks

a well-developed understory (Janzen, 1985; Smith, 1992; but see Corlett, 1986).

Littoral vegetation (Table 1) forms a narrow band in the salt spray zone of the

beach, but is absent at the tidal inlet. Watershed vegetation includes cactus scrub,

deciduous seasonal forest, crops, and pasture. Crab burrows are scattered

throughout the mangrove swamp (Fig. 7a).
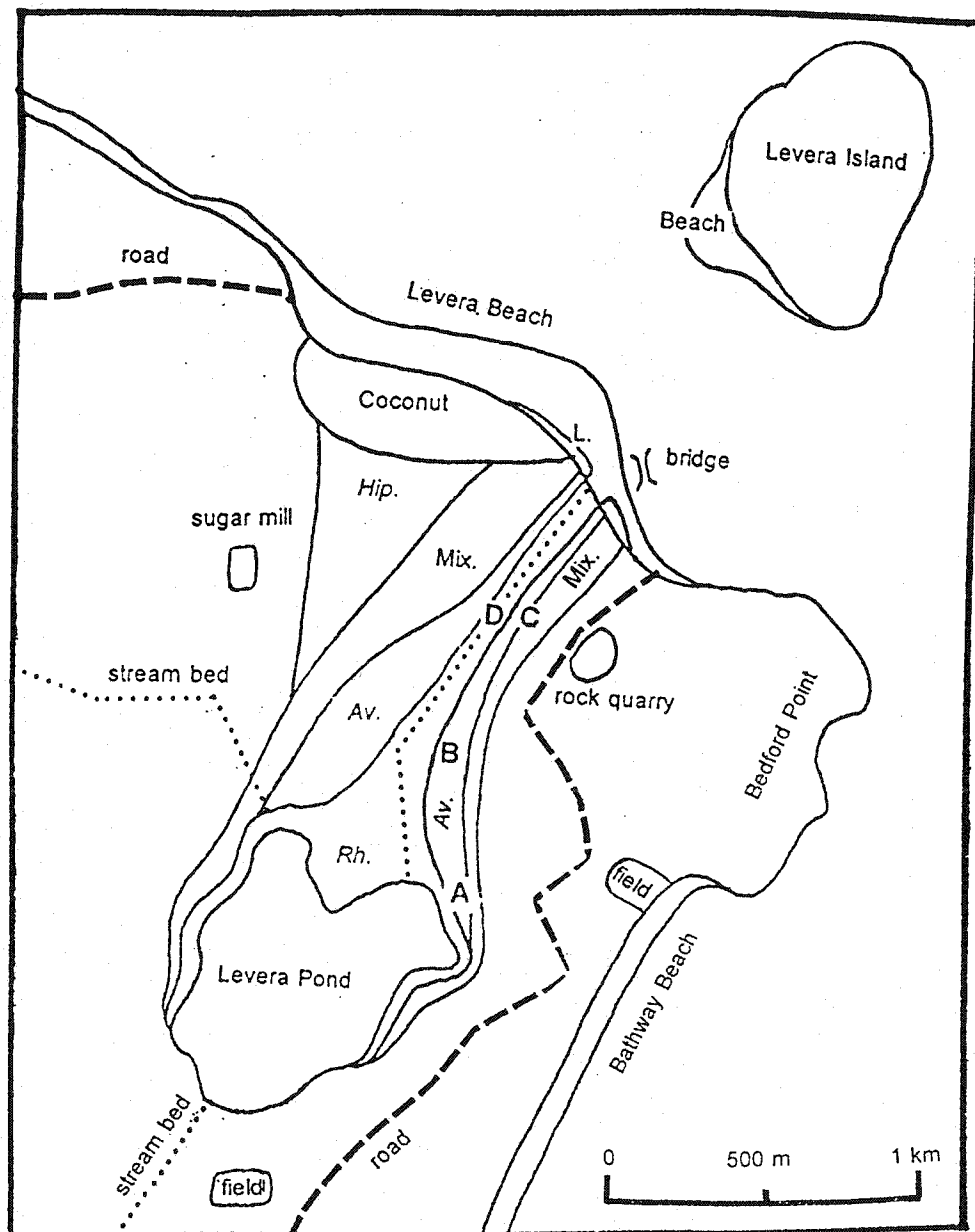
Figure 6. Vegetation zones of Levera Pond. *Hip.* = *Hippomane* zone, Mix. = mixed mangrove zone, *Av.* = *Avicennia* zone, *Rh.* = *Rhizophora* zone, L. = littoral zone, ······ = water course. Tidal inlet is located between the two littoral zones, landward of the bridge. Surrounding vegetation (not indicated) includes cactus scrub and deciduous seasonal forest. Location of sediment cores, A, B, C, and D, are indicated. There is a footpath circling Levera Pond, and several cutlines which are not indicated.

Table 1. Vegetation zones of the mangrove swamp at Levera Pond, Grenada. Constituent species are ranked as abundant (A), common (C), or rare (R).

LITTORAL ZONE
A   Canavalia rosea (Leguminosae)
C   Brachiaria distachya (Poaceae)
C   Coccoloba uvifera (Polygonaceae)
C   Ipomoea pes-caprae (Convolvulaceae)
C   Sesuvium portulacastrum (Portulacaceae)
C   Sporobolus virginicus (Poaceae)
R   Capparis odoratissima (Capparaceae)
R   Clerodendrum aculeatum (Verbenaceae)
R   Eleusine indica (Poaceae)
R   Euphorbia serpens (Euphorbiaceae)
R   Hippomane mancinella (Euphorbiaceae)
R   Jacquinia armillaris (Theophrastaceae)
R   Philoxerus vermicularis (Amaranthaceae)
R   Pithecellobium unguis-cati (Leguminosae)
R   Spigelia anthelmia (Loganaceae)
R   Trianthema portulacastrum (Aizoaceae)

COCONUT PLANTATION
A   Cocos nucifera (Palmae)
R   Psidium guajava (Myrtaceae)

RHIZOPHORA ZONE
A   Rhizophora mangle (Rhizophoraceae)

AVICENNIA ZONE
A   Avicennia germinans (Avicenniaceae)
R   Fimbristylis sp. (Cyperaceae)
R   Laguncularia racemosa (Combretaceae)

MIXED MANGROVE ZONE
C   Avicennia germinans (Avicenniaceae)
C   Conocarpus erectus (Combretaceae)
C   Laguncularia racemosa (Combretaceae)
R   Alternanthera flavescens (Amaranthaceae)
R   Cynodon dactylon (Poaceae)
R   Fimbristylis sp. (Cyperaceae)
R   Panicum maximum (Poaceae)
R   Philoxerus vermicularis (Amaranthaceae)

HIPPOMANE ZONE
A   Hippomane mancinella (Euphorbiaceae)

Figure 7. a) A crab burrow causes disturbance of sediments. Knife is 40 cm long.

b) A boiling pot found adjacent to the foundations of a building which may be the remains of an abandoned sugar mill, northwest of Levera Pond. Note that the pot has been repaired in several places. Dr. McAndrews provides scale.

Human Disturbance

Amerindians inhabited Grenada since at least A.D. 100 (Table 2). However, they were gatherers and primitive agriculturalists (CCA, 1991) with low population densities (Devas, 1974), and therefore had little impact on natural vegetation. The Amerindian diet included maize (*Zea*) and guava (*Psidium guajava*), both of which are found in the pollen diagram, as well as root crops, beans, squash, papaya, and other fruits and vegetables (CCA, 1991).

With European settlement in 1650, there was a shift to export agriculture and monoculture. Environmental impact was probably minor until 1700, due to low population size. Between 1702 and 1834, sugar cane was cultivated on almost all low-lying lands in Grenada. Additional areas were deforested to provide fuel for the sugar boiling houses and rum distilleries. Thousands of slaves were imported, causing rapid population increase (CCA, 1991). Livestock numbers increased, leading to overgrazing in some areas (CCA, 1991). Exports also included cocoa, cotton, coffee, wood, and hides. The abolition of slavery in 1834 caused labour shortages and many sugar estates were abandoned. Emancipated slaves started small subsistence-based farms, which led to the clearing of a large part of the remaining upland natural rain forest. Today little natural vegetation remains (Fig. 8). Primary export crops are nutmeg, bananas, and cocoa, and secondary crops are sugar cane, coconut, and citrus (CCA, 1991).

Grenada is vulnerable to erosion due to steep slopes, erodible clay soils, and rainfall intensities of up to 132 mm/hr (CCA, 1991). Agricultural crops generally

Table 2. Colonization and agricultural history of Grenada. Information drawn from CCA (1991) and Devas (1974).

Date (A.D.)	Event
100	Amerindians (primitive agriculturalists) migrate from South America
700	Arawaks migrate from South America
1498	Columbus sights Grenada, names it "Concepcion"
1500	Caribs migrate from South America and conquer Arawaks
1609-49	several unsuccessful colonization attempts by French and British
1650	first successful French settlement, 200 people; tobacco production begins
1700	indigo and livestock production begins; population 835 people, 64 horses, 569 cattle
1702	sugar cane becomes key crop, cultivated on almost all low-lying land in Grenada; slaves imported
1714	cocoa, coffee, and cotton cultivation begins
1750	population 13,000
1763	becomes British colony
1767	becomes "free port", export expands
1779	becomes French colony
1783	becomes British colony; export of fustic (dye wood), slaves, hides, and wood begins
1834	abolition of slavery causes economic collapse, many plantations and sugar estates are abandoned, emancipated slaves clear a large part of remaining upland natural forest for small subsistence-based farms
1851	population 32,671
1974	Grenada becomes independent
1989	population 97,000; nutmeg, bananas, and cocoa are primary crops and coconut, sugar cane, and citrus are secondary crops
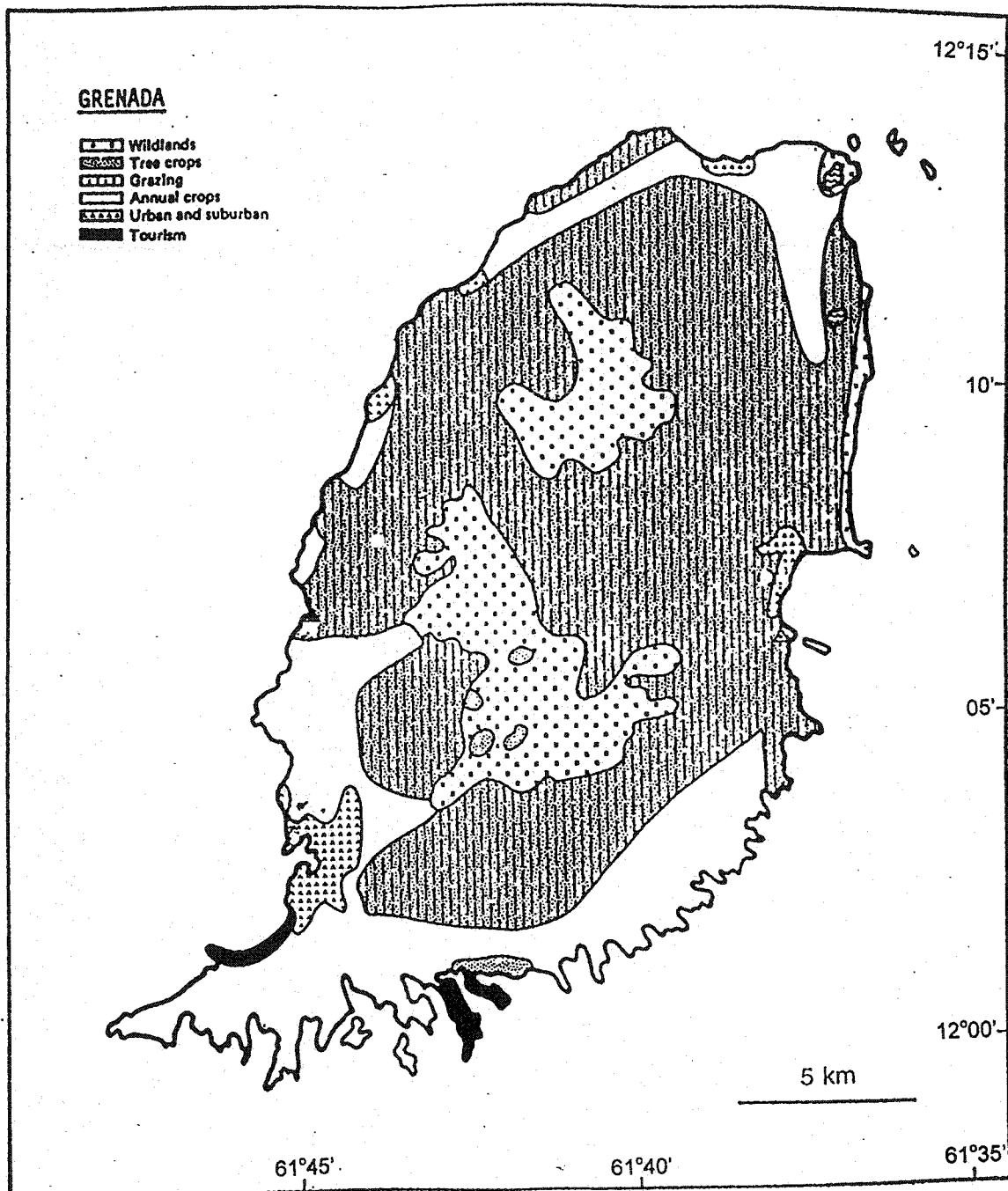
Figure 8. Generalized land use map of Grenada, modified from CCA (1991). Little natural vegetation remains. The Levera pond watershed contains natural vegetation (cactus scrub and deciduous seasonal forest), and annual crops.

provide less protection from erosion than forest because they have fewer strata of vegetation to intercept rain and less extensive root systems to consolidate the soil. Crop soils usually have less humus than forest soils; therefore, they have lower permeability and experience greater surface runoff (Goudie, 1994). The above factors increase the likelihood of floods or mudslips.

Evidence of human disturbance in the Levera area during colonial times includes the remains of a fort and look-out tower on Bedford Point. A large black boiling pot (Fig. 7b) adjacent to the foundations of a building may be the remains of a sugar cane plantation, northwest of Levera Pond (Fig. 6). Today there is a footpath circling Levera Pond, an unpaved road to the east of Levera Swamp, and several footpaths and cutlines through the watershed. Local people cut mangroves for charcoal, fish in Levera Pond, and trap crabs in Levera Swamp. There is a coconut plantation northwest of Levera Pond and several small fields around the periphery of the swamp. Cattle were observed grazing in a field east of Levera Pond.

METHODS

Field Methods

Field work was conducted at Levera Pond in November, 1992. Vegetation zones were mapped using aerial photographs and field observation. Species within each zone were ranked as abundant, common, or rare (Table 1). Plants were collected, identified, and deposited in the Royal Ontario Museum (Appendix 1).

Several pinches of surface sediment (about 1 mL each) were taken from each vegetation zone for pollen analysis. Samples from a given zone were mixed together, to prevent over-representation of local vegetation. Samples represent several years of sediment accumulation and therefore reduce possible bias of seasonal and annual variation in pollen production. Surface litter samples were taken from two 1 m^2 plots in the *Rhizophora* zone, *Avicennia* zone, and mixed mangrove zone. Water samples were taken from the top and bottom of the water column in the centre of Levera Pond (3 m deep) and tested for salinity using a Yellow Springs Conductivity Meter (Model 33).

Sediment cores were taken with a Dachnowsky sampler and modified Livingstone sampler (Wright, 1967). Cores A, B, and C, (444 cm, 445 cm, and 120 cm long respectively) were taken along a transect between Levera Pond and Levera Beach and Core D (205 cm long) was taken 10 m west of Core C (Fig. 6). Further penetration was impeded by coarse mineral sediments. An additional core was taken from the centre of Levera Pond in December, 1993, by Jock McAndrews.

Sediment Analysis

Cores were described visually, and analysed by loss on ignition (Dean, 1974). The outer portion of the cores were scraped off prior to sampling to remove surface contamination. Samples of 0.9 mL were removed at 5 cm intervals. Some sections of Core A (120-140 cm, 140-160 cm) and Core B (300-310 cm, 310-320 cm) were too watery to form a solid core, so only one sample could be taken per section. Samples were oven-dried at 105°C for 24 hours, and then heated in a furnace for one hour at 550 and 1000°C, successively. Weight loss between 105 and 550°C represents organic content. Weight loss between 550 and 1000°C represents CO_2 content of $CaCO_3$. To calculate $CaCO_3$ content, the amount of CO_2 was divided by 0.44 (the fraction of CO_2 in $CaCO_3$), (Dean, 1974). Results were plotted using the computer program CANPLOT (Campbell and McAndrews, 1992).

Particle size of the shelly sand unit of Core A (370-444 cm), Core B (420-445 cm), and Core D (150-205 cm) was determined by dry sieving sediments through a 9.5 mm, 6.3 mm, 4.0 mm, 2.0 mm, 1.0 mm, 710 um, and 297 um mesh.

Dating

Three peat samples from each of Cores A and B were radiocarbon dated at Brock Geological Sciences. Radiocarbon years deviate from calender years due to variations in the $^{14}C/^{12}C$ ratio of carbon dioxide in the atmosphere (Olsson, 1986). Therefore, age was converted to calender (cal) years with the Radiocarbon Calibration Program Rev. 3.0.3 (Stuiver and Reimer, 1993), using a decadal tree-ring dataset (Stuiver and Becker, 1993). A smoothed version of the calibration

curve (150 year moving average) was used, as recommended for samples which have accumulated over long time intervals (Stuiver and Reimer, 1993). The tree-ring dataset is recommended for terrestrial samples. Analysis of litter samples indicates that all identified organic matter is derived from mangroves. However, if there is a component of marine organic matter in the peat, the ages may be somewhat younger than reported. Marine samples have a lower $^{14}C/^{12}C$ ratio than contemporaneous terrestrial samples because carbon in deep ocean water is exchanged so slowly with that of surface water that some radiocarbon decays before exchange. Age of the bottom of Cores A and B was estimated assuming a constant rate of deposition (arbitrarily chosen as 2 cm/year) in the shelly sand unit.

Pollen analysis

Reference pollen slides were made by treating flowers with warm 10% KOH for five minutes to soften them, sieving with a gouch crucible to remove large particles, and then treating with warm acetolysis solution for two minutes to break down cellulose. Samples were mounted on slides with silicone oil and the cover slip sealed with latex paint. Additional reference slides were obtained from the Royal Ontario Museum, Toronto, and the Canadian Museum of Nature, Ottawa. It was difficult to discriminate pollen of *Hippomane mancinella* and *Euphorbia serpens*. Because *Hippomane* is more common in the vegetation, this pollen is referred to as *Hippomane*-type.

Samples of 0.9 mL were removed from Cores A and B at intervals of 5 to 20 cm. Samples were prepared for pollen analysis using standard procedures (Faegri

and Iversen, 1989), as outlined below. Samples were treated with 10% HCl to dissolve carbonates and sieved to remove particles <10 um and >150 um. Most pollen types (including all local to Levera Pond) fall within this size range. However, sieving would have caused the loss of exceptionally small pollen grains (e.g. *Peperomia* and *Piper*) and exceptionally large pollen grains (e.g. *Manihot esculenta* and *Ipomoea quamoclit*) which are present on Grenada. Samples were then treated with warm 10% KOH for five minutes to remove colloids, warm HF for two minutes to dissolve silicates, and warm acetolysis solution for two minutes to break down cellulose. Samples were stained with safranin and mounted in silicone oil. For peat samples, it was necessary to extend KOH treatment to 15 minutes (adding water to prevent concentration of KOH) and to sieve samples again after chemical treatment to remove particles <10 um.

Pollen density can be determined by spiking sediment samples of known volume with a known number of marker particles (Benninghoff, 1962). One tablet containing approximately 11,300 *Lycopodium clavatum* spores in a $CaCO_3$ matrix (Stockmarr, 1971) was added to each sample before treatment. *Lycopodium clavatum* is a suitable marker for tropical pollen because it is a temperate species. Four species of *Lycopodium* have been reported on Grenada (*L. cernuum*, *L. dichotomum*, *L. linifolium*, and *L. taxifolium*); however, these species are distinguishable from *L. clavatum*. Furthermore, marker spores are easily distinguished from other spores because they have been acetolyzed twice (tablet preparation and pollen concentration) and therefore appear darker than other

spores. The ratio of observed to total *L. clavatum* spores was used to determine the quantity of sediment examined in each count, and the pollen density was then calculated, as summarized below.

$$\frac{\text{observed } L. \text{ clavatum}}{\text{total } L. \text{ clavatum}} = \frac{\text{mL sediment examined}}{\text{mL sediment in sample}}$$

$$\frac{\text{observed pollen}}{\text{mL sediment examined}} = \text{pollen density (per mL)}$$

Fossil pollen were counted along traverses spaced 0.5 mm apart at a magnification of 500x using Leitz Wetzlar microscopes linked by a comparison bridge. To determine a desirable sample size, the number of pollen types and percentage of selected pollen types were graphed as a function of sample size (Figs. 9 and 10). Where possible, a minimum of one hundred fossil pollen grains were counted per sample. In a few samples of the clay unit, pollen density was too low to count one hundred grains. A larger sample size (minimum of two hundred pollen grains) was used for surface samples because these results are used to interpret fossil pollen assemblages. *Nymphaea* and microforaminifera were excluded from the pollen sum. Results were plotted using the computer program CANPLOT (Campbell and McAndrews, 1992). Pollen counts are deposited with the North American Pollen Database, Illinois State Museum, Springfield.
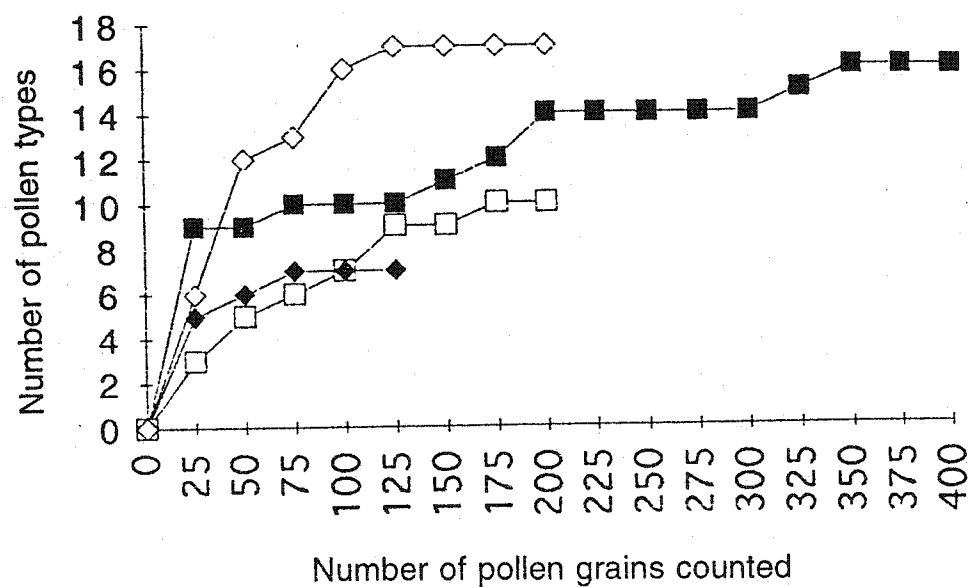
Figure 9. Number of pollen types as a function of sample size. Rate of increase slows at a sample size of about 100 pollen grains. ◇ = Core B, 130 cm, ■ = Core B surface sample, □ = *Hippomane* surface sample, ◆ = Core B, 247 cm.
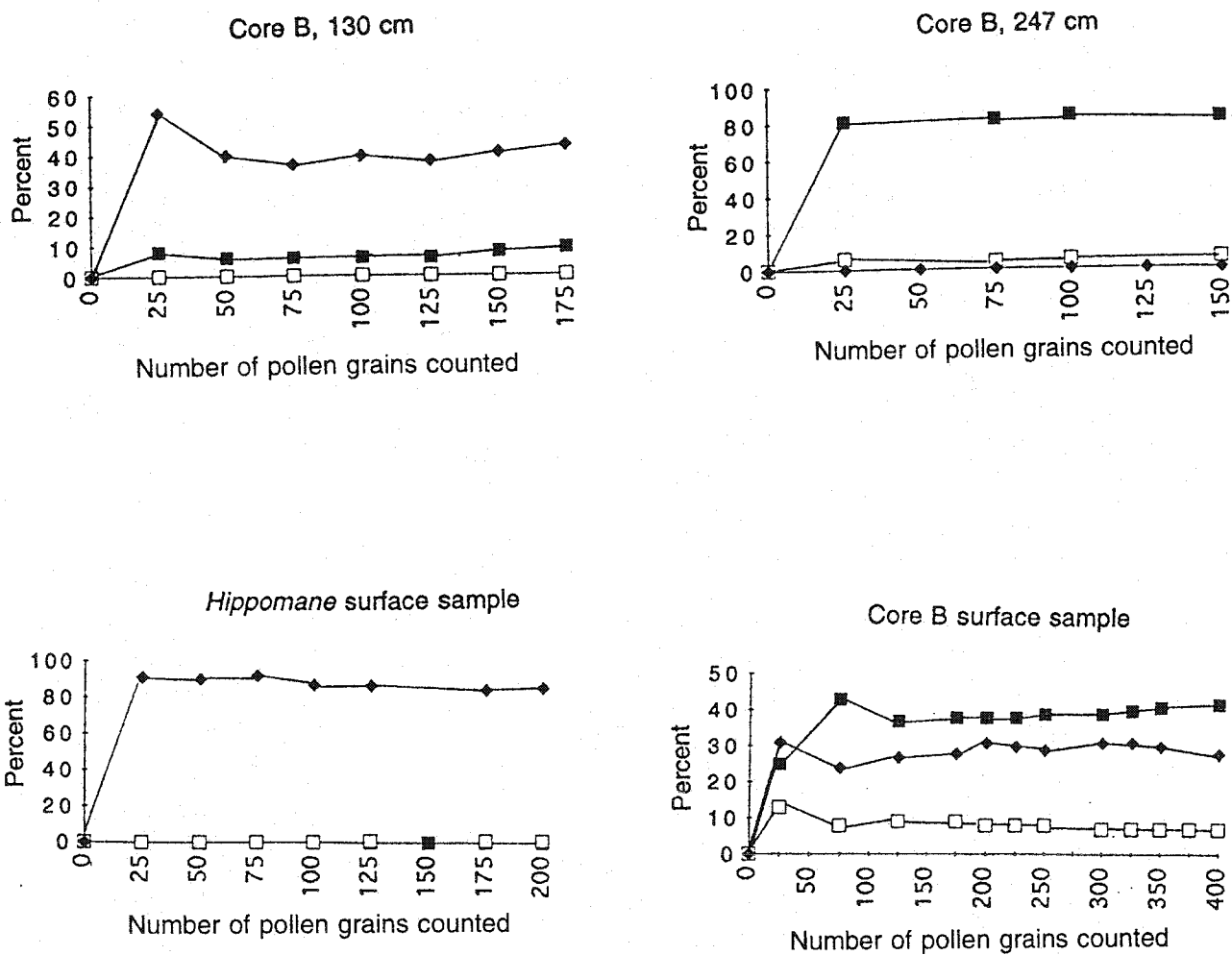
Figure 10. Percentage of selected pollen types as a function of sample size.

♦ = *Hippomane*,   ■= *Rhizophora*,   □= *Conocarpus*. Percentages stabilize before a sample size of 100 pollen grains.

Macrofossils

Reference propagules (fruits, seeds, or seedlings) were mounted on slides with rubber cement. Surface litter samples were sieved through a 500 um mesh. Core samples were analyzed in 20 to 40 cm segments. Core segments were soaked in water for 48 hours to soften sediments, and then sieved through a 297 um mesh. Macrofossils were picked using a Wolfe dissecting microscope at 10x magnification. The presence or absence of charred and uncharred wood was noted. Molluscs, foraminifera, and echinoderm spines were identified by David Barr, Department of Invertebrate Zoology, Royal Ontario Museum. Leaves were identified by comparison with herbarium specimens and propagules were identified by comparision with the reference collection. Two macrofossils which were abundant in the samples could not be identified. Unknown A is a solid, barrel-shaped seed, approximately 1 mm x 0.5 mm, light to dark brown with a dull sheen, and with six dark brown grooves running length-wise. A few specimens have a small point at one end. Unknown B is spherical, approximately 0.5 mm, beige, hairy, spongy, and hollow, with a shiny brown lining inside.

RESULTS

Salinity

Samples from the top and bottom of the water column in the centre of Levera Pond had salinities of 4.1 and 4.2 ppt (parts per thousand), respectively, indicating that Levera Pond is brackish and unstratified. For comparison, distilled water has a salinity of 0 ppt and sea-water has a salinity of approximately 32 ppt. Salinity of Levera Pond may vary over time (increasing during the dry season), and over space (increasing with distance from river inlets). Samples were taken at the end of the rainy season and therefore may have had lower salinity than usual.

Sediment Stratigraphy

Cores A and B have three stratigraphic units: shelly sand, successively overlain by peat and clay (Fig. 11). The shelly sand unit consists of marine shells (intact and broken), coral, sand particles, and a small amount of plant debris. The contact between the shelly sand and peat units appears sharp in Core A. This contact was not recovered for Core B. The peat unit has scattered gastropod shells, which cause fluctuations in the calcium carbonate content. There is a sharp contact between the peat unit and clay unit in both cores. The clay unit can be subdivided into a basal grey clay phase (which contains pyrite, FeS_2) and an upper cinnamon brown clay phase (which does not). The grey/brown contact was not recovered for either core, but the brown phase begins at less than 110 cm depth in Core A and at less than 100 cm depth in Core B. Pyrite is common in mangrove
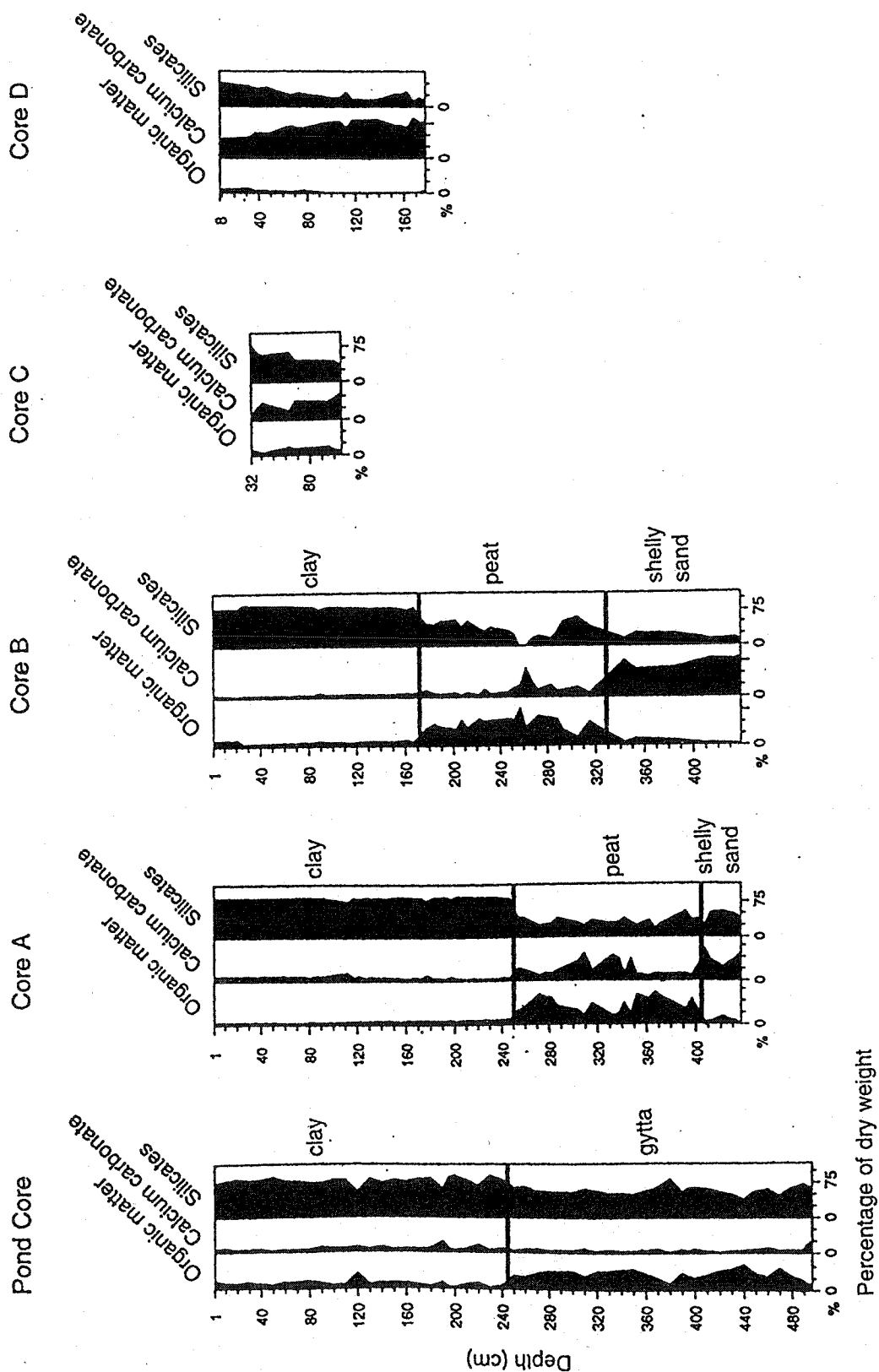
Figure 11. Thermal analysis of five Levera cores. Cores A and B have three stratigraphic units: shelly sand, overlain by mangrove peat, and then clay. The Pond Core has a basal unit of gytta overlain by clay, which correspond to the peat and clay units of Cores A and B. Cores C and D have a higher proportion of calcium carbonate than the clay units of the other three cores because they were taken closer to the sea and therefore receive more tide-transported (shelly) sediments.

sediments, resulting from bacterial reduction of sulphates of marine origin under anaerobic, waterlogged conditions (Marius and Lucas, 1991; Lin and Melville, 1993). The brown clay phase reflects aerobic conditions. The pond core has two stratigraphic units: basal gytta (organic pond mud), overlain by clay, which correspond to the peat and clay units of Cores A and B.

Core C grades from sand at the base of the core to clay at the top, without a sharp contact. Core D grades from shelly sand to sand to clay, without a sharp contact. No radiocarbon dates were made on Cores C and D, but they appear to correspond to the clay unit of the other cores (Fig. 11). Cores C and D have a higher proportion of calcium carbonate (shell and coral) because they were taken closer to the sea, and therefore receive more tide-transported sediments. Particle size is greater in Core D than Core C, as it was taken closer to the path of tidal flow. The basal section of Core D has a similar organic/calcium carbonate/silicate ratio to the shelly sand unit of Cores A and B. However, particle size is smaller in Core D (Fig. 12), suggesting a lower energy environment than experienced in the shelly sand units of Cores A and B. Particle size decreases upward, indicating reduced depositional energy over time.

Radiocarbon and Calender Dates

Radiocarbon dates (Table 3) indicate that the bottom of Cores A and B are about 2500 years old. Peat deposition began just before 2360 ± 240 yr B.P. in Core A and just before 1970 ± 170 yr B.P. in Core B. Clay deposition began less than 500 ± 80 yr B.P. in Core A and less than 230 ± 100 yr B.P. in Core B. (Dates
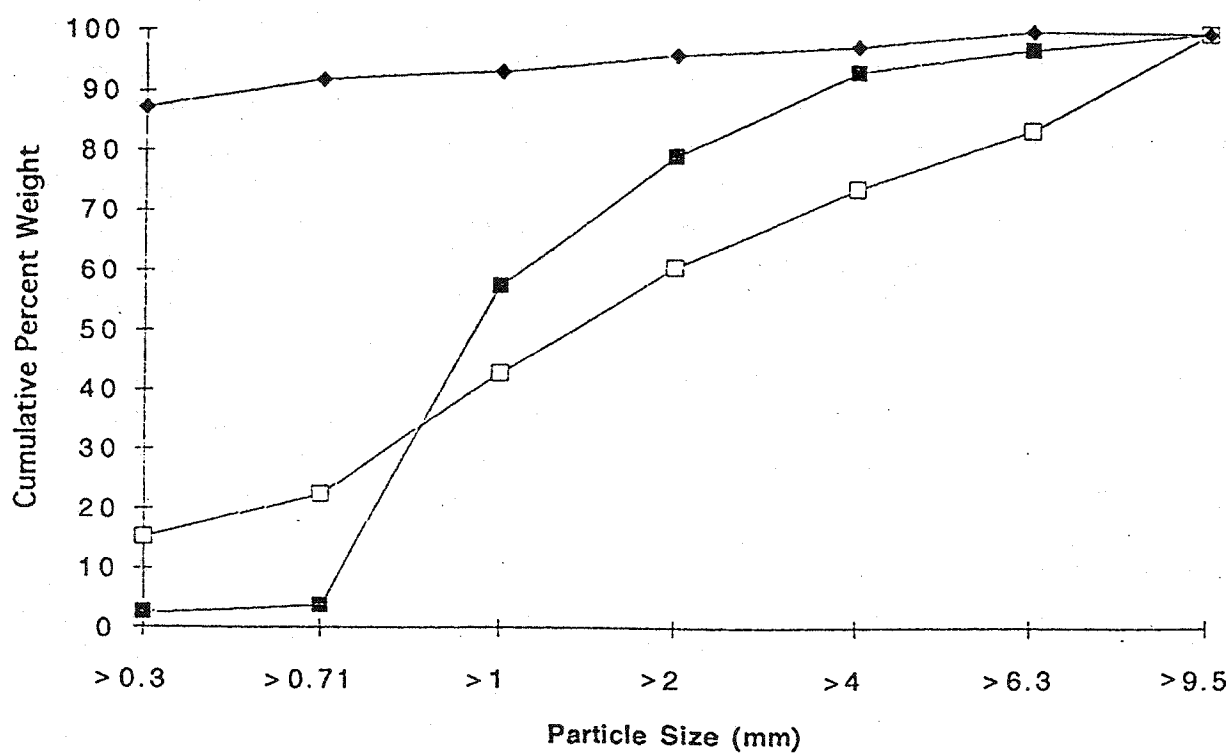
Figure 12. Cumulative particle size of the shelly sand unit of Core A (■), Core B (□), and Core D (♦).
Particles less than 0.3 mm are not included in the diagram.

Table 3. Age of mangrove peat sediments from Levera Pond, Grenada. Radiocarbon dates are reported as years before present (1950) ± one standard deviation. Calibrated (cal.) age range includes values within one standard deviation. More than one calibrated age range may be reported for a sample due to fluctuations in atmospheric $^{14}C/^{12}C$ ratios.

Core	Depth (cm)	^{14}C age (YBP)	cal. age range (YBP)	cal. age range (AD/BC)	Lab. No.[a]
A	252-257	500 ± 80	570-500	AD 1380-1450	BGS 1625
A	330-353	1875 ± 90	1890-1680	AD 60-270	BGS 1699
A	393-411	2360 ± 240	2720-2090	770-140 BC	BGS 1626
B	163-190	230 ± 100	490-270	AD 1460-1680	BGS 1623
			10-0[b]	AD 1940-1955	
B	220-235	1700 ± 90	1700-1490	AD 250-460	BGS 1698
B	284-294	1970 ± 170	2110-1730	160 BC-AD 220	BGS 1624

[a]Brock Geological Sciences

[b]represents a negative age BP (post-1950)

were made near the top of the peat unit, not at the contact). Age similarity confirms that the stratigraphic units of Cores A and B represent the same depositional events. However, peat accumulation and clay deposition began about 300 years earlier in Core A (the landward core) than in Core B (the seaward core), (Figs. 13 and 14). An alternative theory is that peat accumulation was synchronous in both cores, and the radiocarbon dates are slightly inaccurate. This theory is supported by the fact that the peat units are the same length (160 cm, Fig. 11). If peat deposition were synchronous, rate of clay deposition would have been almost twice as high in Core A than in Core B. However, the fact that all three radiocarbon dates are older for Core A than Core B suggests that peat deposition was not synchronous.

A single radiocarbon date can correspond to multiple calender dates, due to past changes in atmospheric ^{14}C levels (Stuiver and Pearson, 1986). One age range is reported for the upper peat unit of Core A: 500-570 cal yr B.P. In contrast, two age ranges are reported for Core B: 490-270 cal yr B.P., and 10-0* cal yr B.P. (where 0* = post-1950). It is unlikely that the latter age range is correct, because there is no corresponding age range for Core A. The clay unit of Cores A and B appears similar and likely corresponds to the same depositional event.

Presence of *Cocos nucifera* pollen at the base of the clay unit in Cores A and B (Figs. 13 and 14) indicates that clay deposition began less than 400 yr B.P. *Cocos nucifera* is native to the Old World tropics (Howard, 1979), and was introduced to the Caribbean after A.D. 1550 (400 yr B.P.) (Patterson and Stevenson, 1977).
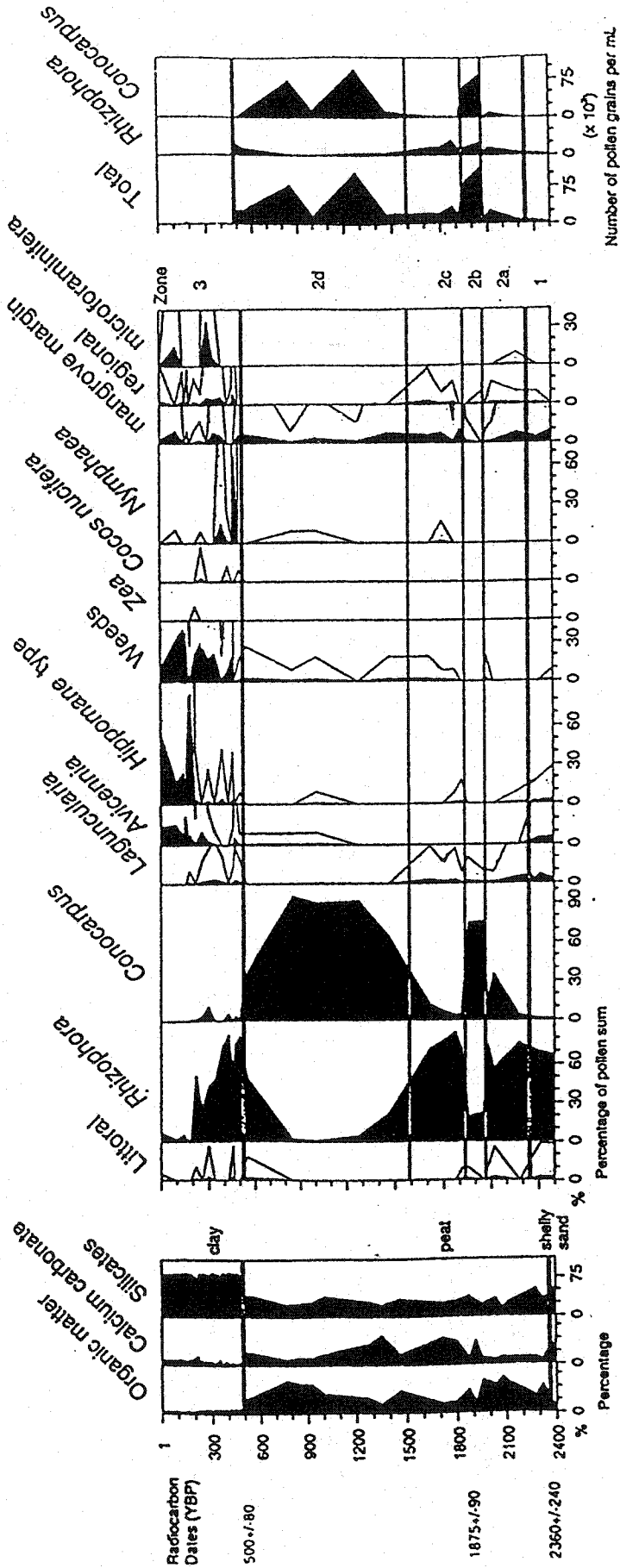
Figure 13. Thermal analysis, pollen percentage, and pollen density of Core A. White curves in the pollen diagram represent 5x exaggeration. *Nymphaea* and microforaminifera were excluded from the pollen sum. *Hippomane* type includes pollen from *Hippomane mancinella* and *Euphorbia serpens*. See Appendix 2 for constituent species of the littoral, weeds, mangrove margin, and regional categories.
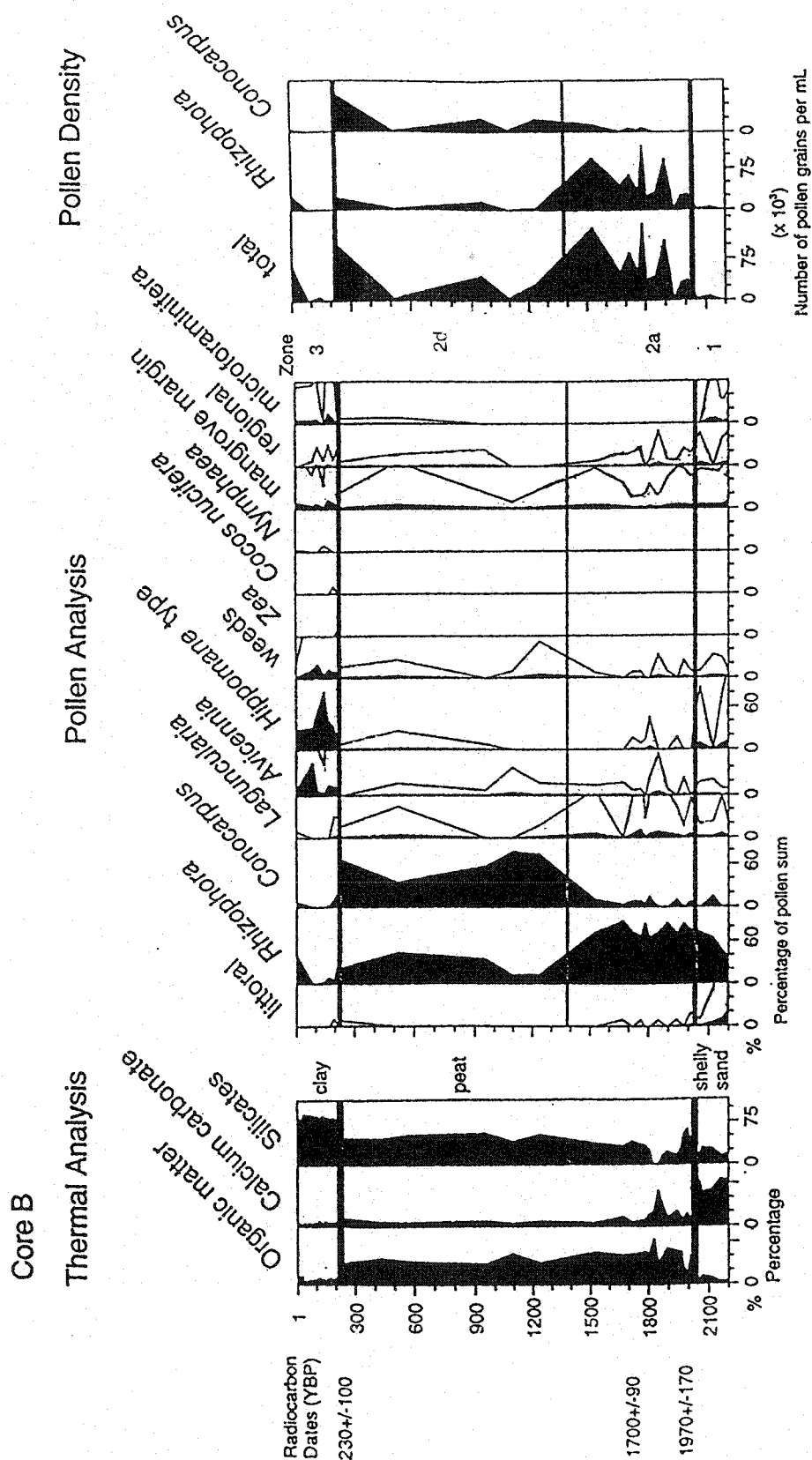
Figure 14. Thermal analysis, pollen percentage, and pollen density of Core B. White curves in the pollen diagram represent 5x exaggeration. *Nymphaea* and microforaminifera were excluded from the pollen sum. *Hippomane* type includes pollen from *Hippomane mancinella* and *Euphorbia serpens*. See Appendix 3 for constitituent species of the littoral, weeds, mangrove margin, and regional categories.

Sedimentation Rates

Sediment accumulation rates were estimated using radiocarbon dates. The peat unit has a sediment accumulation rate of 0.08 cm/yr (12.6 yr/cm) in Core A and 0.06 cm/yr (15.5 yr/cm) in Core B. Sediment accumulation rates were slower during the *Conocarpus* peak (Zone 2d) than during the *Rhizophora* peak.

The clay unit has a sediment accumulation rate of more than 0.5 cm/yr (2.0 yr/cm) in Core A and more than 0.7 cm/yr (1.4 yr/cm) in Core B. Thus, sediment accumulation rates were 6 to 11 times higher during the historic period, indicating higher erosion rates following forest clearance for agriculture and grazing.

Pollen Surface Samples

Surface pollen assemblages (Fig. 15) reflect local mangrove vegetation (Anderson and Muller, 1975; Grindrod, 1985; Tissot, 1990). Between 85 and 100% of identified pollen grains represent species which occur within a 100 m radius of the sample site, 0-4% represent species within 500 m, and 0-11% represent species which occur more than 500 m from the sample site. In contrast, Caratini *et al.* (1973) report up to 25% allochthonous pollen, with highest values near river channels, suggesting water-transport. However, this may be an over-estimate, as unknown pollen and pollen from taxa which were rare in the mangrove zone were classified as allochthonous pollen. The low percentage of allochthonous pollen in mangrove swamps may be partially explained by local abundant pollen producers, causing autochthonous pollen to "drown out" allochthonous pollen. Many upland
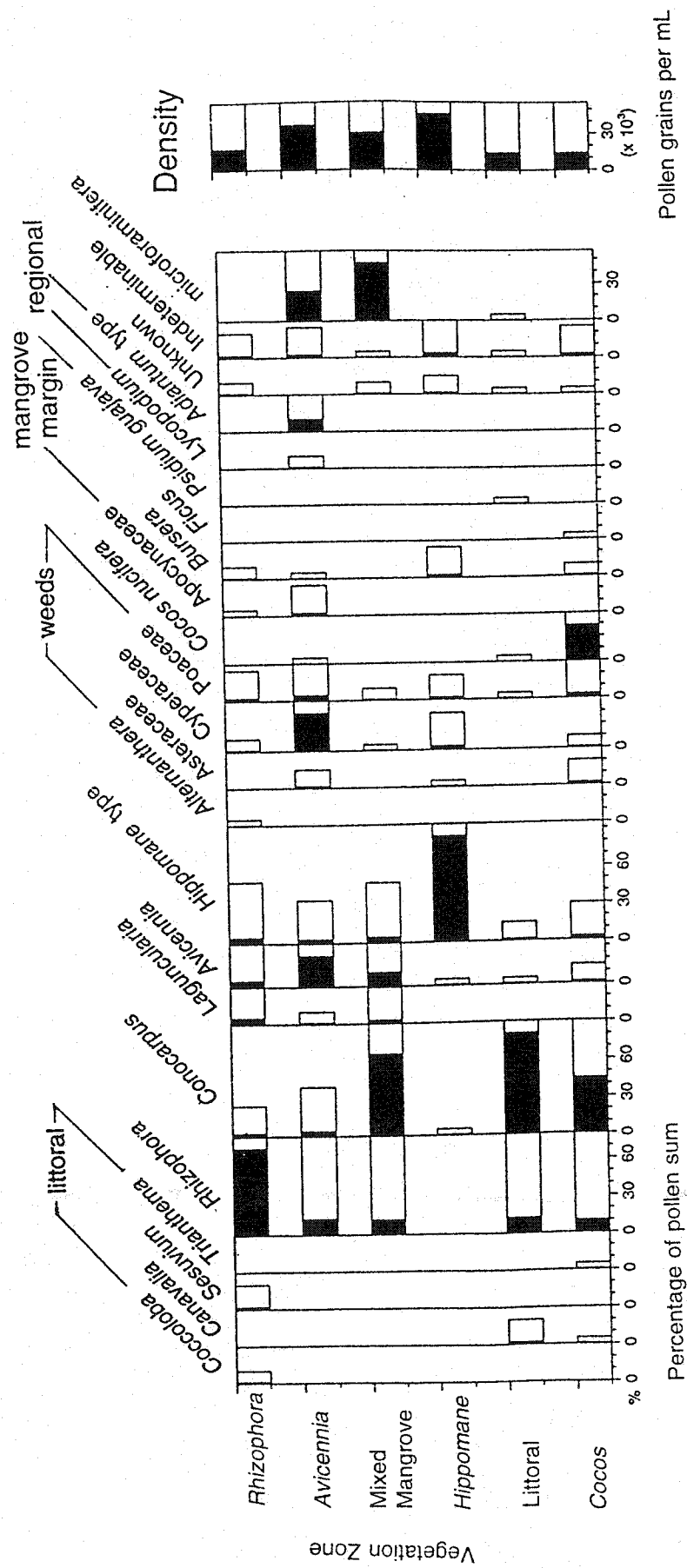
Figure 15. Pollen surface samples from different vegetation zones at Levera Pond. White bars represent 10x exaggeration. Microforaminifera were excluded from the pollen sum.

species are insect-pollinated with limited pollen dispersal. In addition, the closed mangrove canopy reduces influx of allochthonous wind-borne pollen. At Levera Pond, trade winds blow onshore from the east and would therefore be expected to carry less pollen than winds which traverse the land. These factors make Levera Pond an excellent location to study local succession.

Different species vary widely in their pollen production and dispersal capabilities. Therefore it is necessary to use surface samples to calibrate the pollen-vegetation relationship. The use of modern analogues is an effective method of interpreting the fossil record, assuming that the relationship is not obscured by differential pollen preservation. Typical of anemophilous species, *Rhizophora mangle* produces abundant, easily dispersed pollen (Anderson and Muller, 1975). At Levera Pond, 70% *Rhizophora* pollen represents a pure stand, while 10% *Rhizophora* pollen represents adjacent vegetation zones. Somewhat higher values were reported for *Rhizophora* species in Missionary Bay, Australia (Grindrod and Rhodes, 1984), with over 90% *Rhizophora* pollen in the *Rhizophora* zone and 44-59% *Rhizophora* pollen in adjacent zones. Values may be lower at Levera Pond because the *Rhizophora* zone forms a relatively narrow fringe. In addition, *R. mangle* may have lower pollen production than other *Rhizophora* species. *Rhizophora* pollen has been reported nearly 2 km upwind from parent sources (Grindrod, 1985); however, strong localized deposition renders it a useful indicator species (Grindrod, 1988; Ellison, 1989).

Conocarpus pollen is over-represented and easily dispersed. The pollination mechanism is unknown (Tomlinson, 1986), but abundant pollen production suggests anemophily. For example, *Conocarpus* comprises 35% of surface pollen in the *Cocos* plantation, although it is absent from the vegetation. Although *Conocarpus*, *Avicennia*, and *Laguncularia* are equally abundant in the mixed mangrove vegetation (Table 1), *Conocarpus* comprises 65% of the surface pollen, while *Avicennia* and *Laguncularia* pollen comprise only 11% and 3%, respectively. This example also shows that the entomophilous *Laguncularia* is greatly under-represented in surface pollen.

Avicennia is an entomophilous genus which is under-represented in surface pollen (Bartlett and Barghoorn, 1973; Caratini *et al.*, 1973; Vishnu-Mittre and Guzder, 1973). At Levera Swamp 25% *Avicennia* pollen represents a pure *Avicennia* stand with localized patches of *Fimbristylis*, 11% represents a mixed mangrove stand, and up to 5% *Avicennia* pollen indicates adjacent vegetation zones.

Hippomane pollen has strong localized deposition, comprising 85% of surface pollen in a pure stand, and up to 5% in adjacent zones. The pollination biology is uncertain, but conspicuous yellow glands associated with each flower cluster may attract pollinators (Tomlinson, 1986).

Cocos nucifera pollen is under-represented, comprising 30% of surface pollen in a pure *Cocos* stand. *Coccoloba uvifera*, *Canavalia rosea*, and *Sesuvium portulacastrum*, which are common to abundant in the littoral zone, are also under-

represented in the surface pollen. *Ipomoea pes-caprae* which is common in the littoral zone, is absent from surface pollen, as it usually reproduces by vegetative means. The weedy plants, Poaceae and Cyperaceae, have normal representation in the surface pollen (Grindrod, 1985). *Bursera* and Apocynaceae, which grow along the mangrove margin, contribute up to 3% of pollen in the mangrove surface samples, indicating good pollen dispersal.

Chitinous microforaminifera linings (Terasmae, 1958) are present in the littoral surface sample and are abundant in the mixed mangrove and *Avicennia* surface samples. Foraminifera inhabitat a variety of habitats in brackish to saline waters, and therefore indicate marine influence (Murray, 1991a and b).

Fossil Pollen

Cores A and B exhibit three pollen zones, corresponding to the three stratigraphic units (Figs. 13 and 14, Appendices 2 and 3). Zone 1, which corresponds to the basal shelly sand unit, has low pollen density ranging from 3000 to 6000 grains per mL in Core A and 750 to 7500 grains per mL in Core B. Low pollen densities may be caused by (1) low pollen production, (2) high sediment accumulation rates, or (3) post-depositional loss due to decay or winnowing (Vishnu-Mittre and Guzder, 1973). *Rhizophora*, the dominant pollen type in Zone 1, is an abundant pollen producer. Ward (1988) reported low mangrove pollen density due to fungal and bacterial decay. In contrast, pollen from Levera Swamp is well-preserved. Therefore, low pollen density may indicate that the shelly sand unit

(1) was deposited seaward of a *Rhizophora* stand, (2) had a rapid rate of accumulation of marine sediments, and/or (3) experienced post-depositional loss due to winnowing. All three options indicate more direct contact with the ocean than experienced in the peat unit.

Zone 1 is similar to the *Rhizophora* zone surface sample (Fig. 15). Both are dominated by *Rhizophora* and have low representation of *Avicennia*, *Conocarpus*, *Laguncularia*, and *Hippomane*-type pollen. However, the *Rhizophora* surface sample has a higher pollen density. The percentage of littoral species in the *Rhizophora* surface sample is similar to that of Core A, but lower than that of Core B. In Core B, the proportion of littoral pollen declines from 25% at the base of the core to 3% near the Zone 2 contact. Core B has microforaminifera, while Core A and the *Rhizophora* surface sample do not. The pollen assemblage indicates that the shelly sand unit was deposited in or seaward of a *Rhizophora* stand.

Zone 2, which corresponds to the peat unit, is characterized by high but fluctuating pollen densities, ranging from 9500 to 116,000 grains per mL in Core A, and 4000 to 140,000 grains per mL in Core B. Fluctuating pollen densities probably reflect the heterogeneity of peat. Deposition of vegetative matter, such as leaves and wood, would decrease pollen density, while deposition of flowers would increase pollen density. However, there was no correlation between pollen clumps and density peaks. Core A has higher densities of *Conocarpus* pollen, while Core B has higher densities of *Rhizophora* pollen, indicating that Core A (the landward site) is a drier site than Core B (the seaward site).

In Zone 2, there is a general shift from *Rhizophora* dominance to *Conocarpus* dominance, indicating a decrease in relative sea-level. However, the pattern of this succession differs between the two cores. Core A has four subzones, 2a-d, while Core B has only two, 2a and d.

Zone 2a is similar to the *Rhizophora* zone surface sample. However, Core A lacks *Avicennia* pollen and both cores show a slightly higher proportion of *Conocarpus* pollen, reaching up to 30% in Core A. This suggests that Zone 2a represents a pure *Rhizophora* stand, adjacent to a mixed mangrove zone. The mixed mangrove zone would have been similar in composition to the one existing today, but with a lower proportion of *Avicennia* near Core A, and higher proportions of *Conocarpus* near both core sites.

Zone 2b (Core A only) is similar to the mixed mangrove surface sample, but lacks *Avicennia* and *Hippomane*-type pollen and has a slightly higher proportion of *Rhizophora* pollen. This indicates a mixed *Conocarpus/Laguncularia* stand, immediately adjacent to a *Rhizophora* stand. Because there is a steep slope at the coring sites, vegetation zones may occur in narrow bands. Alternatively, *Rhizophora* may have formed a mixed stand with the other mangroves. Zone 2b indicates an abrupt decrease in relative sea-level, which persists for about 12 cm (25 years) of the peat unit. This subzone may be absent from Core B because it is a wetter site. Thus, even with a decrease in relative sea-level, Core B may have remained in the sea-level range dominated by *Rhizophora*. Alternatively, Zone 2b might be an artifact of bioturbation. For example, a disused crab burrow (Fig. 7a)

could have been filled with younger sediments from the *Conocarpus* peak of Zone 2a (Grindrod, 1988).

Zone 2c (Core A only) is similar to Zone 2a, indicating a *Rhizophora* stand, adjacent to a mixed *Conocarpus/Laguncularia* zone. *Nymphaea* pollen also appears in Zone 2c. Most *Nymphaea* species occur in fresh-water, but some occupy slightly brackish water, stagnant or flowing, in coastal lowlands (Wiersema, 1987).

Zone 2d is similar to the mixed mangrove surface sample. However, Core A has a higher proportion of *Conocarpus* pollen than the surface sample, suggesting *Conocarpus* was dominant and *Avicennia* rare. In contrast, Core B has more *Rhizophora* and less *Conocarpus* pollen than the mixed mangrove surface sample, confirming that Core B was a wetter site than Core A.

Zone 3, which corresponds to the clay unit is characterized by low pollen densities ranging from 150 to 3000 grains per mL in Core A and 900 to 6700 grains per mL in Core B (excluding the surface sample). Pollen is well preserved; therefore, destruction by fungi or bacteria is not a likely explanation. Sediment accumulation rates are 6 to 11 times higher in the clay unit than the peat unit, which would dilute autochthonous pollen rain. A slight increase in allochthonous pollen in Zone 3 may be due to increased allochthonous sediment input. In addition, trees were cut to make a footpath and road adjacent to the coring sites, which would cause a slight decrease in pollen production.

The pollen assemblage changes abruptly in Zone 3, indicating human disturbance. The reason for the *Conocarpus* decline is unknown, but may reflect changing edaphic conditions. *Conocarpus* may also have been felled to create the foot-path. Core B has a lower proportion of *Rhizophora* pollen than Core A, in contrast to the peat unit. *Rhizophora* dominates the grey (pyrite-rich) clay unit of Core A, and declines toward the top of the core. The shift from *Conocarpus* dominance in Zone 2d to *Rhizophora* dominance in the lower clay unit of Core A may indicate a rise in water level at Levera Pond. Deforestation increases watershed runoff (Goudie, 1994), causing lake levels to rise (Dearing and Foster, 1986). Core B, which is further from Levera Pond, would be less affected by the rise. In support of this theory, *Nymphaea* pollen is abundant in the lower clay unit of Core A, suggesting pond overflow. *Avicennia* and *Hippomane*-type pollen increase in Zone 3, especially the upper brown clay unit. The increase in *Hippomane* reflects a shift to drier mineral soils. Weed pollen also increases due to forest clearance. *Zea* and *Cocos nucifera* pollen appear in Zone 3. *Zea* was cultivated by Amerindians, Europeans, and slaves (CCA, 1991). *Cocos nucifera* was introduced to the New World for cultivation after A.D. 1550 (Patterson and Stevenson, 1977). Microforaminifera are present in both cores, indicating brackish conditions.

Plant Macrofossils

Macrofossils usually reflect local vegetation, although they may be transported by water or animals (Faegri and Iversen, 1989). All identifiable components of mangrove litter were locally deposited (Fig. 16). However, a large proportion of litter (twigs and debris) were not identified. Debris is mainly composed of leaf fragments which resemble mangrove leaves. In the *Rhizophora* zone and *Avicennia* zone, the canopy dominant contributes the largest proportion of litter biomass. *Laguncularia* propagules are present in both zones, although mature *Laguncularia* are absent from the *Rhizophora* zone and rare in the *Avicennia* zone (Table 1). *Laguncularia* produce abundant fruit; however, seedling mortality in the first year is almost 100% (Tomlinson, 1986). The two *Rhizophora* samples are almost identical, reflecting the homogeneity of the *Rhizophora* zone. The two *Avicennia* samples are similar, but one has a higher proportion of *Laguncularia* than the other. The two mixed mangrove samples differ, reflecting the heterogeneity of vegetation in this zone. The samples contain little or no *Conocarpus*, although *Conocarpus* is common in the vegetation (Table 1). This indicates that *Conocarpus* has a lower rate of leaf and propagule production and/or a higher rate of decomposition, and may explain why peat accumulated more slowly during the *Conocarpus* pollen peak (Zone 2d) than the *Rhizophora* pollen peak (Zone 2a).

Fimbristylis seeds were found in *Rhizophora* and *Avicennia* litter (Fig. 17). Poaceae seeds were found in Rhizophora and mixed mangrove litter. *Polygonum* was found in *Rhizophora* litter, although it was not observed in local vegetation or

Litter Biomass
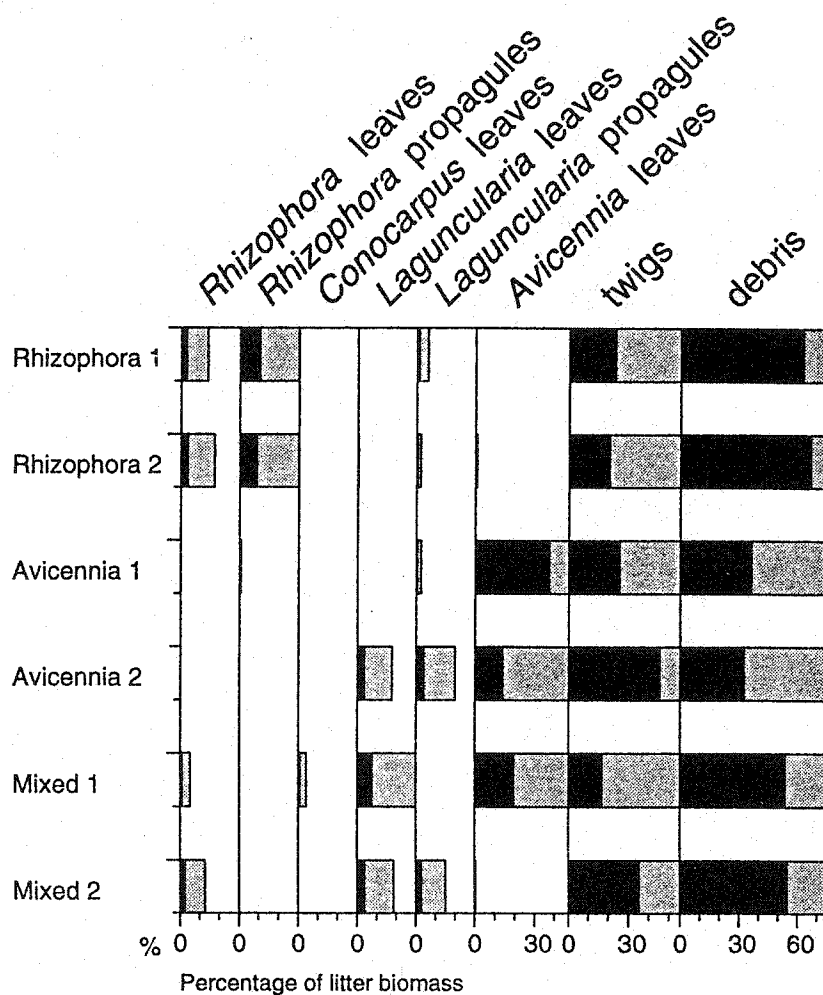
Figure 16. Percent contribution to litter biomass of the *Rhizophora* zone, *Avicennia* zone, and mixed mangrove zone. Grey bars represent 5x exaggeration. One litre of litter was examined for each sample. Replicate samples are shown for each zone. Propagules from species other than *Rhizophora* and *Laguncularia* contributed <1% of litter biomass and were excluded from the diagram. Twigs were not identified. Debris is mainly composed of leaf fragments, which resemble mangrove leaves.

Litter Propagules
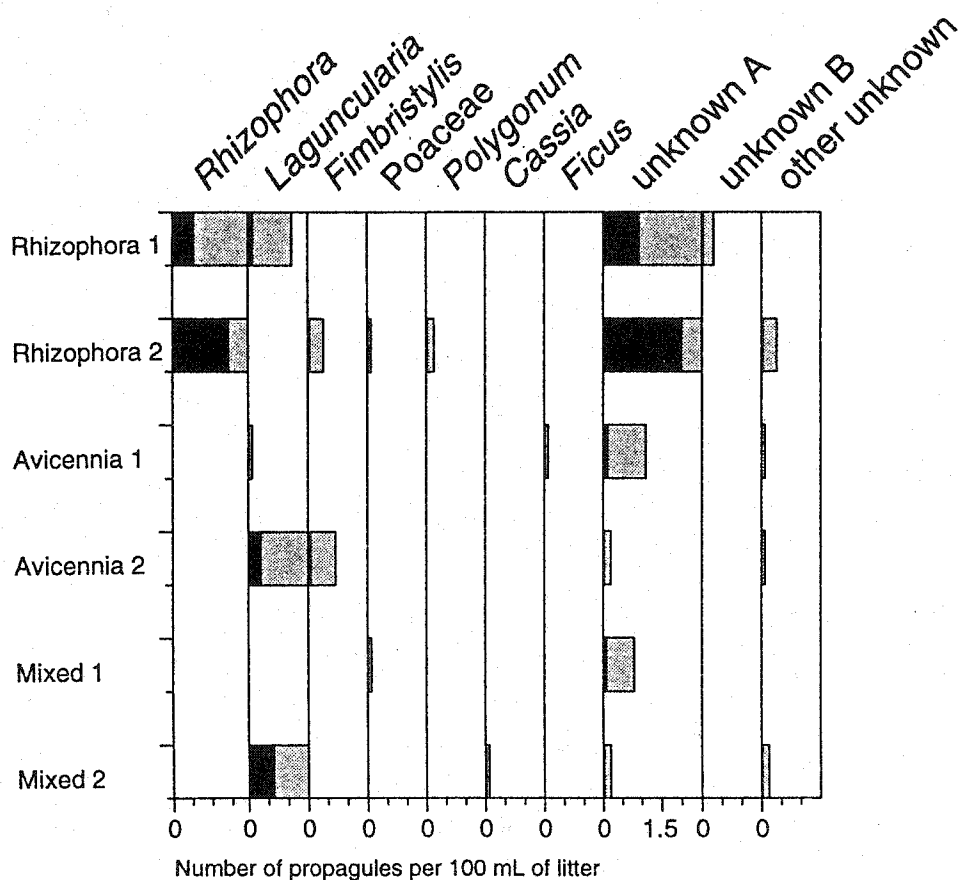
Figure 17. Number of propagules per 100 mL of litter from the *Rhizophora* zone, *Avicennia* zone, and mixed mangrove zone. Grey bars represent 5x exaggeration. One litre of litter was examined for each sample. Replicate samples are shown for each zone. Unknown A is a solid, barrel-shaped seed, approximately 1 mm x 0.5 mm, light to dark brown with a dull sheen, and with six dark brown grooves running length-wise. Unknown B is spherical, approximately 0.5 mm, beige, hairy, spongy, and hollow, with a shiny brown lining inside.

surface pollen. *Cassia* occurred in one of the mixed mangrove samples, while *Ficus* occurred in one of the *Avicennia* samples. Both plants grow along the mangrove margin. Unknown A occurred in all mangrove zones, whereas Unknown B was restricted to one of the *Rhizophora* samples.

The *Rhizophora* propagule in Core A (Fig. 18) corresponds to a *Rhizophora* pollen peak of Zone 3 (Fig 13). The *Conocarpus* propagules of Core A correspond to the *Conocarpus* pollen peak of Zone 2d. *Polygonum* seeds occur in Core B (Fig. 19), although they are absent from the pollen assemblage (Fig. 14). *Polygonum* is an herb with cosmopolitan distribution, ranging from garden weeds to wet habitats (Howard, 1988). *Nymphaea* macrofossils are abundant in Core A, but absent in Core B, in support of the pollen trend. This reflects the fact that Core A was taken closer to Levera Pond, where *Nymphaea* is likely to grow. *Nymphaea* macrofossils and pollen both peak near the bottom of Zone 3, suggesting pond overflow. Unknown A occurs in all lithological units, but is most abundant in *Rhizophora* peat (Zone 2a). Unknown B is most abundant in *Rhizophora* peat, but also occurs in the shelly sand unit of Core A. Wood occurs in the peat unit of both cores, and the clay unit of Core B. Charred wood occurs in the clay unit and prehistoric peat unit of Core B. Wood may be charred due to natural fire or Amerindian activity.

Other macrofossils

White gastropods, ranging in size from 0.5 mm to 5 mm, were present in the litter of all mangrove zones. This species has few diagnostic characters and could
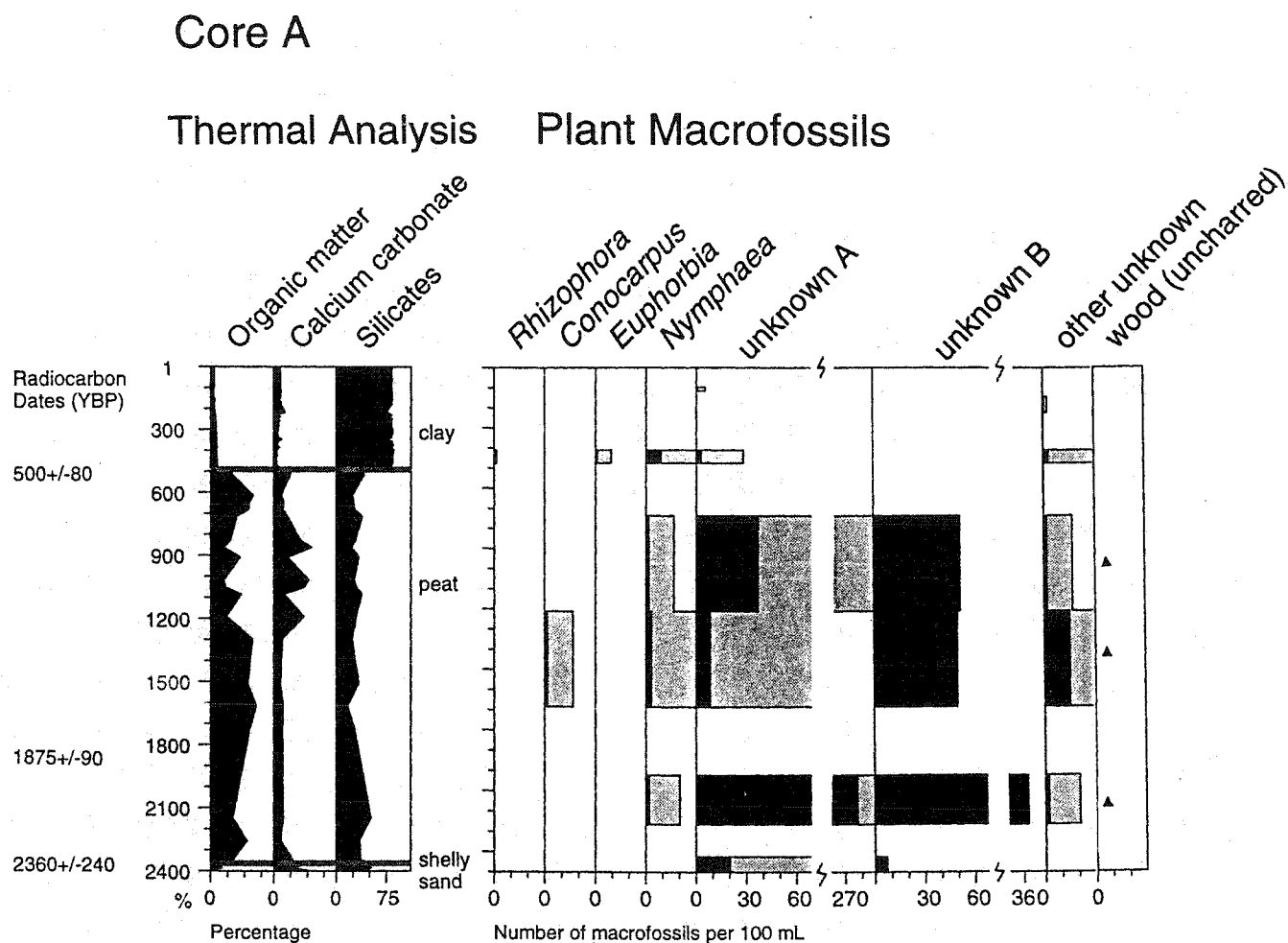
Figure 18. Number of propagules per 100 mL of sediment from Core A. Presence of wood is

indicated by a triangle (▲). Grey bars represent 10x exaggeration. Gaps represent sections of the

core which were not analyzed. Unknown A is a solid, barrel-shaped seed, approximately 1 mm x

0.5 mm, light to dark brown with a dull sheen, and with six dark brown grooves running lengh-wise.

Unknown B is spherical, approximately 0.5 mm, beige, hairy, spongy, and hollow, with a shiny

brown lining inside.

Core B

Thermal Analysis

Plant Macrofossils

Organic matter
Calcium carbonate
Silicates

Polygonum
unknown A
unknown B
other unknown
wood (uncharred)
wood (charred)

Radiocarbon
Dates (YBP)

230+/-100

1700+/-90

1970+/-170

1
300
600
900
1200
1500
1800
2100

clay

peat

shelly
sand

% 0   0   0   75
Percentage

0   6 0   6   0   0   6 0   0

Number of macrofossils per 100 mL of litter

Figure 19. Number of propagules per 100 mL of sediment from Core B. Presence of wood is indicated by a triangle (▲). Samples which contained no plant macrofossils are indicated by an asterisk (★) at the left margin. Gaps represent sections of the core which were not analyzed. Unknown A is a solid, barrel-shaped seed, approximately 1 mm x 0.5 mm, light to dark brown with a dull sheen, and with six dark brown grooves running length-wise. Unknown B is spherical, approximately 0.5 mm, beige, hairy, spongy, and hollow, with a shiny brown lining inside.

not be identified (David Barr, personal communication, 1994). Gastropods are common in all mangrove zones (Hutchings and Saenger, 1987); therefore, it is likely that they were deposited *in situ*. Similar gastropods are scattered throughout Cores A and B, with greatest abundance in the peat unit.

Litter samples also contain echinoderm spines and marine shells, indicating periodic tidal inundation. *Avicennia* litter and mixed mangrove litter contain foraminifera including *Amphistegina*, which indicates shallow marine water (Francine McCarthy, personal communication), and cf. *Ammonia beccarii* and cf. *Trochammina inflata*, which indicate the upper quarter of the intertidal zone (Scott and Medioli, 1986). However, no macrofo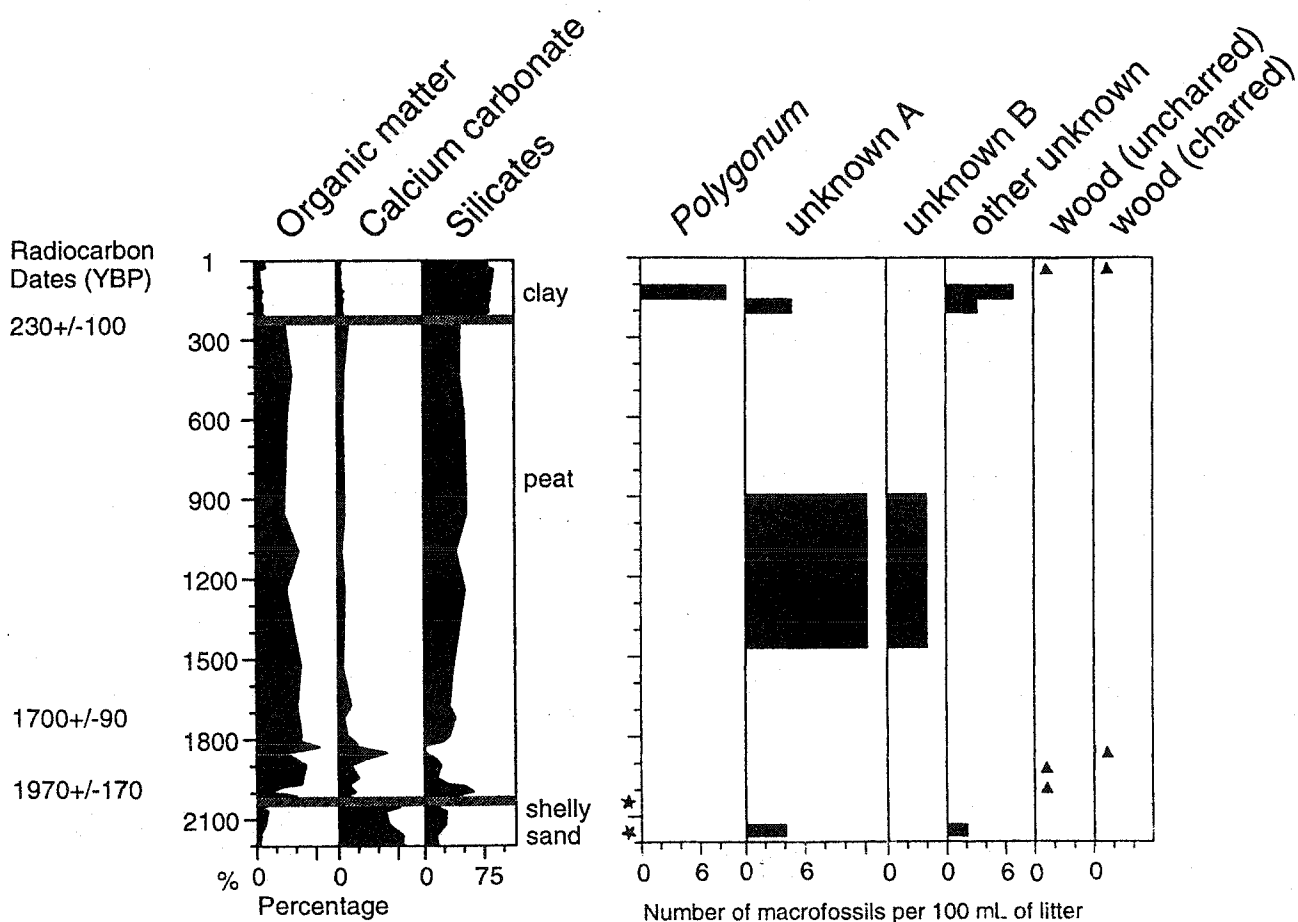ssil foraminifera were observed in the cores. Calcareous foraminifera (such as *Ammonia*) are seldom preserved in subsurface sediments (Scott and Medioli, 1986). Organic foraminiferal tests (such as *Trochammina*) are destroyed by oxidative bacteria if left to stand at room temperature for extended periods (Scott and Medioli, 1986). Litter samples were analyzed immediately after drying, whereas core samples were stored for over one year before analyzing. Therefore, absence of foraminifera in the cores does not prove absence at time of deposition.

The shelly sand unit of Cores A and B contains echinoderm spines and a variety of marine molluscs, including Muricidae cf. *Nucella*, Dentaliidae cf. *Dentalium laqueatum*, Corbulidae cf. *Corbula*, Lucinidae cf. *Phacoides*, and Veneridae cf. *Cyclinella/Callista*. This indicates that the ocean was the main source of sediment in the shelly sand unit.

DISCUSSION

Origin of shelly sand unit (Zone 1)

Cores A and B have three lithological units: shelly sand, overlain by mangrove peat, and then clay. Large particle size in the shelly sand unit indicates a higher energy environment than today. A sharp contact between shelly sand and *Rhizophora* peat indicates a sudden decrease in energy of deposition. Abundant marine shells and coral indicate that the sea was the main source of sediment in the shelly sand unit. This suggests a more direct connection with the ocean than today. Dominance of *Rhizophora* pollen indicates that the sample was taken in or seaward of a *Rhizophora* zone. Because the bottom of the core was not radiocarbon dated, rate of sediment accumulation in the shelly sand unit cannot be determined. It may have been deposited suddenly, in a storm, or gradually, as a beach deposit. Both possibilities are discussed below.

Storm theory

The shelly sand unit may have been deposited in a single high energy event, such as a hurricane. Storm surges cause erosion and redistribution of sediments (King, 1972). In 1960, a cyclone eroded beaches on Mauritius Island and deposited sand and coral debris at the storm swash limit (McIntire and Walker, 1964). High winds and waves associated with hurricanes can defoliate and uproot mangroves, leaving deposits of sediment and organic debris (Roth, 1992). In 1971, Cyclone

Althea deposited poorly sorted shell and sand debris in some areas of a mangrove forest in Bowling Green Bay, Queensland (Hopley, 1974). In addition, much organic debris was deposited in almost all areas affected by the storm (Hopley, 1974). In contrast, the shelly sand unit of Cores A and B contains very little organic matter. It seems unlikely that a storm which was capable of depositing at least 1 m of sediment (Core B), would not also have caused major vegetation damage. Therefore, it is unlikely that the shelly sand unit was deposited by a hurricane.

Bay theory

A more plausible explanation is that the mangrove swamp was formerly a bay and the shelly sand unit represents a beach deposit. This theory is supported by several lines of evidence. Low pollen density and low proportion of organic matter suggest that the cores were taken seaward of the *Rhizophora* zone. Abundance of littoral pollen in Core B suggests that it was taken close to the salt spray zone.

This indicates that relative sea-level during Zone 1 was at least 1 m higher than today. Mangroves would have been limited to sheltered, low-lying areas around the periphery of the bay. Where elevation rises steeply, as to the east, mangroves may have been excluded.

Mangrove Expansion

Zone 2 is characterized by mangrove peat and high pollen densities, suggesting that the mangrove swamp had begun expanding into the bay. The pollen assemblage indicates a transition from a pure *Rhizophora* stand (2a) to a mixed mangrove stand (2d) due to a progressive drying of the sediments. Expansion of the mangrove swamp indicates a decrease in relative sea-level. This could be caused either by a fall of gauge sea-level or a rise of the land. Sea-level curves for the West Indies indicate that gauge sea-level rose slowly during the late Holocene (Fig. 1). Therefore, a decrease in relative sea-level would have been caused by movement of the land. Two possible mechanisms, sediment accumulation and tectonic uplift, are discussed below.

Sediment Accumulation

Rate of sediment accumulation may have outpaced sea-level rise during the late Holocene. Levera Island refracts waves (Fig. 5a), and focusses sediments onto what is now Levera Beach. The sediment-focussing process may have caused a double spit to form and grow into a cuspate beach barrier across the mouth of the bay (Fig. 20). This barrier eventually grew into a tombolo (sand spit) linking the two islands. A beach barrier would shelter the embayment, explaining the contact between high energy shelly sand and low energy *Rhizophora* peat. The reduction in energy would encourage the accumulation of terrigenous sediments, which might otherwise have been washed out to sea. Sediment accumulation provides a

A. Bay (ca. 550 B.C.)
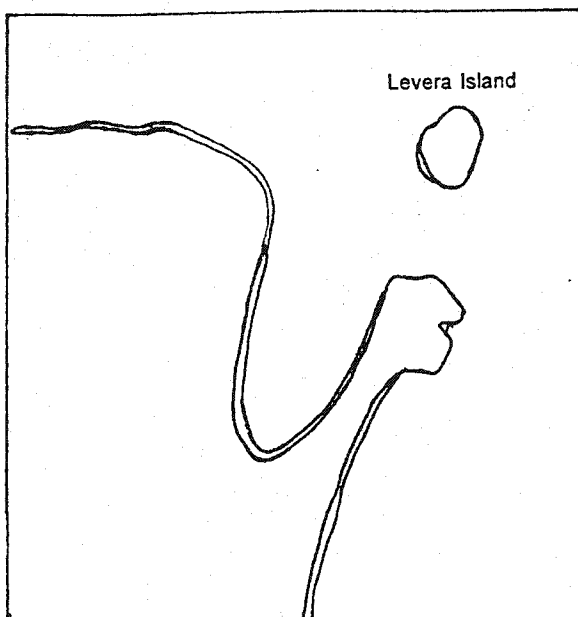
B. Paired spits (ca. 350 B.C.)
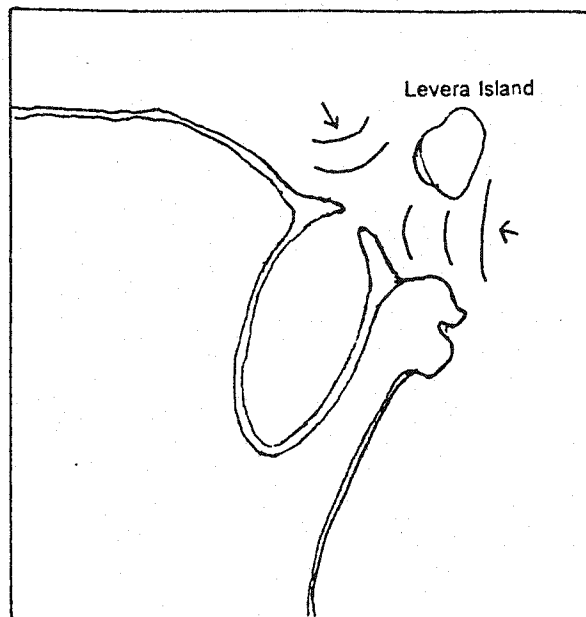
C. Cuspate spit (today)
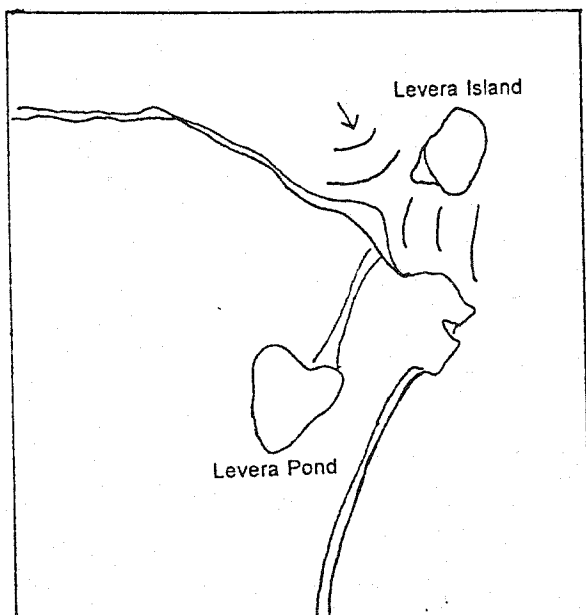
D. Tombolo (A.D. 1950)
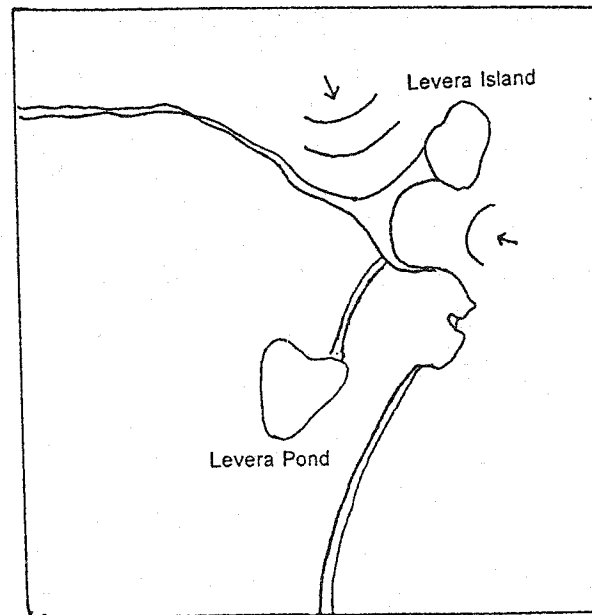
Figure 20. Proposed history of Levera Pond. A) Approximately 2500 yr B.P. (ca. 550 B.C.), mangroves were confined to the periphery of a bay. A shelly sand beach was deposited.

B) Approximately 2300 yr B.P. (ca. 350 B.C.), paired spits formed at the mouth of the bay.

C) The paired spits grew into a cuspate beach barrier which sheltered the embayment.

D) The cuspate beaches of Levera Pond and Levera Island became linked as a tombolo. In the 1970s, erosion reduced the tombolo to two cuspate spits, as shown in C.

substrate for mangrove growth, allowing expansion of the swamp. Mangroves contribute to soil build-up by slowing water velocity and consolidating sediments with their roots (Woodroffe, 1992), and by depositing organic debris. Radiocarbon dates indicate that the mangrove swamp prograded into the Core A site about 300 years earlier than the Core B site.

Tectonic Uplift

Raised shore platforms in the Levera area and adjacent islands suggest an abrupt 3 m decrease in relative sea-level. Tectonic uplift is a feasible explanation, because Grenada's location near the Caribbean Tectonic Plate boundary makes it vulnerable to tectonic activity (CCA, 1991). However, core lithology and pollen do not support a 3 m tectonic uplift during the last 2500 years. Coseismic uplift can be detected by a sudden shift in lithology or pollen assemblage, incongruent with modern successional sequences (Ellison, 1989). However, *Rhizophora* remains the dominant pollen type throughout the shelly sand unit and lower peat unit. A sharp contact between the two units suggests a sudden decrease in energy of deposition, and perhaps a decrease in relative sea-level. It is possible that tectonic uplift occurred at this time, reducing marine incursion into the bay. However, a gradual process of sediment accumulation would still be necessary to explain why the mangrove swamp expanded into the Core A site 300 years earlier than the Core B site. The transition from *Rhizophora* peat to mixed mangrove peat is not incongruent with modern successional sequences, as mixed mangrove occurs

immediately landward of the *Rhizophora* zone in some areas of Levera Pond today. It is possible that tectonic uplift contributed to the drying of sediments, but again, a gradual process of sediment accumulation is necessary to explain why the mixed mangrove zone succeeded the *Rhizophora* zone 300 years earlier at Core A than at Core B.

Thus, sediment lithology, pollen, and macrofossils indicate a decrease in relative sea-level and in energy of deposition over the last 2500 years. Formation of a beach barrier and accumulation of sediments allowed mangroves to expand into the bay. *Rhizophora* was the first to colonize the new sediments, followed by mixed mangrove vegetation. Tectonic uplift may also have contributed to the decrease in relative sea-level.

Late-Holocene expansion of mangrove swamps was reported in locations with an abundant sediment source (Wijmstra, 1969; Van der Hammen, 1974; Woodroffe *et al.*, 1985; Tissot, 1987; Parkinson, 1989; Tissot and Marius, 1992). As rate of gauge sea-level rise decelerated, it was outpaced by sediment accumulation. In contrast, marine transgression of mangrove swamps continued on low, flat islands which lack an abundant sediment source (Woodroffe, 1981). It is not surprising that the Levera mangrove swamp expanded during the late Holocene. Levera has a steeply sloped watershed, providing abundant terrigenous sediments. Sediment erosion increased during the historic period, and probably accelerated the expansion of the swamp. Levera is situated in the lee of Levera Island, which focusses marine sediments onto Levera Beach. However, since 1971, sediment

erosion has outpaced sediment accumulation, and the tombolo which linked Levera Island and Levera Beach has been reduced to two cuspate spits. Increased beach erosion was reported elsewhere on Grenada and other Eastern Caribbean islands during this period (CCA, 1991).

Human Disturbance

Mangrove peat is overlain by clay, which represents rapid erosion during the historic period. Ternan *et al.* (1989) states that erosion is not a widespread problem in Grenada. However, sediment accumulation rates at Levera Pond were 6 to 11 times higher during the historic period than the preceeding period. If sediment accumulation continues, Levera Pond will fill in, (unless rate of sediment accumulation is exceeded by sea-level rise or land subsidence). High historic erosion rates have been reported for other Caribbean islands (Lugo *et al.*, 1981; Bjork and Digerfeldt, 1991).

Presence of *Cocos nucifera* at the base of the clay unit indicates that clay deposition began after A.D. 1550. It is unlikely that clay deposition occurred between A.D. 1550 and A.D. 1700, as population density and agricultural intensity were low (CCA, 1991). Clay deposition may have begun in the 1700's, with sugar cane cultivation. Between 1702 and 1834, sugar cane was cultivated on almost all low-lying lands in Grenada. A large boiling pot found adjacent to the foundations of a building may be a remnant of an abandoned sugar estate. Clay deposition continues today, although the sugar estate has been abandoned. The road to

Levera Beach is unpaved and may be a major source of clay sediments. An increase in weed pollen reflects local disturbance, and farming and grazing of the watershed.

Further Studies

Our results indicate that a mangrove swamp invaded a bay. To refine the pattern of invasion, it would be necessary to core other areas of the swamp. A longer core would illustrate the response of Levera Pond to rapid sea-level rise during the late Pleistocene and early Holocene. Barring tectonic uplift, a regressive sediment sequence (freshwater peat overlain by mangrove peat) is predicted. A longer core of Levera Pond might provide information about the age and origin of the basin. It would be worthwhile to compare the history of Levera Swamp with mangrove swamps occupying drowned river valleys on the south end of Grenada. If tilting of the island occurred during the Holocene, the southern mangrove swamps would have experienced a greater rise in sea-level.

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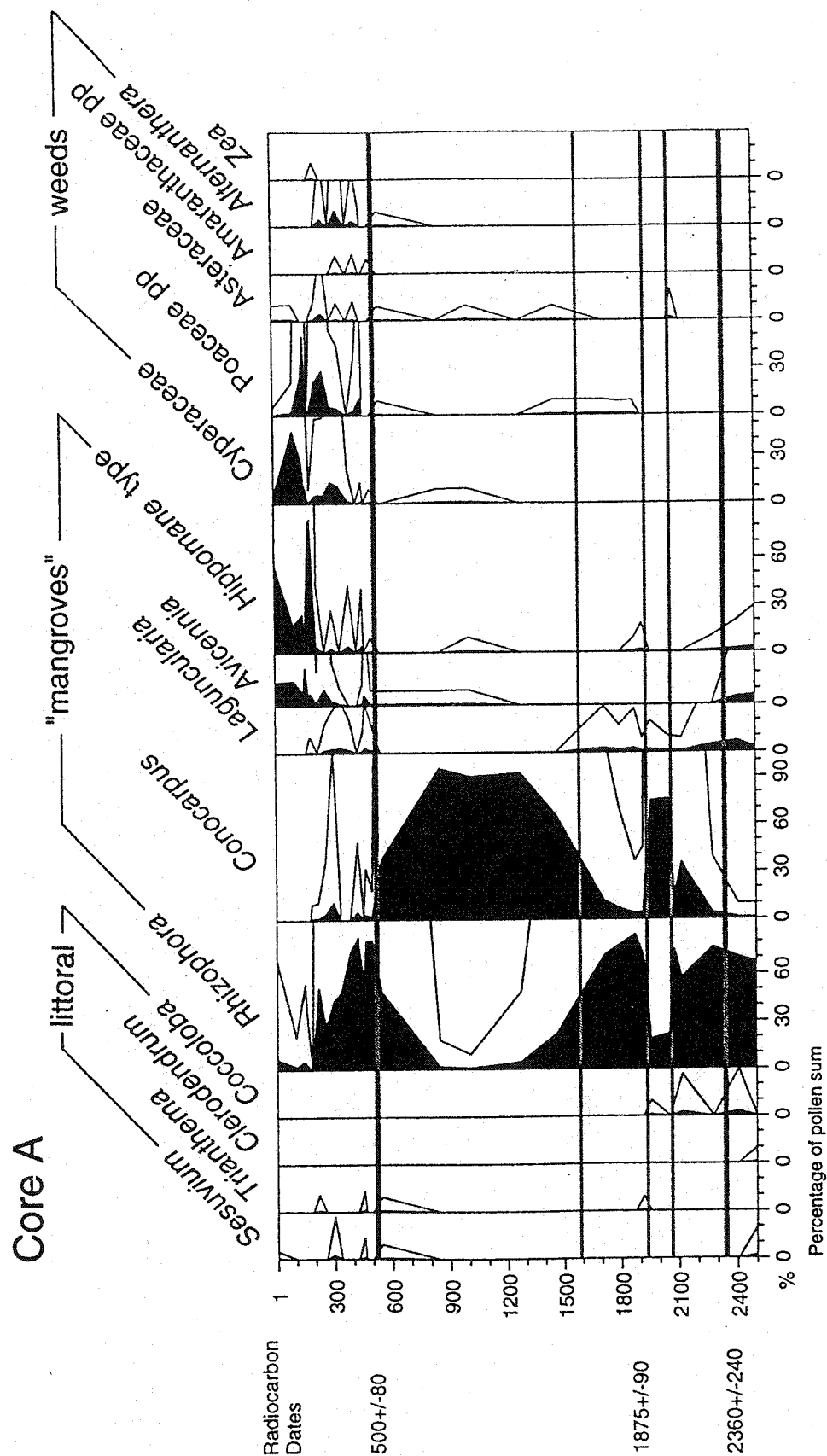
Appendix 1. List of plants collected in Levera area of Grenada in November 1992 and June 1993. The Levera Pond location also includes Levera Hill. Compiled by K. Barbour.

Genus	Species	Date	Location
Avicennia		19930607	Bedford Point
Bourreria		19930607	Bedford Point
Capparis		19930607	Bedford Point
Citharexylum		19930607	Bedford Point
Coccoloba		19930607	Bedford Point
Cordia		19930607	Bedford Point
Dichantium		19930607	Bedford Point
Enicostema		19930607	Bedford Point
Erithalis	fruticosa	19921105	Bedford Point
Genipa	americana	19930607	Bedford Point
Sesuvium		19930607	Bedford Point
?Trichilia		19921103	Levera Pond
Alternanthera	flavescens	19921103	Levera Pond
Annona		19930608	Levera Pond
Boerhavia		19930608	Levera Pond
Bourreria	succulenta	19921103	Levera Pond
Bourreria	succulenta	19921107	Levera Pond
Brachiaria	distachya	19921105	Levera Pond
Bunchosia	polystachia	19921103	Levera Pond
Bursera	simaruba	19921107	Levera Pond
Capparis		19921103	Levera Pond
Capparis	odoratissima	19921103	Levera Pond
Casearia		19930608	Levera Pond
Cassia		19930608	Levera Pond
Chamaesyce	mesembrianthemifolia	19921103	Levera Pond
Citharexylum	spinosum	19921103	Levera Pond
Clerodendrum	aculeatum	19921105	Levera Pond
Coccoloba	uvifera	19921103	Levera Pond
Cordia	obliqua	19921107	Levera Pond
Crateva	tapia	19921107	Levera Pond
Croton		19930608	Levera Pond
Croton	flavens	19921103	Levera Pond
Croton	hircinus	19921103	Levera Pond
Cuscuta	americana	19921103	Levera Pond
Desmanthus	virgatus	19921103	Levera Pond
Desmodium	triflorum	19921103	Levera Pond
Diospyros	inconstans	19921107	Levera Pond
Epidendrum		19930608	Levera Pond
Evolvulus		19921103	Levera Pond
Fimbristylis	ferruginea	19921107	Levera Pond
Ipomoea	pes-caprae	19921103	Levera Pond
Lantana	involucrata	19921103	Levera Pond
Malachra	alceifolia	19921103	Levera Pond
Ocimum		19930608	Levera Pond

Appendix 1 (continued).

Genus	Species	Date	Location
Pithecellobium	unguis-cati	19921103	Levera Pond
Polypodium		19930608	Levera Pond
Psychotria	microdon	19921107	Levera Pond
Randia	aculeata	19921103	Levera Pond
Rauvolfia	viridis	19921103	Levera Pond
Sarcostemma	clausum	19921103	Levera Pond
Sesuvium	portulacastrum	19921103	Levera Pond
Tabebuia	heterophylla	19921103	Levera Pond
Tournefortia	caribaea	19921107	Levera Pond
Tridax	procumbens	19930608	Levera Pond
Vernonia	cinerea	19921105	Levera Pond
Acacia	nilotica	19921105	Levera Pond Beach
Acanthocereus	tetragonus	19921105	Levera Pond Beach
Blutaparon	vermiculare	19921105	Levera Pond Beach
Canavalia	rosea	19921105	Levera Pond Beach
Capraria	biflora	19921105	Levera Pond Beach
Cassia	obtusifolia	19921105	Levera Pond Beach
Cracca	caribaea	19921105	Levera Pond Beach
Cynodon	dactylon	19921105	Levera Pond Beach
Eleusine	indica	19921105	Levera Pond Beach
Erythroxylum		19921105	Levera Pond Beach
Euphorbia	serpens	19921105	Levera Pond Beach
Fimbristylis	cymosa	19921105	Levera Pond Beach
Fimbristylis	ovata	19921105	Levera Pond Beach
Fimbristylis	spadicea	19921105	Levera Pond Beach
Guettarda	odorata	19921105	Levera Pond Beach
Jacquemontia	pentantha	19921105	Levera Pond Beach
Jacquinia	armillaris	19921105	Levera Pond Beach
Jacquinia	armillaris	19921105	Levera Pond Beach
Justicia	sphaerosperma	19921105	Levera Pond Beach
Opuntia	dillenii	19921105	Levera Pond Beach
Panicum	maximum	19921105	Levera Pond Beach
Pilosocereus	royeni	19921105	Levera Pond Beach
Spigelia	anthelmia	19921105	Levera Pond Beach
Sporobolus	virginicus	19921105	Levera Pond Beach
Trianthema	portulacastrum	19921105	Levera Pond Beach
Tillandsia		19921105	Levera Pond Beach

Appendix 2. Complete pollen diagram for Core A, Levera Pond. *Nymphaea* and microforaminifera were excluded from the pollen sum. White curves represent 10x exaggeration. The group "mangroves" includes two mangrove associates: *Conocarpus erectus* and *Hippomane mancinella*.
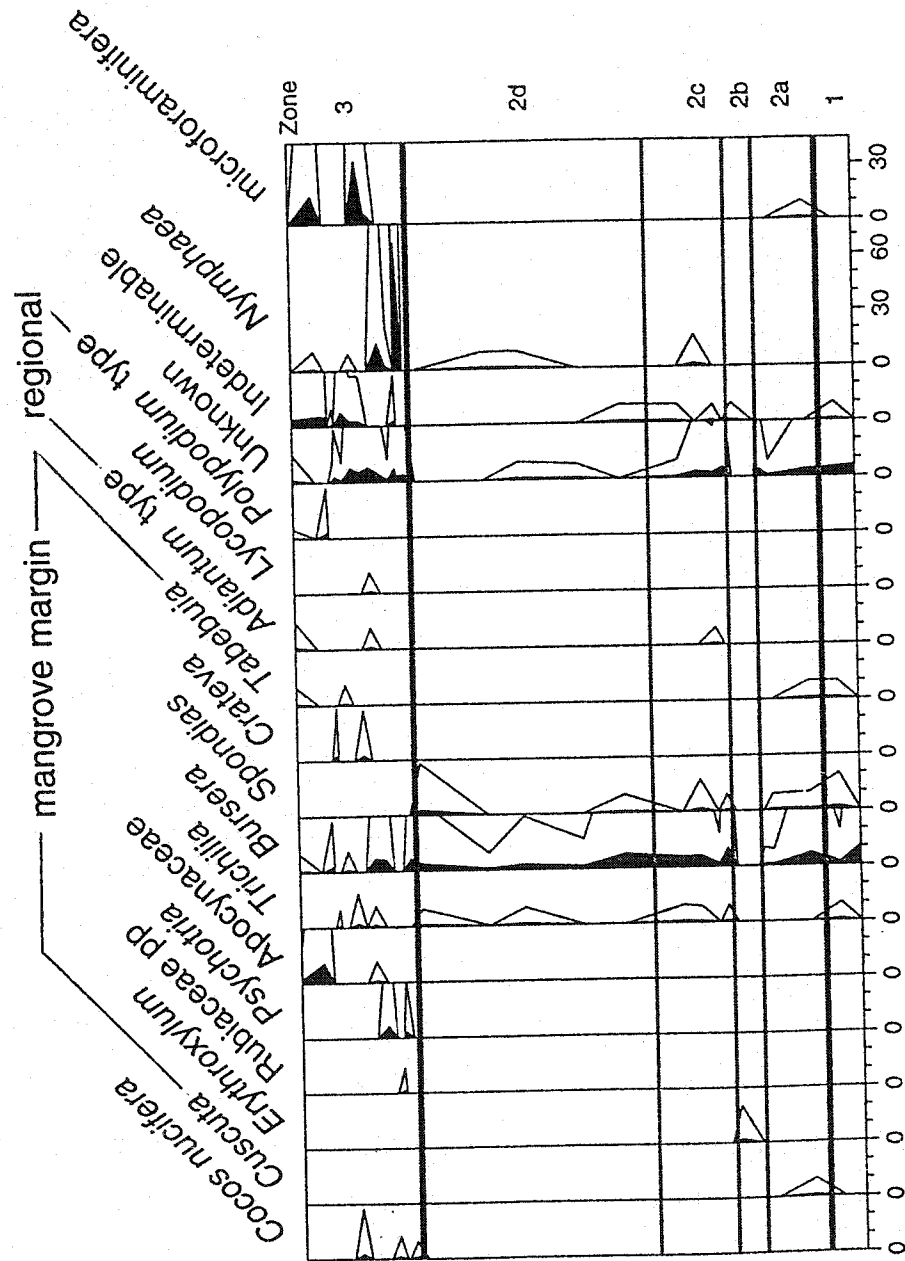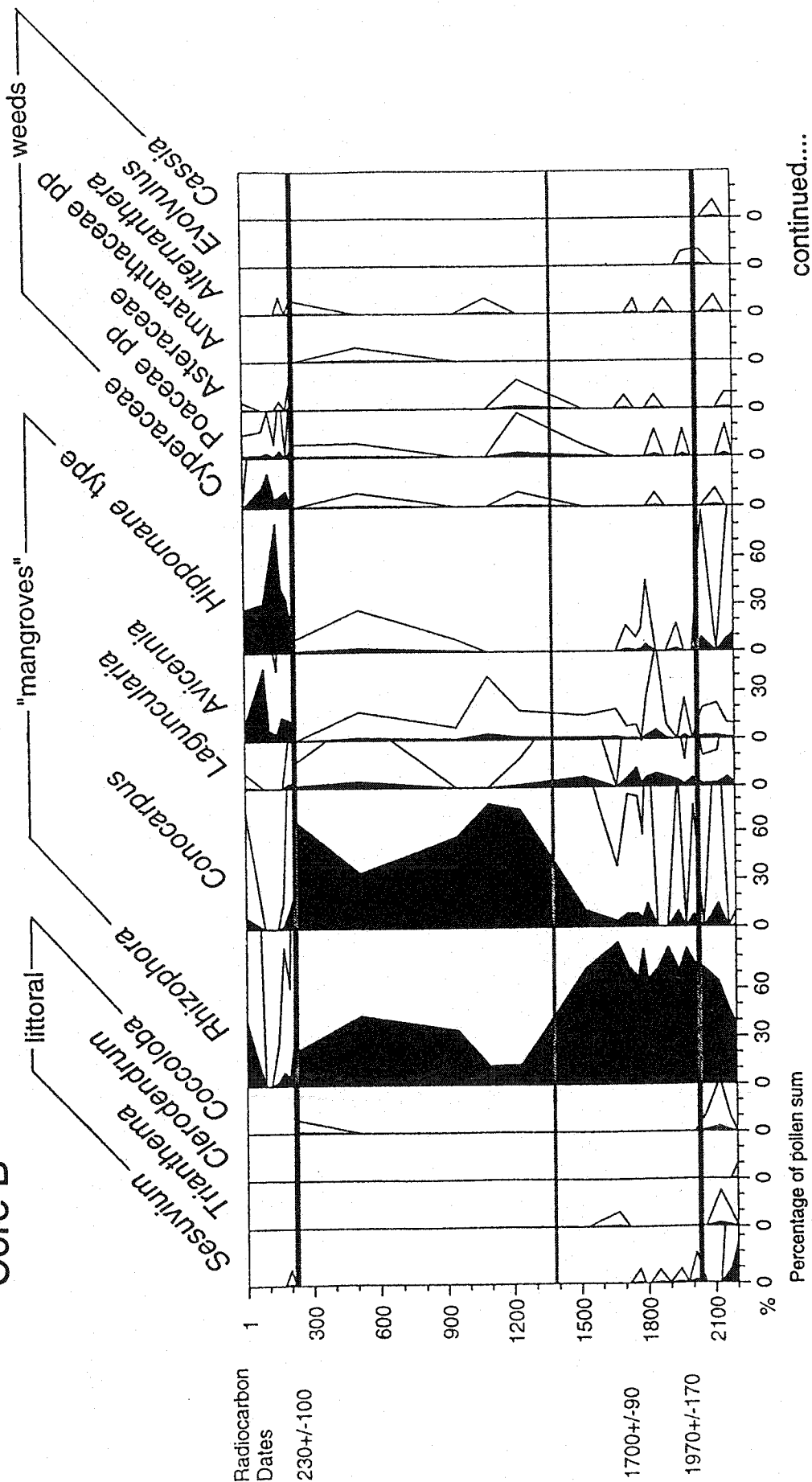
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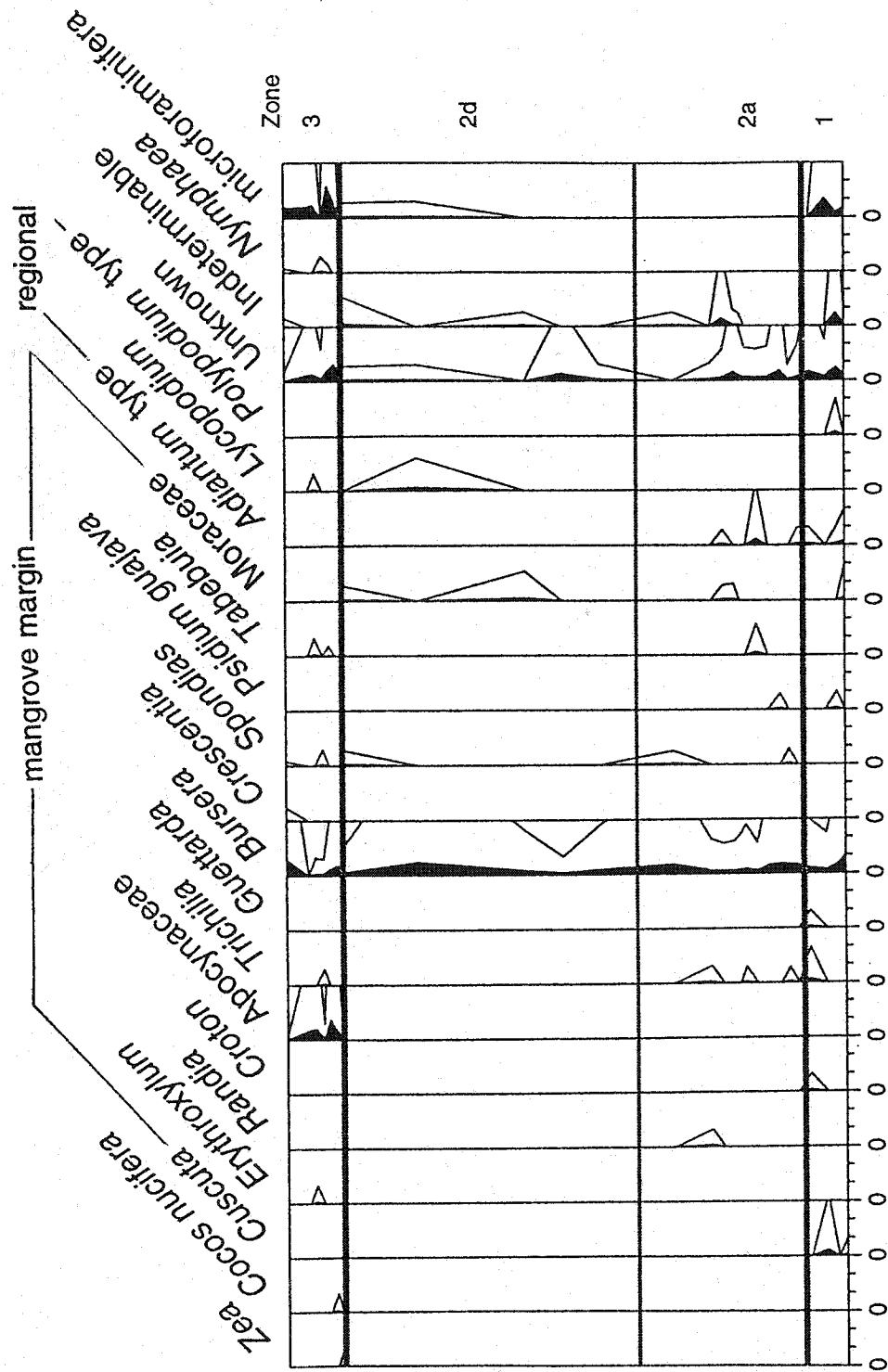Appendix 2, continued.

Appendix 3. Complete pollen diagram for Core B, Levera Pond. *Nymphaea* and microforaminifera

were excluded from the pollen sum. White curves represent 10x exaggeration. The group

"mangroves" includes two mangrove associates: *Conocarpus erectus* and *Hippomane mancinella*.

Appendix 3, continued.