Master of Science
Course ***ISATEC***

MSc Thesis in International Studies in Aquatic Tropical Ecology

Long term effect of hurricane disturbance and recovery based on vegetation coverage, biomass and productivity estimates of the Turneffe mangrove forest in Belize

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Abstract

In October 1961, Hurricane Hattie, a Category 5 hurricane (Saffir-Simpson Hurricane Scale), hit the Belizean coastal area. The eye of Hurricane Hattie passed directly over Turneffe Atoll. This storm destroyed entire islands as well as most of the vegetation and human habitation in a 40-km wide swath across Turneffe. To examine long-term recovery from hurricane damage, I established permanent plots at three sites at Turneffe, which fell within the zone of catastrophic disturbance and suffered the most intense storm damage. For comparison, I established additional plots at East Snake Cay (ESC), a mangrove island approximately 100 km to the south, which was well outside the zone of catastrophic disturbance during Hattie and received minimal damage. Forty years after the catastrophic effects of Hurricane Hattie, recovery of aboveground biomass at Turneffe is much lower when compared to ESC. Vegetation coverage estimates for Turneffe show that the three sites, Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay V (DMCV) have *Rhizophora mangle, Avicennia germinans*, and *Laguncularia racemosa*, and the mangrove associate *Conocarpus erectus*. This is also true for the ESC site.

Rhizophora mangle was the dominant specie in all sites regardless of the level of structural complexity. Estimates from aerial photographs of SC, BCC, and DMCV show that *R. mangle* covered approximately 38, 57, and 46%, respectively, of the total cay area. The Turneffe sites that experienced severe erosion following Hurricane Hattie have recovered most of the cay substrate. SC and DMCV have increased in size from their pre-hurricane dimensions whilst, ESC has decreased in size due to erosion. Estimates from the present study show that SC, BCC, and DMCV have accumulated an aboveground biomass of 8.64, 10.33, and 5.44 kg · m^{-2}, respectively, in the 40 yrs since Hurricane Hattie. These values are very low when compared to ESC where current aboveground biomass was estimated at 32.04 kg · m^{-2}. Litter fall estimates are available for the Turneffe sites only. Values extrapolated from the five months sampling period (October - 02 to February - 03), for mean yearly production shows that BCC had the highest litter fall rates (936.95 g · $m^{-2}yr^{-1}$), followed by SC (824.43 g · $m^{-2}yr^{-1}$) and DMCV (705.2 g · $m^{-2}yr^{-1}$). A significant amount of bird guano amongst the litter fall was found in two of the three sites (SC and BCC), which is believed to be seasonal since input was highest for the month of October and coincided with the fruiting season of cay forest from the larger neighboring islands.

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1 Introduction

Mangrove forests along many tropical coastlines are frequently and severely damaged by hurricanes that differ in scale, intensity, and frequency. Disturbance can be defined generally as any relative discrete event in time that disrupts ecosystem, community, or population structure and changes resource or substrate availability or the physical environment (White and Pickett 1985). Hurricanes and tropical storms are a frequent and natural form of major disturbance throughout the Caribbean basin, though large hurricanes capable of causing catastrophic damage (classified as Category 5 on the Saffir/Simpson damage potential scale by the U.S. National Weather Service) are less frequent. Although rare, they are thought to play a major role in the organization of Caribbean ecosystems (Lugo et al. 1976). Along these coasts, mangrove forests receive the full brunt of hurricanes as well as anthropogenic damage. Because the frequency of such storms at any one site is usually well within the potential lifetime of individual trees (Stoddart 1963), these disturbances influence the mangrove stands and their associated community dynamics. Depending upon the position of particular mangrove forests relative to the tracks of intense tropical cyclones (hurricanes, typhoons), the frequency of large-scale, stand-replacing disturbances may vary markedly among mangrove sites (Sherman et al. 2000). Spatial patterns of hurricane damage are complex and may result from interactions among micro- and macro-topography, forest structure, and composition (Brokaw and Grear 1991).

Available literature exists documenting the ability of mangrove forest to regenerate following hurricanes. However, changes that occur in vegetation following major disturbances by hurricanes and storm tides have not been reported for long-term recovery -over 40 years (Sherman et al. 2000). Most tropical research in the area of disturbance ecology focuses on systems which are disturbed at the scale of small gaps whose frequency of occurrence is high (Denslow 1980; White and Pickett 1985; Denslow 1987). Little is known, on the contrary, about the effects of infrequent large-scale disturbances such as Category 5 hurricanes after an extended period. Whether rare large disturbances are qualitatively different from numerous small disturbances remains an unresolved issue in ecology, in part because of an insufficiency of long-term data on the effects of large scale disturbances and the impossibility of replicating such events (Turner et al. 1997). Hurricanes are events that operate at scales and intensities that are more conducive to long-term ecological research. They occur in the Caribbean with predictable frequencies, in the order of several decades for hurricanes with very severe effects and the order of years for lesser storms (Weaver 1986). Studies with forests in general have showed that forest characteristics are frequently measured by biomass, tree density, number of tree species, basal area, wood volume, wood density, aboveground primary productivity, and complexity index change in predictable patterns over periods of 40 years following a hurricane (Crow 1980; Weaver 1986). If the structural and floristic characteristics of tropical island forests result from hurricane recurrence (Doyle 1981; Lugo and Snedaker 1974), the flora and the structure of each forest type, should in turn, reflect the disturbance history for the forest cover.

In 1960, D.R. Stoddart surveyed the group of cays along the Belizean barrier reef system, including the Turneffe Atoll which is approximately 51 km off the coast of Belize. In October 1961, Hurricane Hattie, a Category 5 (Saffir-Simpson Hurricane Scale) hurricane, hit the Belizean coastal area. The path of the eye of Hurricane Hattie passed directly over Turneffe Atoll. This storm changed and vanished some of the islands that Stoddart had mapped the previous year.

Based on the available information and literature, sites were selected accordingly, and site visits on the eastern side of the atoll were conducted at the beginning of the study for the Turneffe area. A gradient of disturbance intensity along Hurricane Hattie's path was also used during the selection of sites. The overall goal of this study was to quantify the level of recovery of mangrove forest in the Turneffe area of specific islands based on previously mapped areas. Recovery was put in context with available literature from the region with respect to biomass and productivity estimates. Island-level changes were based on available maps from before and after Hurricane Hattie provided by Stoddart (1963 and 1982) and on contemporary georeferenced aerial photographs of the three sites in Turneffe.

It is now 40 years since this major disturbance happened. This time span is considered as the number of years hypothesized for complete recovery of mangroves ecosystems (Lugo et al 1976). In the Neotropics, it has been noted that one of the principle difficulties is that anthropogenic influence is so common in coastal areas, and few opportunities exist where recovery from a natural disturbance can be examined in the absence of confounding human-caused damage. Turneffe Atoll provides a unique opportunity for a follow-up study on the mangrove forest ecosystem. The atoll has received little anthropogenic impacts since Hurricane Hattie due to the remoteness of the area and the extent of damage on the previous human settlements.

1.1 Hurricane Hattie disturbance at Turneffe Atoll

In 1960, D.R. Stoddart surveyed the group of cays along the Belizean barrier reef system, including the Turneffe Atoll. In October 1961, Hurricane Hattie, a Category 5 (Saffir-Simpson Hurricane Scale) hurricane, hit the Belizean coastal area. The path of the eye of Hurricane Hattie passed directly over Turneffe Atoll. This massive storm had sustained winds that exceeded 241 km/hr and gusts more than 322 km/hr, (NOAA 2003). Hurricane Hattie completely transformed, reorganised and vanished some of Turneffe’s islands that Stoddart had surveyed the previous year. Within a few months after the storm, Stoddart revisited and remapped the same areas that he had surveyed in 1960 (Stoddart 1963). In addition, he mapped the directions of both wind and currents during the storm and correlated these with wave patterns. He also plotted the extent and direction of tree falls in relation to wind and waves. He evaluated and mapped the damage to the Belizean Barrier Reef and the fringing reefs at Turneffe including the small sand and shingle cays that are found in gaps along the narrow eastern reefs. Stoddart's published studies from immediately before and after the storm’s effect, detailed maps and data of the vegetation, geomorphologic features, and human activities of these islands. Additional information on Hurricane Hattie damage is provided by Vermeer (1963).

1.2 Belize hurricane synopsis since 1961

Belize's coastal areas have been hit several times by hurricanes since Hurricane Hattie. The following list makes note of the hurricanes that have made landfall in Belize with Category 4 on the Saffir-Simpson Hurricane Scale; however, Hurricane Hattie still holds the record of being the last major hurricane, Category 5, since 1961. In 1978, Hurricane Greta, Category 4, hit Belize making landfall in Stann Creek, south of Belize City. As recently as 2000, Hurricane Keith, Category 4, stalled just off the northern coast of Belize. Keith affected the northern coastal islands as a Category 3 hurricane (Beven 2001). The storms effect was also experienced on the north part of the Turneffe Atoll causing considerable defoliation and tree death to extensive mangrove areas (pers. obs.) Hurricane Iris, Category 4 hurricane, (Avila 2001), made landfall in southern Belize causing severe damage to the mangroves of the Monkey River area. Close analysis of the storm record since Hurricane Hattie was used to select sites and rule out direct catastrophic damage so that I could assess recovery from Hurricane Hattie on the eastern side of Turneffe Atoll and a fourth site on the southern coastal area of Belize (Toledo). I also used a map, courtesy of the Belize World Wildlife Fund (WWF), that includes the tracks of all hurricanes that made landfall in the coastal areas of Belize from 1851 to 2001 (Reefs at Risk Caribbean Threat Assessment Workshop Miami – October 2002, data courtesy of Chris Landsea). The chart is color coded for different intensity hurricanes and shows only one hurricane track in red line (Category 5), which was Hurricane Hattie. In addition, I consulted the UNISYS Internet Weather Database to verify the hurricanes that have affected the Belizean coastal area (UNISYS Corp. 2003).

1.3 Scope of Study

The objective of this study was to give springboard information for assessing long-term patterns of recovery from hurricanes by comparing and contrasting forest conditions after 40 years from a devastating hurricane. The pre-hurricane vegetation structure, which was based on maps and descriptive data provided by Stoddart (1963), was compared with gathered data during this study. Furthermore, I examined the effects of pre-existing land use on the resilience of mangrove ecosystems, comparing damage and recovery patterns at Turneffe in areas that were heavily impacted by human activities when the storm hit. I compared three sites at Turneffe Atoll that suffered severe to near-complete destruction with East Snake Cay, an area along the southern coast of Belize that sustained only slight storm damage.

The study was based on the following hypotheses:

1) The mode of recovery in mangrove ecosystems is a function of the severity of the disturbance, the type of forest stand prior to the impact, and extent of the area affected.

2) Mangrove forest biomass after a major hurricane, is still after 40 years, significantly lower than a relatively undisturbed mangrove forest.

2 Materials and Methods

2.1 General description of study area

Belize is located on the Caribbean coast of northern Central America. It shares a border on the north with Mexico, on the west and south with Guatemala (Fig. 2.1). To the east it faces the Caribbean Sea. The barrier reef flanks much of the 386 km of predominantly marshy coastline. These shallow coastal waters are sheltered by the barrier reef with many small islands called Cays. The small cays, totaling about 689 km^2, dot the reef. Most cays are less than 1.0 m above sea level and subject to periodic inundation (Hartshorn et al. 1984). The area of the country totals 22,960 km^2, 3% of the land area is comprised of the cays (Murray et al. 2003).

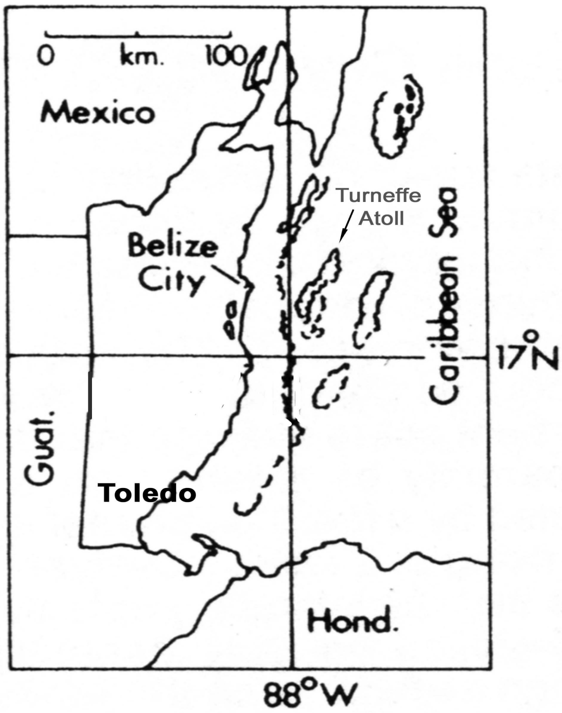

Figure 2.1. Map of Belize showing general location of the three atolls (modified after Rützler and Macintyre 1982)

Belize is home to three of the four atolls found in the Caribbean (Fig. 2.1). Turneffe Atoll, the largest of the three found in Belize, is located approximately 51 km off the coast of Belize. It spans about 50 km at its maximum length and 16 km at its widest point. The Turneffe area of land is estimated at 16 km^2; mangroves covering approximately 64% of the area. On its western side it is covered by several intertidal mangrove cays. Sandy cays are usually found between the channels on the inner edge of the eastern side, and the atoll itself is surrounded by an extensive fringing reef. A chain of islands surrounds three lagoons, the northern lagoon, the central lagoon, and the southern lagoon. Windward and leeward mangrove forests encircle deep lagoons with restricted circulation. In contrast, the northernmost part of Turneffe Atoll has no extensive mangrove development, and the northern lagoon is well circulated. Gishler (2003) suggested that the Turneffe Islands are located in a protected, low energy position in the lee of Lighthouse Reef. Due to its remoteness, Turneffe is free from allochtonous and fluvial discharge from the mainland.

2.2 Climate and physicochemical regime

Belize lies in the transition from subtropical to tropical conditions. Northern Belize experiences a subtropical climate, whilst the south of Belize is exposed to the tropical rainforest conditions (BNMS 2003). The country lies in the trade wind belt; consequently, winds from the east and northeast predominate for most of the year. The climate is characterized by a rainy and a dry season. Most rainfall occurs during June to November. Mean annual rainfall across Belize ranges from 1524 mm in the north to 4064 mm in the south. Except for the southern region, the amount of rainfall varies from year to year (BNMS 2003). Data gathered at the Meteorological Station in Belize City from the different stations throughout the country show that the rainy season begins in early May in the southern part of the country, progressing to the north of the country in early June. The main synoptic features that are responsible for the rainfall are tropical waves, tropical storms, and hurricanes that generally occur throughout the Caribbean from June to November. Records show that a peak activity for tropical waves occurs during June and July. Tropical storms and hurricanes peak during September and October. However, there are great variations from year to year and winds from the north to northwest, called "northerns", are also common. They affect rainfall distribution and, therefore, climatic conditions during October to April. The peak activity is usually during December and January. The dry season is considered from November to May with April being the driest month (BNMS 2003).

Average air temperatures range from 24°C during the "northerns" to 27°C in the summer. Seaward of the Turneffe Atoll, winds are northerly (1 m/s). However, the current flows westward around the northern part of the atoll; thus, creating a southerly drift along the leeward side (Holtermann and Garcia 1998).

Records of weather data for the Turneffe and coastal areas have never been kept for extended periods. For the Turneffe Atoll area, at the Calabash Cay station Belize (CCB), weather data were collected for January 1996 to December 1997 as part of the CARICOMP project (UNESCO 1998). Mean monthly maximum and minimum air temperature for those two years was 30.1 °C, and 23.4 °C respectively. Mean cumulative rainfall for 1996 and 1997 was 1901 mm and 1847 mm, respectively. An offshore island, Carrie Bow Cay, located in the central province of the barrier reef has also produced records for the years 1993 to 1996 for the CARICOMP project (UNESCO 1998). During this time, the mean monthly maximum temperature was 34.6 °C with a minimum of 22.5 °C. Cumulative rainfall at Carrie Bow for 1996 and 1997 was 1691 mm and 1883 mm, respectively. Walton Smith in Gishler and Hudson (1998) observed extreme fluctuations in water temperature and salinity in the southern lagoon, Turneffe, with maximum values of 31°C and 70‰, respectively. Between December 2000 and December 2001, Gishler (2003), deployed two data loggers in the Turneffe lagoons. Temperature recordings ranged from 22 - 32 ºC and salinity fluctuated from 34.2 - 42.5 ‰.

2.3 Vegetation type

The mangrove flora of the Atlantic seaboard is limited to 10 species, which is far fewer than the 60 reported fort the Indo-Pacific region where mangroves attain there maximum taxonomic development (Lugo and Snedaker 1974). In Belize, there are three true mangrove species: *Rhizophora mangle, Avicennia germinans* and *Laguncularia racemosa.* A fourth species, *Conocarpus erectus*, is an important mangrove associate in Belize that is transitional between the true mangroves and non-mangrove species (Feller and Sitnik 1996). The total distribution of Belize's mainland mangrove area was estimated at 57109 ha, which is 72.7% of the total mangrove coverage (Murray et al. 2003). Turneffe's area of 7420 ha, covers 9.4% of the total mangrove area. Minty et al. (1995) identified five major vegetation types for the Turneffe area: (i) Mangrove (ii) Beach Thicket (iii) Broken Palmetto Thicket (iv) Broken Palmetto-Buttonwood Thicket and (v) Cay Forest.

The mangrove association varies from tall monospecific stands of *R. mangle, A. germinans* and *L. racemosa*, to extensive stands of dwarf forest usually found on the inner borders of the lagoons. Fringing mangroves occur on the lee of the windward coral rubble and sand cays such as Soldier Cay and Dead Man Cay V. Stunted mangrove stands are also found on the windward side of the islands where they may be influenced by the winds and the lack of soil (pers. obs.). At Turneffe, I have observed mangroves growing on peat, sand and coral rubble.

The Beach Thicket is usually found on the windward sand or coral rubble ridges. The prevailing winds are a major influence for the stunted growth of this particular stand. The unevenness in canopy structure is what gave rise to the name Broken Palmetto Thicket. This vegetation type is comprised primarily of the palm known as the Palmetto, *Thrinax radiata.* The Broken Palmetto Thicket occurs on drained peat and organic sand.
The Broken Palmetto-Buttonwood Thicket is comprised primarily of Buttonwood (*Conocarpus erectus),* almost to the exclusion of the Palmetto species. This association grows on drained peat.

Cay Forest is considered as the climax association of the higher elevation cays (Minty et al. 1995). These cays provide a higher elevation; thus, the influence of salinity is minimal or absent, as observed to a lesser extent at SC. This vegetation type is usually restricted to sand ridge areas and occurs on organic sands (Minty et al. 1995).

2.4 Selection and description of study sites

The unique data provided by Stoddart (1962, 1963) and Stoddart et al. (1982) were used as the basis for the selection of sites. The information from these publications was unique in the sense that it provides detailed descriptive information and maps of the eastern side of Turneffe pre- and post Hurricane Hattie. Prior to Hurricane Hattie, Stoddart (1962) reports the existence of thriving communities (900 people in seven to eight settlements), which were engaged in fishing, extensive coconut plantations, pig farming, and sponge growing.

It is now 40 years since that major disturbance and the area has not been resettled extensively. Namely, the only human activities are three resorts operating on the eastern side of the atoll; two research centres, and some sparsely scattered temporary fishing camps. Stoddart's original data and maps (1962, 1963) provided the basis for selection of study sites for forest structure comparisons and experiments. Each of the islands mapped by Stoddart was categorized based on intensity of hurricane damage, land use at time of the storm, and forest type. Sites were selected along a disturbance severity gradient (Fig 2.2a). Three reef islands on the eastern side of the atoll were selected for the study, listed from a north to south orientation - Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay V (DMCV) and a fourth site which fell outside the zone of catastrophic disturbance from Hurricane Hattie was selected for comparative reasons - East Snake Cay (ESC), southern Belize, Toledo (Fig. 2.2b).

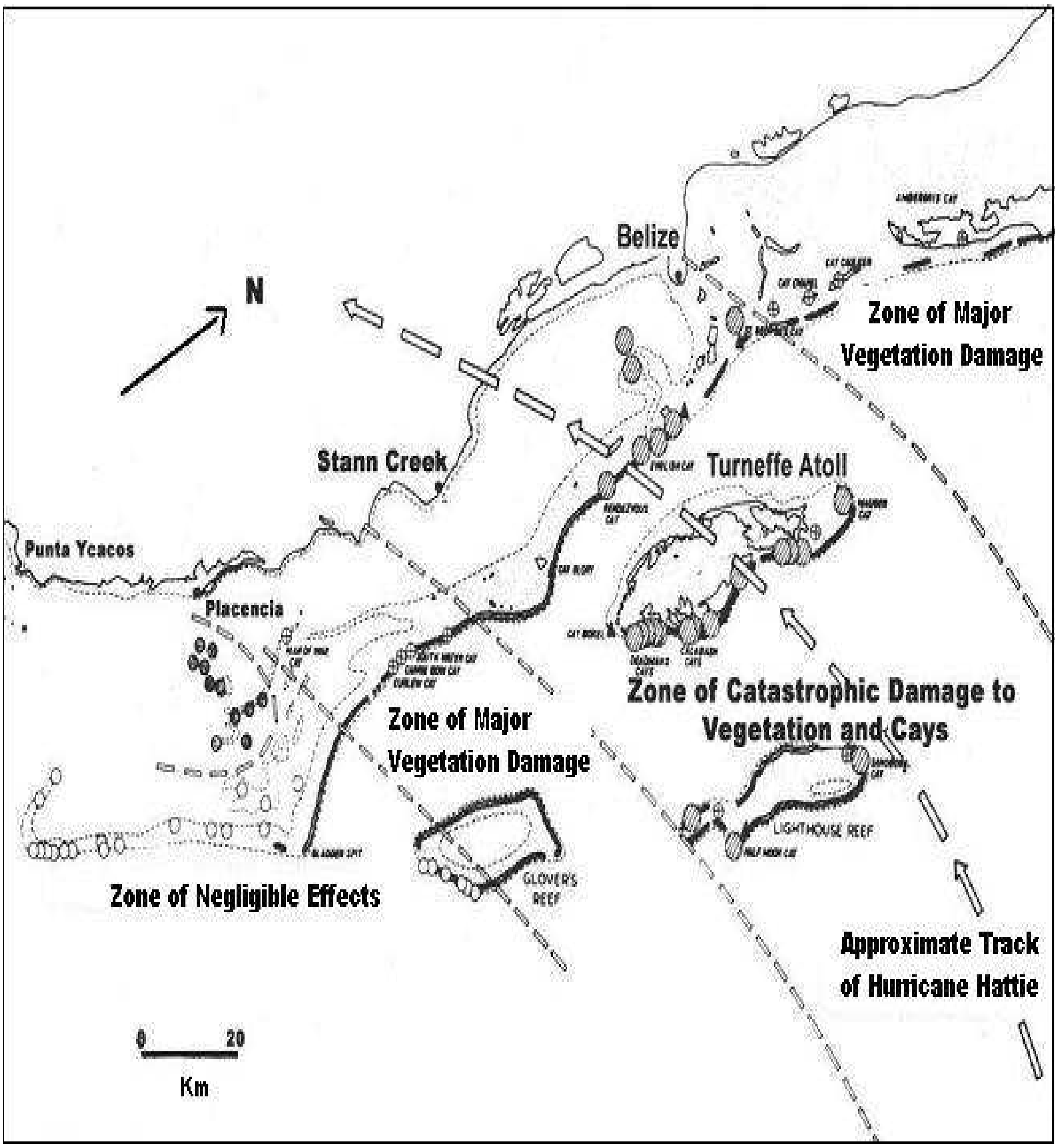

Figure 2.2a. Zones of hurricane damage to reef and cays (modified after Stoddart 1963).

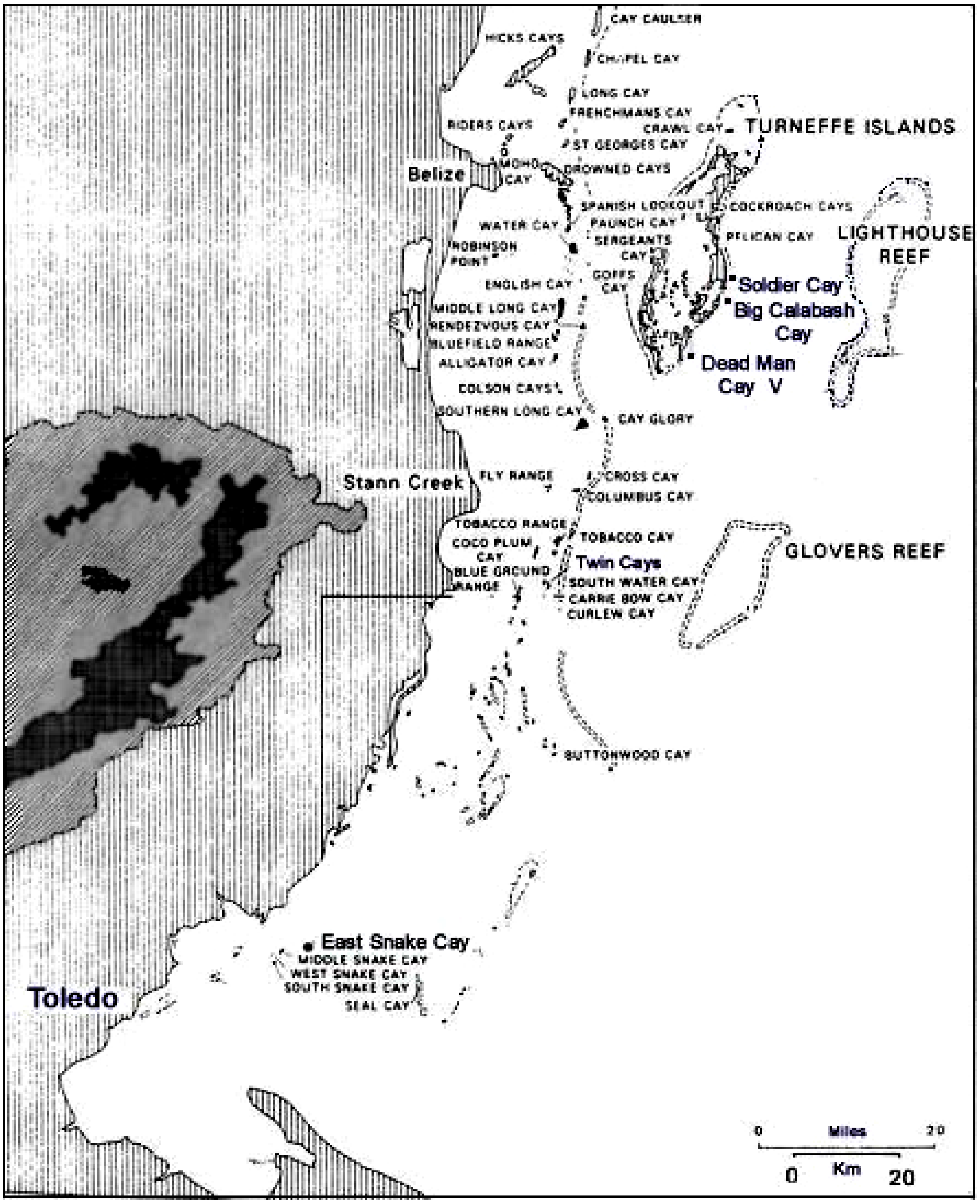

Figure 2.2b. Location of study sites for Turneffe and East Snake Cay, Toledo, southern Belize (modified after Stoddart 1982).

The following descriptions of the physiographic features of the cays are summarized based on Stoddart's observations (1962, 1963 and 1982). These summaries include observations immediately before and after Hurricane Hattie for the Turneffe sites (SC, BCC, and DMCV) and the available description of ESC during his 1961 visit. Each of the study sites is juxtaposed with the present physiographic features that were observed during this field study.

Soldier Cay (SC)

Soldier Cay, a reef island, is located on the easternmost point of the east reef on Turneffe (17°19'N and 87°47'W). Before Hurricane Hattie, SC was planted with coconuts (*Cocos nucifera*) 40 feet high (12 m). The natural vegetation had been almost entirely removed. Numerous *R. mangle* seedlings were growing in the shallow water along the west and south shores of the cay (Stoddart 1962). His report further makes reference to several houses and sheds on the island.

On his second visit after the storm, Stoddart (1963) reported that SC had been completely transformed. The salient features were no longer recognizable. The island surface was a flat low-lying area with exposed coconut roots and scattered fresh coral blocks. There was marginal erosion on all sides of the island. In terms of vegetation, all except four of the coconut trees had disappeared along with the associated understory. The houses and sheds had disappeared with the exception of some posts. Stoddart (1963) reported that there were no *R. mangle* seedlings around the cay and describes the cay as a bleak and desert place almost devoid of soil.

At the time of my study SC was covered with lush vegetation, primarily mangroves. The dominant species was *R. mangle* found on the fringe of the island with average heights of 5 m within the established plots; however, all mangrove species found in Belize are present including the mangrove associate, *C. erectus*. The island can be described as a Fringing *R. mangle* with the Beach Thicket Association where inundation does not occur due to protection of elevated coral rubble around the island's periphery. The cay was also rich in a diversity of none-mangrove plants. Certain plant species that were identified include the *Thrinax radiata*, *Coccoloba uvifera*, *Terminalia catalpa*, and a couple of stunted coconuts. The cay's approximate dimensions was 78 m at it widest point and 134 m in length. Interestingly, on the southern end of the cay, there was a conspicuous belt of monospecific stand of *R. mangle* trees with approximate heights of 1.5 to 3 m. The belt itself measures approximately 139 m in length and its width varies between 2 to 5 m. The stand seemed to be thriving on an elevated pile of coral rubble that was prominent on the seaward shore and was abutted on the leeward side by the shallow lagoon.

Big Calabash Cay (BCC)

Big Calabash Cay is located on the eastern side of the atoll, (17°17'N and 87°48'W), south of SC and northeast of Calabash Cay, Belize (CCB) – which is the location of the University of Belize, Institute of Marine Studies field station. Stoddart (1962) described BCC as a uniformly low and sandy cay, 155 m long and 32 - 50 m wide. The island had no shingle but several places on its banks were lined with conch shells that were usually used to help against erosion. The vegetation had been removed for the cultivation of coconuts forming a ragged canopy of 6 to 9 m with sparse growth of grasses beneath the cocal plantation. At the time of Stoddart's visit (1962), people living on BCC were raising pigs on the island. Peripheral mangroves, chiefly *R. mangle* seedlings, were close inshore with a couple of taller *A. germinans* trees to the north end of the island. The island was inhabited for many years and had several houses because it was the center of the sponge industry between 1900 and 1939.

After Hurricane Hattie when Stoddart (1963) made his second visit, he describes BCC as severely affected. From his calculations, the seaward shore retreated from 1.8 to 11 m and the leeward shore retreated between 4.6 to 9 m. The cocal forest almost completely disappeared with the exception of five coconut trees. Interestingly, the original ground vegetation survived, but all the *R. mangle* seedlings were swept away. The houses were also washed away by the storm.

At the time of my study, BCC was covered primarily with mangrove vegetation. *Rhizophora mangle* dominates the forest composition; however, all three mangrove species including *C. erectus* were found on the island. The fringing mangrove had an average height of 4.7 m within the established plots. The island's periphery was completely encircled by *R. mangle,* but other mangroves occur interspersed along its fringe. However, the majority of these other species occur inshore approximately 8 to 10 m from the island's borders. Different species of grasses occur inshore underneath the *A. germinans, L. racemosa* and *C. erectus* trees along with a couple of stunted coconuts. The island measures approximately 147 m at its maximum length and between 40 to 50 m for its width. Interestingly, house foundations described by Stoddart (1962, 1963) can still be found on the southeastern end of the island.

Dead Man Cay V (DMCV)

On the windward side of the southeastern part of Turneffe, there is a group of five cays on the reef flat called the Dead Man Cays. DMCV is the southern-most cay on Turneffe Atoll selected for this study (17°11'N and 87°51'). Pre-hurricane description by Stoddart (1962), described DMCV as a sand cay with very little shingle. The triangular-shaped cay had dimensions of a little over 46 m at its east west length, while the west side measured approximately 64 m. The cay consisted of two sections. On the east side of the island, the first section was a low-lying humic sandy area with the vegetation cleared for coconuts. On the west side, the second section was adjacent to the sand area, and consists entirely of *R. mangle* with little or no dry land (with approximate dimensions of 64 and 32 m). The eastern side had an old gnarled *A. germinans*. An important note added by Stoddart (1962) was the presence of two distinct islands at the location of DMCV, which were charted by Owen (1830). Stoddart suggested that both cays had merged into one over the past 130 years at the time of his study.

After the storm, Stoddart (1963) described the cay as the subject of erosion on all shores, whereby surface sand was stripped away over about half of the area along with a remainder of the old *A. germinans* stump. Most of the coconuts were destroyed, and the *R. mangle* stand was much defoliated.

At the time of this study, there were interesting features for the DMCV site. As with the other sites, the vegetation was dominated by *R. mangle.* However, all three species were found within the cay along with the *C. erectus* species. The mean canopy height of the fringing mangrove where the plots were established was at 3.7 m. Nevertheless, a well developed *A. germinans* tree on the northern part of the island towered at 7.5 m high. The cay was devoid of coconuts and maintained a similar vegetation distribution as described by Stoddart (1962), in the sense that the western side was almost entirely populated by *R. mangle* whilst the eastern half of the cay consists of a mixed forest dominated by the *L. racemosa* with a variety of understory shrubs. However, no coconuts were found. The cay has approximate dimensions of 105 m at its maximum length and 65 m at its widest point.

East Snake Cay (ESC)

East Snake Cay lies outside the zone of catastrophic disturbance from Hurricane Hattie. ESC (16°12'N and 88°30'W), which is located about 14 km from the mainland in the southern part of Belize (Toledo district), was selected as a reference site for comparative reasons. Information about ESC is available from Stoddart (1982) from his brief 1961 expedition. He described ESC as a sand cay with shingle ridges with significant amount of corals around them. At the time of his visit, ESC was a densely vegetated sand cay, surrounded entirely by shingle ridges. Of interest was the presence of an inner shallow moat with mangroves and a cut through the rampart at the northern tip of the cay. The whole system was 260 m long with up to 110 m wide. The shingle rampart was limited to *Ipomea* sp. and *R. mangle* vegetation. The sand cay south of the rampart was covered with a dense cocal forest along with other species – *Thrinax radiata, Coccoloba uvifera, Terminalia catalpa*, and *Ficus* sp. (20 species of plants were recorded including the *R. mangle, A. germinans* and *C. erectus*).

During my surveys, ESC's vegetation was very similar to the findings reported by Stoddart (1982). The fringing *R. mangle* dominated the northern and entire eastern part of the island, as well as all that area surrounding and enclosing the moat. I also noted a cut through the shingle rampart at the northern part of the cay. Interestingly, this particular feature seemed to allow the entrance and exit of tidal currents as well as wind generated high water. Similar to Stoddart’s findings, I found all mangrove species and the mangrove associate at ESC. However, in addition to Stoddart's list, *L. racemosa* occurred in both the mid-eastern and mid-western sections of the cay, which was not mentioned in Stoddart’s report of 1982. Mean heights within the established plots was 7.3 m; however, a *R. mangle* tree within the plot towered at 19 m and several trees within the cay were estimated at over 19 m high. A well developed cay forest covers the southern and central part of the island. The automatic lighthouse on ESC that was noted by Stoddart is still standing. However, another lighthouse structure has since been constructed close to the older one at the southern end of the island. The older one was made out of concrete and a newer modern one was made out of steel. These structures made it easy to superimpose maps for comparisons. ESC has approximate dimensions of 189 m at its maximum length and 100 m at its widest point.

2.5 Field study

2.5.1 CARICOMP goal and approach

Caribbean Coastal Marine Productivity (CARICOMP) is a scientific regional monitoring program that has a network of approximately 24 sites in 16 countries including marine laboratories, parks, and reserves. This program is geared at gathering data to study land and sea interactions and processes primarily of three coastal ecosystems in the Caribbean: mangroves, corals reefs and sea grass beds. The CARICOMP program produced a manual to provide the basic support for scientific data gathering especially with the intention of having standard methods for research (CARICOMP Level I Methods Manual 2002). The advantage of the manual is to provide relatively simple techniques with the use of easily available equipment in order to guarantee frequent, regular, and reliable data for the region. Such a manual adds to the benefit of compiling reliable data that can be easily compared since the same methodology is used.

For this study, the CARICOMP Methods Manual Level I (2002) was adapted in conjunction with the methods described by Shaeffer-Novelli and Cintrón (1986), to measure forest structure and productivity of the selected sites.

2.5.2 Establishment of study units (plots) and in-situ measurements

Structure of the mangrove vegetation was described based on the values obtained from the three permanent plots established in each site (total of 0.03 ha per site). The

CARICOMP methodology was adapted for this particular study. Thus, a fringing *Rhizophora* forest was selected. Three plots measuring 10 x 10 m were established per site. Plots were oriented parallel to the shoreline with distances of 3 to 4 m between plots, and were labeled as A, B, and C. The three plots were constructed by marking the corner at the left side as the zero point and taking compass bearings for the orientation of the plots (Fig. 2.3). I used a compass and a measuring tape to complete the 10 x 10 m square. The corners were marked with pvc pegs at the corners where trees were not available. The borders of the plot were lined with a fluorescent string to facilitate the easy recognition of all trees that fell within the plots. I used Global Positioning System (GPS) to determine the coordinates of the zero points of all plots.

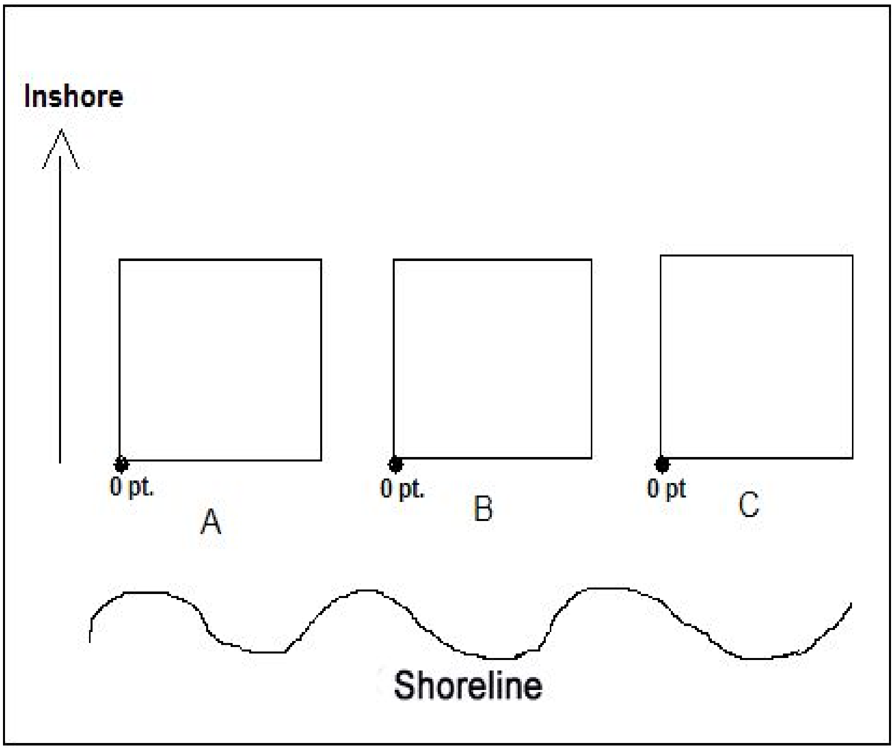

Figure 2.3. Orientation and layout of plots relative to the shoreline.

For each plot, all mangrove trees with trunk diameter at or greater than 2.5 cm were (i) numbered and labeled with an aluminum tag, (ii) identified to species, (iii) measured as follows:

Diameter

Diameter is closely related to stand development and is used for forest stand characterization. Diameter at breast height (dbh), was measured in cm with a graduated foresters tape around the tree trunks which gave the girth values of the trees in cm. Dbh was measured at 1.3 m trunk height for all species except *R. mangle.* For that species, the dbh was taken immediately above the buttress roots. All measured trunks, at the respective dbh position, were marked with a foresters all weather crayon. In the case of trees with more than one trunk, each trunk was considered as a separate tree. It can be problematical to determine where to take the dbh measurements especially in mangrove forests. For this reason, a list of criteria recommended by Cintrón and Shaeffer-Novelli (1984) were taken into account: (i) when a stem forks below breast height, or sprouts from a single base close to the ground or above it, then each branch was considered as a separate trunk; (ii) situations where the stem forked at breast height or slightly above, measurements were taken just below the swelling caused by the fork; (iii) in the case of *R. mangle,* dbh was measured just above the highest buttressing root - which is considered as the uppermost supporting root, (adopted from the CARICOMP Methods Manual 2002); (iv) in cases where at the point of measurement the tree trunk had abnormalities, measurements were taken slightly above or below the swelling.

Height

Total height is the linear vertical distance between the ground and the tip of the tree crown. Height was measured in m for all identified trees ≥ 2.5 cm dbh within the plot from sediment surface to highest leaves. Height was measured with the aid of a graduated telescoping measuring rod. For tall trees (> 7 m), a Laser instrument (Laser Technology Inc.) was used to measure the height.

2.5.3 Data Analysis

Aboveground biomass

Aboveground biomass is defined as the amount of standing organic matter per unit area at a given time. The amount of biomass stored in a forest is a function of the system's productivity, age, and organic matter allocation and exportation strategies (Cintrón and Shaeffer-Novelli 1984). Height and dbh values were used to calculate aboveground biomass for the established mangrove plots (Cintrón and Shaeffer-Novelli 1984) and the dbh value alone was used with a conversion factor using Golley et al (1962) equation to calculate a second biomass values. Both calculations were performed in order to compare values and are reported in Appendix, Table. A.1–A.4.

Biomass calculations were conducted by non-destructive means. The biomass was calculated using the dbh to weight conversion factor, given by the equation of Golley et al. (1962):

Biomass (g) = dbh(cm) x 3390

A second calculation was performed for individual tree biomass using the equation developed by Cintrón and Shaeffer-Novelli (1984).

$$\text{Biomass (g)} = b\,[(\text{dbh})^2\,(\text{height})]^m$$

where b and m are constants designated by the values 125.9571 and 0.8557, respectively. Calculations yield biomass values in wet weight for the living biomass expressed in kg · m^2.

Basal Area

Basal area is a simple and good measure of the overall stand characterization and development, and can be related to wood volume and biomass (Cintrón and Shaeffer-Novelli, 1984). Diameter is closely related to stand development and is easily converted to basal area (cross section of a stem at the point where dbh is measured), defined as the area occupied by tree stems expressed as m^2 per hectare. Given by the formula:

$$\text{Basal area} = \sum \pi r^2$$

A total of nine stations from the published literature were selected for comparison. Table 3.4a shows information on the sites used for comparison. The literature reports values for basal area, and biomass (CARICOMP 2002). CARICOMP data were selected based on this primary criterion: for all selected sites, general descriptions are reported on the UNESCO 1998 publication. Furthermore, sites from the CARICOMP literature were selected based on: (i) plots established in fringing mangrove stands (ii), *R. mangle* dominated plots (iii), estimated values were selected from the most recent survey and (iv), calculations for estimated biomass using Cintrón and Shaeffer-Novelli (1984) allometric equation. It should be noted that the published literature values varied from different years 1993 to 1998. Table 2.1a, presents the estimated values reported by CARCICOMP (2002), whilst Table 2.1b, reports the values gathered during the time of this investigation.

Table 2.1a. Basal area and biomass estimates for nine CARICOMP designated sites. Biomass calculated using Cintrón and Shaeffer-Novelli allometric equation (data taken from CARICOMP 2002)

Country	Station	Year	Plot	Basal Area (m^2 ha)	Biomass (kg · m^{-2})
Bahamas	Blackwood Bay	1996	A	2.69	0.72
San Salvador	Blackwood Bay	1996	B	6.94	2.07
BBB	Blackwood Bay	1996	C	2.60	0.85
			Mean	**4.08**	**1.21**
Barbados	Graeme Hall Swamp	1998	A	59.40	40.64
GHSB	Graeme Hall Swamp	1998	B	21.35	17.61
	Graeme Hall Swamp	1998	C	27.57	22.86
			Mean	**36.10**	**27.04**
Belize	Calabash Caye	1996	A	29.79	11.69
CCB	Calabash Caye	1996	B	25.85	9.87
	Calabash Caye	1996	C	35.67	12.26
			Mean	**30.43**	**11.28**
Belize	Twin Cays	1993	A	21.55	7.05
TCB	Twin Cays	1993	B	17.59	6.13
	Twin Cays	1993	E	15.59	3.04
			Mean	**18.24**	**5.40**
Bermuda	Hungary Bay	1998	A	29.04	11.15
HBB	Hungary Bay	1998	B	24.49	9.72
	Hungary Bay	1998	C	25.63	10.45
			Mean	**26.39**	**10.44**
Bonaire	Lac Bay Mangrove	1997	A	21.37	9.36
LBMB	Lac Bay Mangrove	1997	B	20.01	8.50
	Lac Bay Mangrove	1997	C	12.69	5.32
			Mean	**18.02**	**7.73**
Colombia	Chengue Bay	1998	A	47.16	25.32
CBC	Chengue Bay	1998	B	45.76	20.93
	Chengue Bay	1998	C	38.40	15.74
			Mean	**43.77**	**20.66**
Puerto Rico	La Parguera	1994	A	26.62	11.08
LPPR	La Parguera	1994	B	16.00	6.32
	La Parguera	1994	C	18.58	7.38
			Mean	**20.40**	**8.26**
Venezuela	Tumba Cuatro	1994	A	4.75	2.93
Morrocoy	Tumba Cuatro	1994	B	24.40	13.55
TCV	Tumba Cuatro	1994	C	22.17	10.59
			Mean	**17.11**	**9.02**

Table 2.1b. Basal area and biomass estimates for the four sites under investigation. Biomass calculated using Cintrón and Shaeffer-Novelli allometric equation (data gather in 2002).

Country	Station	Year	Plot	Basal Area (m2/ha)	Biomass (kg/m2)
Belize	Soldier Cay	2002	A	23.59	9.78
Turneffe	Soldier Cay	2002	B	14.13	5.13
SC	Soldier Cay	2002	C	31.36	11
			Mean	**23.03**	**8.64**
Belize	Big Calabash Cay	2002	A	27.95	11.09
Turneffe	Big Calabash Cay	2002	B	28.57	11.31
BCC	Big Calabash Cay	2002	C	22	8.58
			Mean	**26.17**	**10.33**
Belize	Dead Man Cay V	2002	A	16.01	6.08
Turneffe	Dead Man Cay V	2002	B	19.94	6.06
DMCV	Dead Man Cay V	2002	C	14.08	4.18
			Mean	**16.68**	**5.44**
Belize	East Snake Cay	2002	A	35.12	21.03
Toledo (southern Belize)	East Snake Cay	2002	B	65.11	38.69
ESC	East Snake Cay	2002	C	70.31	36.39
			Mean	**56.85**	**32.04**

Measurements of productivity (litter fall), salinity, and pH

Productivity was assessed by quantifying litter fall. Litter fall was collected with litter traps attached under the mangrove canopy. The amount of litter shed by mangrove trees was investigated only for the Turneffe sites. Unfortunately, litter fall collection was only possible for five months between October 2002 and February 2003. Only three sites were also assessed for litter fall production, SC, BCC, and DMCV located in Turneffe. Due to the remoteness of the site, ESC was not included for the assessment of litter fall. During the sampling period, only one litter trap went missing for the month of January 2003 at SC (Trap ID – SC-B7). However, data were extrapolated for that specific trap from the previous months.

The litter traps were constructed out of pvc pipes (1/2” diameter) with dimensions of 0.5 x 0.5 m, thus, completing a square of 0.25 m^2. Plastic screening (1 mm mesh size) was used to complete the body of the basket to ensure that rain did not stay within the basket, thus preventing biodegradation before the retrieval of the samples from the field. The baskets were approximately 16 cm deep to ensure that the litter was not blown out of the traps by wind. The litter traps were secured beneath the mangrove canopy to the roots of the mangroves with monofilament from its four corners. The baskets were suspended approximately 1 m above the highest tide level.

For each plot, 10 litter traps were deployed, and each trap was labeled according to the site location, plot letter, and number of trap. Five traps were tied parallel to the shoreline within the plot and five perpendicular to the shore line. All litter traps were tied in a north-south direction, starting with litter trap 1 to 5, and in the east-west direction, traps 6 to 10. This technique was used in order to ensure that the samples could be traced back to its origin without any complication in case of any interesting observation or for facilitating collection of samples. In all, 30 litter traps were deployed per site, giving a total of 90 traps for the Turneffe sites.

The leaf litter for all traps was collected at the ending of each month for the months of October 2002 to February 2003. Litter fall was collected in zip lock bags for transportation and labeled according to the traps identification number. Once at the field station, litter was immediately transferred to paper bags using the same identification number corresponding to each litter trap. Litter fall was then oven dried at 70°C for 72 hours until constant dry weight was obtained. Each litter trap sample was sorted separately into all its possible identifiable components called 'categories' and weighed to 0.01 g to obtain its dry biomass. I observed that the dried samples could not be left outside of the oven before sorting due to the high humidity of the environment. Therefore, the sorting had to be done as soon as the bags were retrieved from the drying oven.

Litter fall literature review

For evaluation of litter fall results, published and unpublished literature for the Caribbean were analyzed in order to put my data into a regional context. Special interest was placed on sites that shared similar characteristics and on those that had enough data for comparisons. Data were downloaded from the CARICOMP website data center (CARICOMP 2002).

In order to extrapolate the data for yearly estimates, for the Turneffe sites, the litter fall values excluding guano and miscellaneous, were calculated for individual plots (g dry matter weight · $m^{-2}day^{-1}$) and the rates were multiplied with a total of 365 days which was in turn divided by the number of sampling times (total of 15 sampling times = 3 plots per site x 5-mo sampling period).

Salinity and pH measurements

Coincident with litter fall collection, soil physicochemical parameters were measured. Interstitial water was collected with the aid of a "sipper". The sipper was constructed with a 50 ml syringe attached to a clear narrow diameter, flexible plastic tube. The tube was then attached to another straight and sturdy piece of fibreglass tubing, 45 cm in length, which was plugged at the bottom. The last 6 cm of the fiberglass tube were perforated with tiny holes to allow the inflow of interstitial water when suction was applied from the syringe.

I used this sipper to collect interstitial water samples from all plots at 30 cm below the sediment surface. The first sample of extracted water by the sipper was always discarded due to its debris and sediment disturbed content from insertion of the fiberglass tubing. Subsequent clear samples were used to fill sample vials of 80 ml. Samples were tested for salinity content and pH at the field station using a handheld refractometer and YSI 556 MPS (Multi Probe System, YSI incorporated, Yellowsprings, OH). The aliquot was analyzed at the field station on the same collection date to prevent any possible contamination or changes in sample properties.

Interstitial water samples were taken at each plot at three locations: at the 5 m point on the x border (parallel to the shore line), at the middle of the plot (5m x, 5 m y coordinate), and at the far end border towards the inside of the island (5m x, 10m y coordinate). Salinity values were obtained for November 2002 to February 2003, and pH values for December 2002 to February 2003.

Nutrient Use Efficiency and Resorption Efficiency

Nutrient Use Efficiency (NUE) is defined as the mass of nutrient required to produce a given quantity of biomass. In practice, NUE is the inverse of the concentration at senescence or when a leaf is shed by the plant. Resorption Efficiency (RE) is a measure of the translocation of nutrients from leaves back into the plant during senescence (Vitousek 1982).

Phosphorus NUE and RE have been shown to reflect nutrient availability in Red mangrove forests (Feller et al. 1999). Thus, I used these values as indices to compare potential differences in soil fertility among my sites. The concentration of phosphorus (P) in *R. mangle* leaves was estimated for mature and senescent leaves for all four sites. To calculate the percentage of P resorbed prior to leaf fall, leaf samples were harvested from *R. mangle* trees at each site. Five pairs of mature green and fully senescent (yellow) leaves were randomly collected per plot. Three pairs came from the upper most canopy and two pairs from the mid canopy section. Fully senescent yellow leaves were taken from basal positions on first order branches; fully mature green leaves were also collected from penapical positions from the same branches. Senescent leaves were collected on the basis that with the slightest pressure a leaf detached from the branch.

Harvested leaves were labeled with a Sharpie® marker according to the site and plot and were sealed in zip lock bags. Once at the station, the green and senescent leaves harvested from all plots were pined on a flat surface along with a scale and were photographed with a digital camera. Senescent and green leaves were placed into paper bags and oven dried at 70°C for 72 hours to obtain a constant dry weight. The digital images were used to measure surface leaf area using image analysis software (SPSS, SigmaScan Pro. 4). I conducted this part of my research at the Smithsonian Environmental Research Center, Edgewater, MD, USA.

Leaves were oven dried once more for 12 hours before being ground with a Wiley mill to pass through a 20 - 0.38 mm mesh screen. A total of five senescent leaves per plot were ground together and five green leaves per plot were also ground together and sealed in airtight vials (n= 24 samples). Concentrations of P were determined by Agricultural Analytical Services Laboratory, Pennsylvania State University, University Park, PA, USA. Results were reported in percentage of P per site per plot (Appendix, Table A.8).

RE was calculated as the percentage of P (mass P per unit leaf area) recovered from senescent leaves prior to leaf fall (Feller et al. 1999).

I used the following formula for Resorption Efficiency of Phosphorus (RE_P)

$$RE_P = 100 \; \frac{\left[P \; (g/cm^2 \; in\, mature\, green\, leaves) \; - P \; (g/cm^2 \; in\, senescent\, leaves) \right]}{P \; (g/cm^2 \; in\, mature\, green\, leaves)}$$

NUE of phosphorus (NUE_P) was calculated as the inverse of their concentrations (g nutrient/g biomass) in senescent leaves (senescent leaves biomass per unit of nutrient) from each of the samples collected per plot.

Georeferencing of maps and photographs for calculating area and vegetation coverage

Georeferencing is a task of establishing the relationship between page coordinates or simply topological positions like headlands, bays and other landmarks on a planar map or photo and known real world coordinates. This can be done with Environmental Systems Research Institute (ESRI), so that it can then be integrated with Geographic Information Systems (GIS) data (K. Dietmar per. comm.).

Maps of the selected sites produced by Stoddart (1963, 1982) before and after the storm were used for comparing island changes. The periphery of all four cays were marked with a Geographic Positioning System (GPS) with a hand held Garmin 12 XL, (Garmin Corporation 1998). GPSed coordinates were taken at 5 to 10 m interval along the periphery of the sites in order to get an accurate contour of the cays. A descriptive map from the four sites was produced while on the field, specifically highlighting the distribution of mangroves for future calculations. Aerial photographs were obtained of the three sites in Turneffe in March 2003 (courtesy of Smithsonian Institution and the LightHawk organization).

With these available resources, it was possible to georeference both maps and aerial photographs in order to quantify area of the study sites. Furthermore, with the aerial photographs, it was possible to calculate vegetation coverage of the three sites in Turneffe, based on ground truthing information from the field. Georeferencing was made possible through the Department of Aquatic Ecology within the department of Biology at the University of Bremen. The program used was ArcGIS (version 8.2) a desktop-GIS by ESRI. For the purposes mentioned above, the ArcInfo part of the GIS application was used.

Image data sources including scanned paper maps and aerial photos become powerful when re-projected as image maps for use as a background or base map on which other spatial data were overlaid. It was possible to establish an image-to-world relationship between image and map coordinates and re-project an image into a georeferenced image map. This process assigns real-world coordinates to all of the pixels contained in the image file. With this concept in mind, reference points from the GPS data were used to find locations in the real-world. The concept relies on ground control points whose geographic coordinates are known, determined by GPS readings. The points were then cross-checked into two kinds of maps (i) the vector (shape files) and (ii) the Grid (TIFF files). Maps from (Stoddart 1963, 1982) were scanned and TIFF files were created. The TIFF files were then overlaid and georeferenced to their corresponding current coordinates using the GPS coordinates stored in a point-shape file. Common features seen on both the historic maps and photos that corresponded to the coordinates were selected (as a rule of thumb a minimum of five points is recommended). For this work, averages of eight to 12 points were selected. This process warps the historic image or photo to its approximate geographic location. Georeferencing establishes the image's spatial location and creates a world file which was used to position correctly the image when opened with the GIS software. The advantage of these files was not only having a position but also the scaled location (in m, km, etc.). Shape files were then used to paint polygons of different sizes and attributes, by enclosing the periphery of the photo or map in question. The outer polygon, mapping the contour of the cays, was then dissecting in its different sub-polygons depending on the area in question to be calculated, e.g., vegetation type or erosion after hurricane. Each polygon could be filled with a particular attribute and a name was assigned for further calculations, e.g., total areas or percent cover of a specific feature. The polygons constructed using the scanned paper maps were used specifically to calculate the area eroded after the hurricane. The aerial photos were used to calculate size and geophysical changes since the storm and to determine the percent cover of the different vegetation types (specifically mangroves).

Statistical Analysis

Statistical analysis was performed with the statistical program SPSS for Windows, (Standard Version. Release 10.0.5, 1999. SPSS Inc). A GIS program was also used for the georeferencing of the aerial photographs to calculate area and percent vegetation coverage.

For biomass, basal area and nutrient content, I used one-way ANOVA to determine differences among sites and post hoc tests for multiple comparisons among sites. When an ANOVA found a significant main effect, Fisher's Least Significant Difference Test was used to perform multiple pairwise comparisons. One-way ANOVA's were also used to compare the methods proposed by Golley et al. (1962), and Cintrón and Shaeffer-Novelli (1984).

3 Results

3.1 Vegetation coverage

Each site has been described for vegetation coverage, forest structure, biomass and productivity. Vegetation coverage was calculated based on the outcome from the georeferenced aerial photographs (Turneffe sites only – Figures 3.1a, b, and c). For ESC the descriptive vegetation was from the three plots established and visual observations. As shown in Figure 3.2, *R. mangle* was the dominant species and ranges from 38.7 to over 50% of the total cay area. SC, BCC, DMCV, and ESC areas were approximately 1.03, 0.70, 0.45, and 1.29 ha respectively. The area of ESC was calculated based on the georeferencing of a scanned map. For this site the vegetation coverage was not calculated due to the lack of aerial photograph. The three mangrove species were found at all sites including *C. erectus*. For the SC site all three mangrove species were present however, the quantification of the area covered by the *L. racemosa* species was not possible from the aerial photograph and as such was included in the mixed mangrove vegetation. It should also be noted that all species area coverage's represent underestimation since all species occur within the well mixed mangrove vegetation category with the exception of DMCV. The aerial photograph for DMCV was better in clarity and the forest composition less mixed than the other sites. The characteristic coverage of this site was approximated for all its identifiable features. Non mangrove species were found in all four sites; however for the Turneffe sites the calculated area was within the range of 3 to 5% of the total area. One striking category found only at DMCV was dead mangrove patches located at the eastern and southeastern side of the cay.

Figure 3.1a. Georeferenced aerial photograph of Soldier Cay – Turneffe Atoll, Belize (modified after Feller 2003)

Figure 3.1b. Georeferenced aerial photograph of Big Calabash Cay – Turneffe Atoll, Belize (modified after Feller 2003)

Figure 3.1c. Georeferenced aerial photograph of Dead Man Cay V – Turneffe Atoll, Belize (modified after Feller 2003)

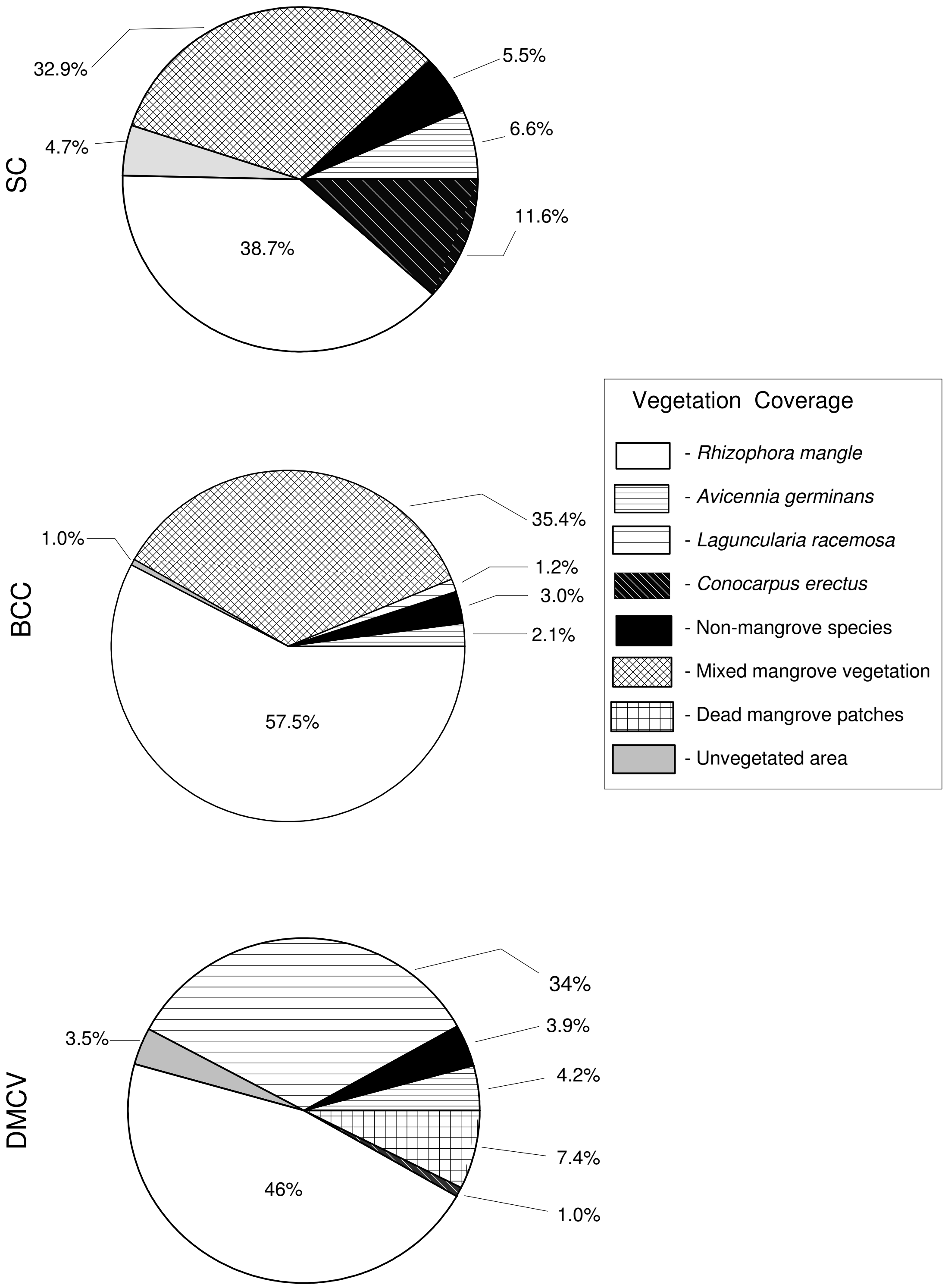

Figure 3.2. Pie chart showing percent Cay coverage of three sites - Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay V (DMCV) in Turneffe Atoll, Belize.

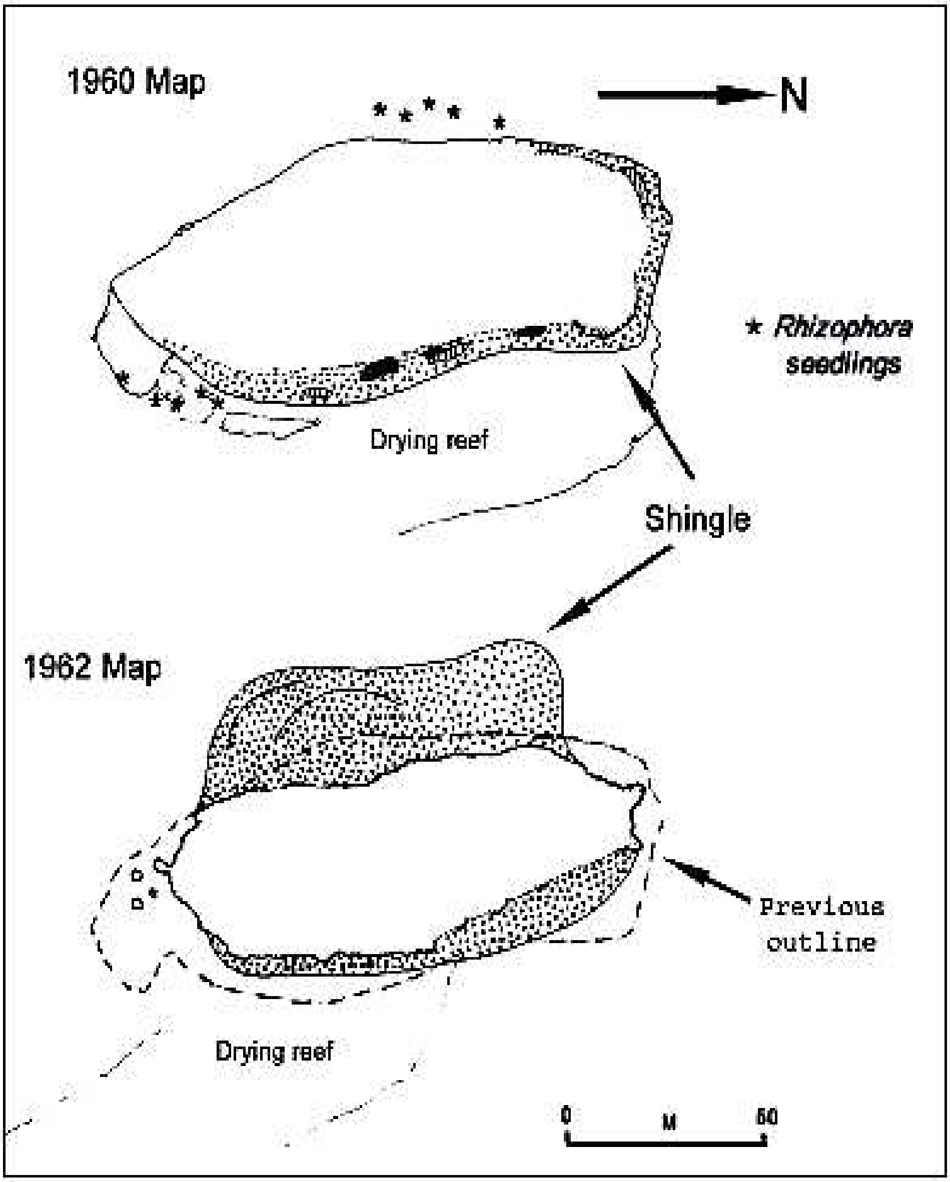

Figure 3.3a. Map of Soldier Cay area, for the year, 1960 and after Hurricane Hattie 1962 (modified after Stoddart 1962).

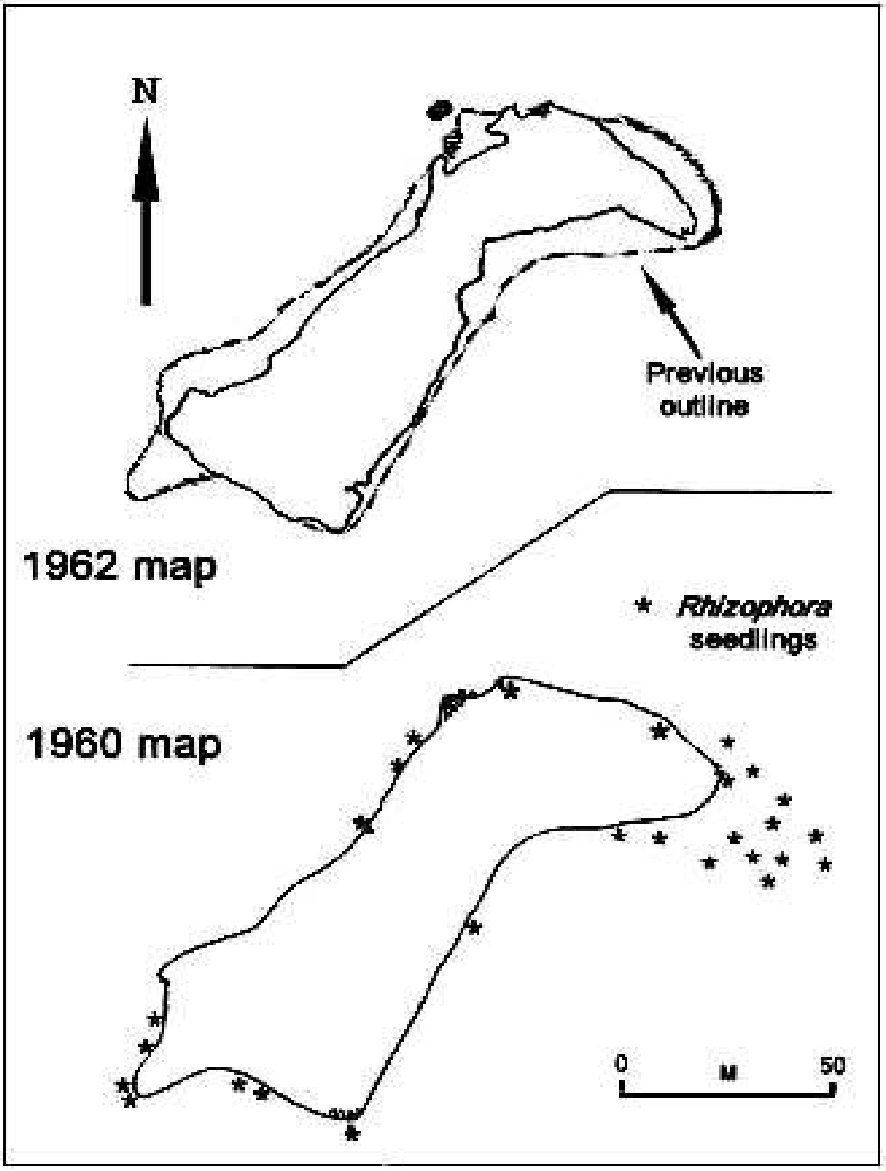

Figure 3.3b. Map of Big Calabash Cay area, for the year 1960 and after Hurricane Hattie 1962 (modified after Stoddart 1962).

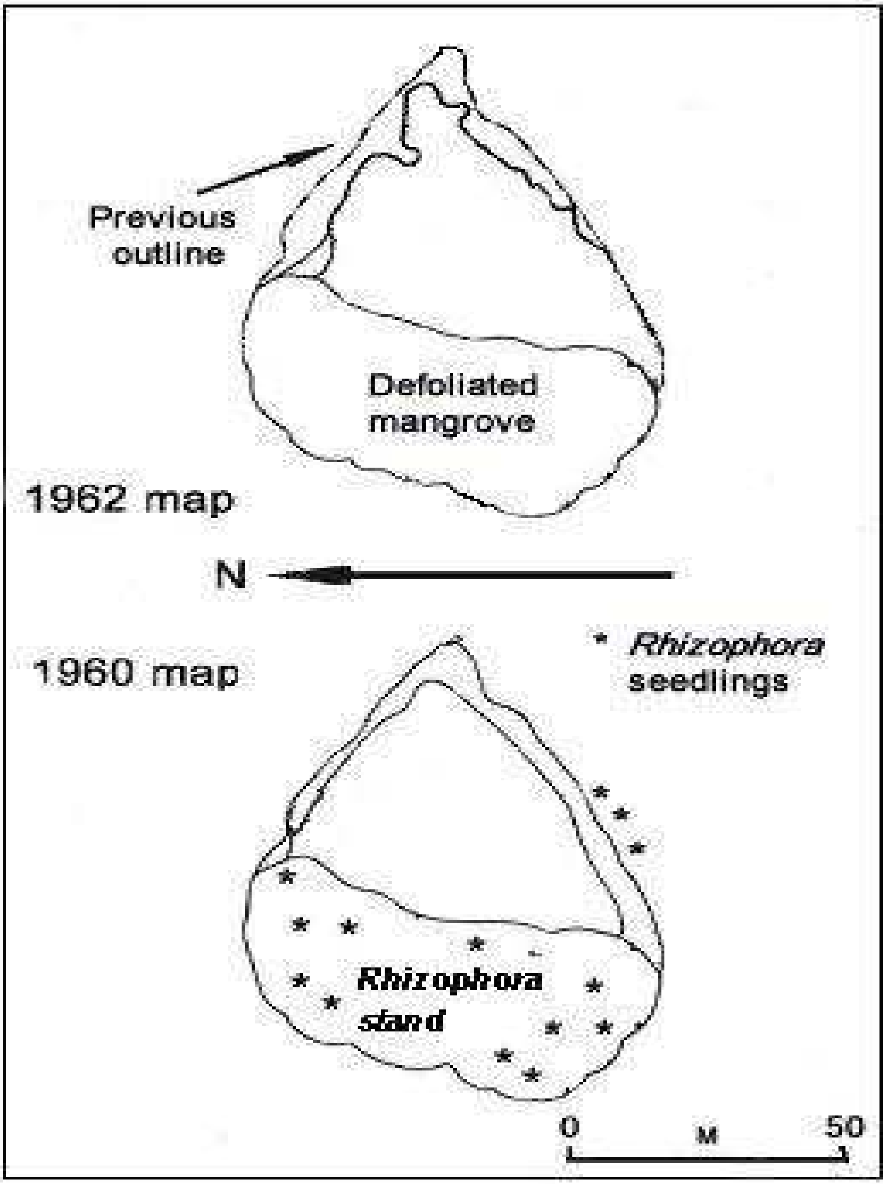

Figure 3.3c. Map of Dead Man Cay V area, for the year 1960 and after Hurricane Hattie 1962 (modified after Stoddart 1962).

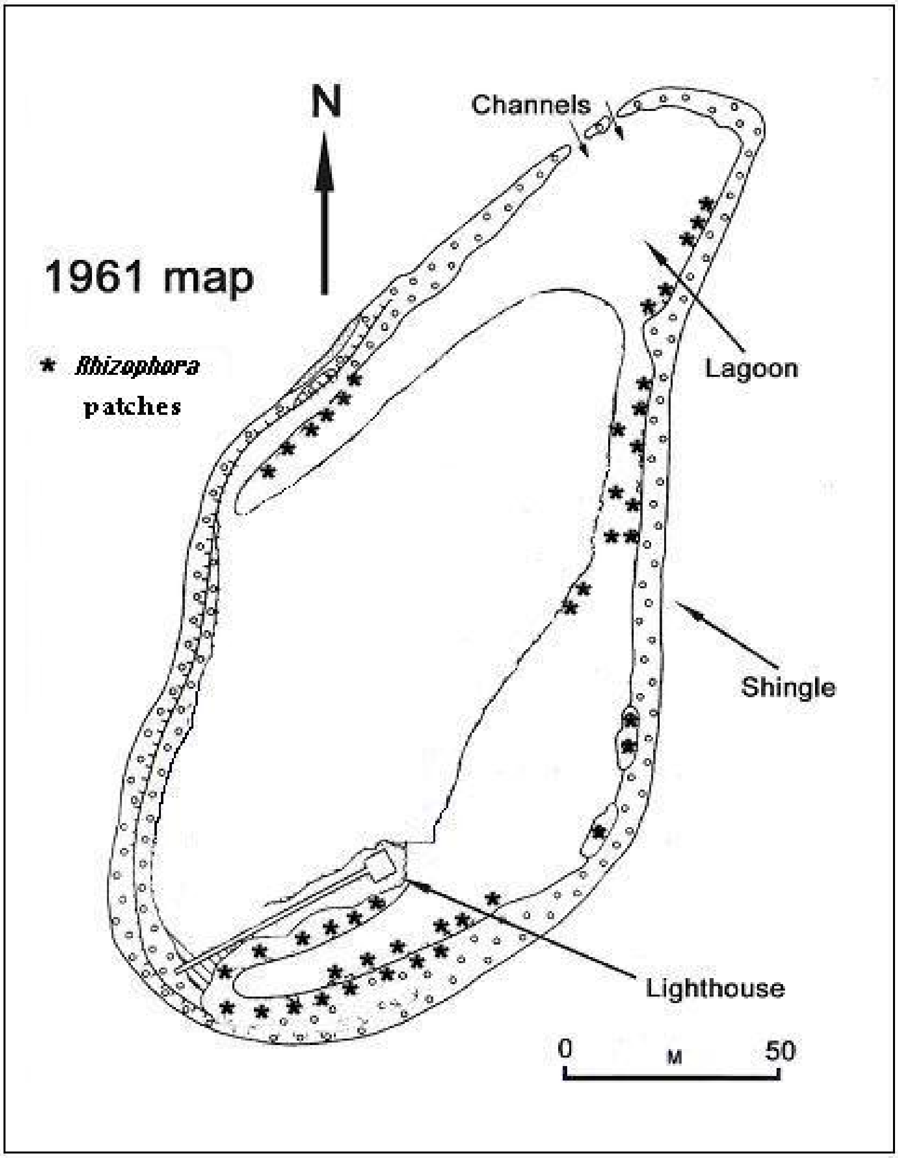

Figure 3.3d. Map of East Snake Cay area for the year 1961 showing the shingle rampart that encircles the entire cay and the presence of *R. mangle* (modified after Stoddart 1982).

Based on the maps produced by Stoddart (1963, 1982) before and after the storm (Figures 3.3a, b, c, and d); results of Table 3.1 show how the cays have changed in dimensions since 1961. The area of SC was severely destroyed during the storm; consequently it lost approximately 39% of the cay surface to erosion. BCC was similarly affected losing 31% of its original area to erosion. On the other hand DMCV experienced 11% erosion from the calculations obtained.

Table 3.1. Summary of Cay dimensions before Hurricane Hattie (1960), after Hurricane Hattie (1962) and 2003 area estimates.

Site	ha
SC – 1960	0.61
SC - 1962	0.37
SC- 2003	1.03
BCC - 1960	0.75
BCC - 1962	0.52
BCC - 2003	0.70
DMCV - 1960	0.36
DMCV - 1962	0.32
DMCV - 2003	0.45
ESC - 1961	2.00
ESC - 2003	1.29

A further comparison for the calculated areas show that SC has regained the area lost during the storm and has managed to colonize more area. Calculations show that approximately 0.42 ha of cay substrate and vegetation has been acquired since before the storm. For BCC it falls short of 0.05 ha from its original dimension before the storm. DMCV also shows that the area after the storm has been recovered and a further 0.09 ha has been acquired as cay substrate and vegetation.

An ESC map published by Stoddart in 1982 was georeferenced to make calculations on the physiological changes of the cay since 1961. Estimates from the calculations conducted shows that ESC has decreased in size. These estimates reflect that ESC has lost approximately 0.71 ha of cay substrate (area). Field observations during the survey confirm the changes in width after the measurements were taken with a measuring tape. The eastern and southeastern side of the cay had suffered considerable erosion. The conclusion was further supported based on the available map and the position of the lighthouse structure described in Stoddart's map (1982).

3.2 Forest Structure

From the mangrove vegetation charts, it was possible to ascertain that *R. mangle* was the dominant species for the Turneffe sites (Figure 3.2). Mangrove tree density for the sites was calculated for SC at 610 trees/0.1 ha, for BCC 850 trees/0.1 ha, for DMCV 1390 trees/0.1 ha and for ESC 236 trees/0.1 ha. Furthermore, in the Appendix, Table. A.1-A.4 describes the structural parameters that were used to calculate aboveground biomass. Both height and dbh show similar tendencies for the four study sites (Figure 3.4).

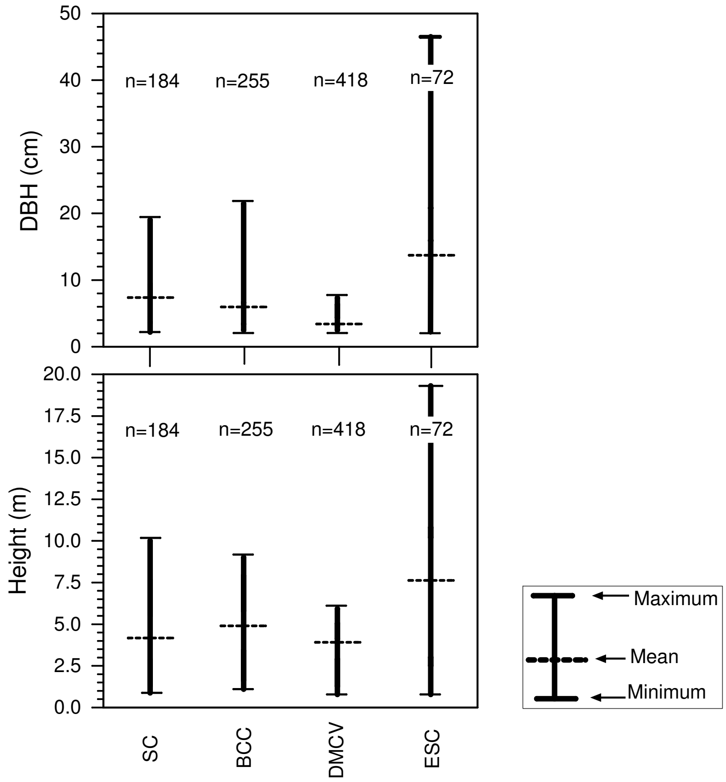

Figure 3.4. Maximum, minimum and mean values for mangrove height and diameter at breast height (DBH) for the four sites, Soldier Cay (SC), Big Calabash Cay (BCC), Dead Man Cay V (DMCV), and East Snake Cay (ESC).

Table 3.2 shows the result of a one-way ANOVA to compare methods by Golley et al. (1962) and Cintrón and Shaeffer-Novelli (1984) for the results of biomass calculations. Golley's values are not statistically different for the 4 sites ($P > 0.05$), while the same test for the Cintrón and Shaeffer-Novelli calculations reflect the opposite ($P < 0.05$). The latter values take into account the height of the trees measured within the plots. Thus, the biomass estimates are more accurate. Based on this outcome, further calculations and comparisons were made with the Cintrón and Shaeffer-Novelli allometric equation.

Table 3.2. Results of one-way analysis of variance (ANOVA) to compare two methods to estimate biomass in four sites: Soldier Cay, Big Calabash Cay, Dead Man Cay V, and East Snake Cay. Probability values < 0.05 indicate significant difference.

Biomass		df	F	P
Golley et al. 1962	Between Groups	3	1.615	0.261
	Within Groups	8		
	Total	11		
Cintrón and Shaeffer-Novelli 1984	Between Groups	3	16.75	0.001
	Within Groups	8		
	Total	11		

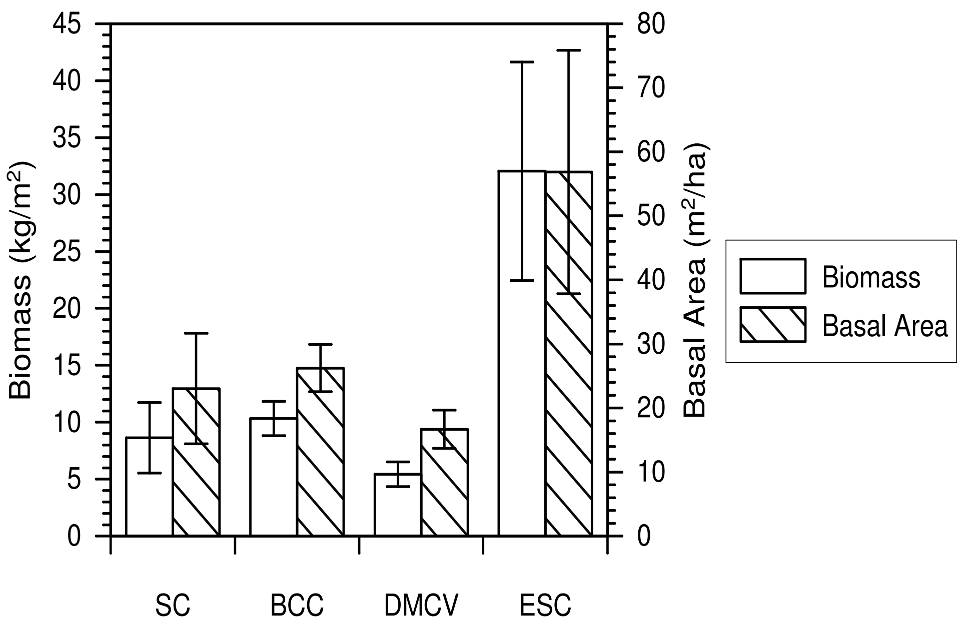

Figure 3.5. Mean biomass and basal area ± standard deviation for the four sites: Soldier Cay (SC), Big Calabash Cay (BCC), Dead Man Cay V (MCV) and East Snake Cay (ESC).

Basal area was estimated along with biomass for all sites. Figure 3.5 shows the values obtained for both biomass and basal area for the sites under investigation.
Biomass and basal area were relatively low at SC, BCC, and DMCV, but there were no significant differences among these three sites ($P > 0.05$). However, values for ESC were much higher and significantly different with almost three times more biomass and basal area than any of the sites at Turneffe.

There was significant difference in biomass among 13 mangrove sites, which included my four sites and nine sites in the CARICOMP network (ANOVA $P < 0.05$). Pairwise comparisons of sites showed that ESC was significantly different from the Turneffe sites as well as seven of the CARICOMP sites (Table 3.3).

Table 3.3. Pairwise comparison of 13 sites (four study sites plus nine selected CARICOMP sites) for differences of mangrove biomass. Values are probabilities. Numbers in bold indicate significant pairwise comparisons.

	SC	BCC	DMCV	ESC	BBB	GHSB	CCB	TCB	HBB	LBMB	CBC	LPPR
BCC	1.000	X	-	-	-	-	-	-	-	-	-	-
DMCV	1.000	1.000	X	-	-	-	-	-	-	-	-	-
ESC	**0.005**	**0.001**	**0.000**	X	-	-	-	-	-	-	-	-
BBB	1.000	1.000	1.000	**0.000**	X	-	-	-	-	-	-	-
GHSB	**0.009**	**0.027**	**0.001**	1.000	**0.000**	X	-	-	-	-	-	-
CCB	1.000	1.000	1.000	**0.002**	1.000	**0.050**	X	-	-	-	-	-
TCB	1.000	1.000	1.000	**0.000**	1.000	**0.001**	1.000	X		-	-	-
HBB	1.000	1.000	1.000	**0.001**	1.000	**0.029**	1.000	1.000	X	-	-	-
LBMB	1.000	1.000	1.000	**0.000**	1.000	**0.005**	1.000	1.000	1.000	X	-	-
CBC	0.505	1.000	0.070	0.742	**0.005**	1.000	1.000	0.069	1.000	0.292	X	
LPPR	1.000	1.000	1.000	**0.000**	1.000	**0.007**	1.000	1.000	1.000	1.000	0.403	X
TCV	1.000	1.000	1.000	**0.000**	1.000	**0.012**	1.000	1.000	1.000	1.000	0.635	1.000

Legend: Soldier Cay (SC), Big Calabash Cay (BCC), Dead Man Cay V (DMCV), East Snake Cay (ESC), Blackwood Bay, Bahamas (BBB), Graeme Hall Swamp, Barbados (GHSB), Calabash Cay, Belize (CCB), Twin Cays, Belize (TCB), Hungary Bay, Bermuda (HBB), Lac Bay Mangrove, Bonaire (LBMB), Changue Bay, Colombia (CBC), La Parguera, Puerto Rico (LPPR) and Tumba Cuatro, Venezuela (TCV)

CCB and TCB, which are CARICOMP designated sites in Belize, were not different from SC, BCC and DMCV at Turneffe. But, they were significantly different from ESC. Both ESC and GHSB had the maximum mean values for biomass, 32.04 and 27.04 kg · m^{-2} respectively, and were significantly different to 10 other sites. However, ESC and GHSB were not significantly different. The range of mean values for biomass at the 13 sites range from an upper limit of 32.04 kg · m^{-2} at ESC to a lower limit of 1.21 kg · m^{-2} at BBB (Table 3.4). Even though the CARICOMP plots were situated in the best locations available at a given site, the site description for BBB indicated that this system was under stress (CARICOMP 2002), which probably affected its biomass estimates.

Table 3.4. Descriptive statistics for biomass per plot (kg · m^{-2}) of 13 sites (four study sites plus nine selected CARICOMP sites).

Sites	N	Mean biomass (kg · m-2)	Std. Dev.	Minimum (kg · m-2)	Maximum (kg · m-2)
SC	3	8.64	3.10	5.13	11.00
BCC	3	10.33	1.52	8.58	11.31
DMCV	3	5.44	1.09	4.18	6.08
ESC	3	32.04	9.60	21.03	38.69
BBB	3	1.21	0.74	0.72	2.07
GHSB	3	27.04	12.07	17.61	40.64
CCB	3	11.27	1.25	9.87	12.26
TCB	3	5.41	2.10	3.04	7.05
HBB	3	10.44	0.72	9.72	11.15
LBMB	3	7.73	2.13	5.32	9.36
CBC	3	20.66	4.80	15.74	25.32
LPPR	3	8.26	2.50	6.32	11.08
TCV	3	9.02	5.48	2.93	13.55

Legend: Soldier Cay (SC), Big Calabash Cay (BCC), Dead Man Cay V (DMCV), East Snake Cay (ESC), Blackwood Bay Bahamas (BBB), Graeme Hall Swamp Barbados (GHSB), Calabash Cay Belize (CCB), Twin Cays Belize (TCB), Hungary Bay Bermuda (HBB), Lac Bay Mangrove Bonaire (LBMB), Chengue Bay Colombia (CBC), La Parguera Puerto Rico (LPPR), and Tumba Cuatro Venezuela (TCV).

3.3 Litter fall

Leaf litter was collected from October 2002 to February 2003. The time interval included the last part of the rainy season, which occurs between June and November in Belize. Litter fall reported in the literature are usually associated with climatological data (temperature and or rainfall). Because the Turneffe field station lacks extensive weather data, the reported values were from the CARICOMP site on Calabash Cay. Monthly mean rainfall weather data (1996-1997) were used to create a two year rainfall graph (Figure 3.6). Each litter fall sample from the three sites was carefully sorted into 15 to 16 separate categories. Litter fall data were collected at SC, BCC, and DMCV, but not from ESC. Figure 3.7 shows the mean monthly values of dry weight litter fall for the three sites including the values of an additional component of bird guano. The data reflects litter fall for the Turneffe sites (SC, BCC, and DMCV).

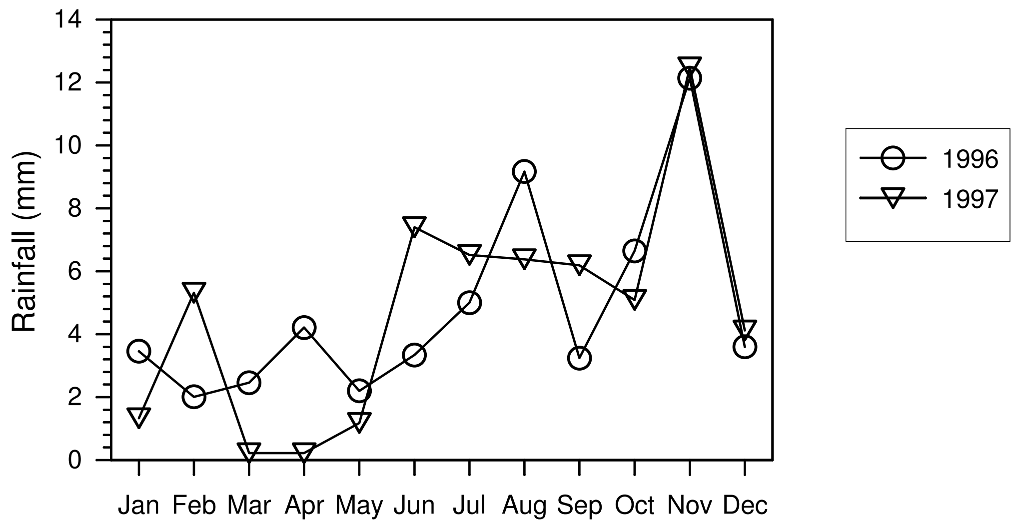

Figure 3.6. Mean monthly rainfall at Calabash Cay, Belize for 1996-1997. (Redrawn from CARICOMP 2002).

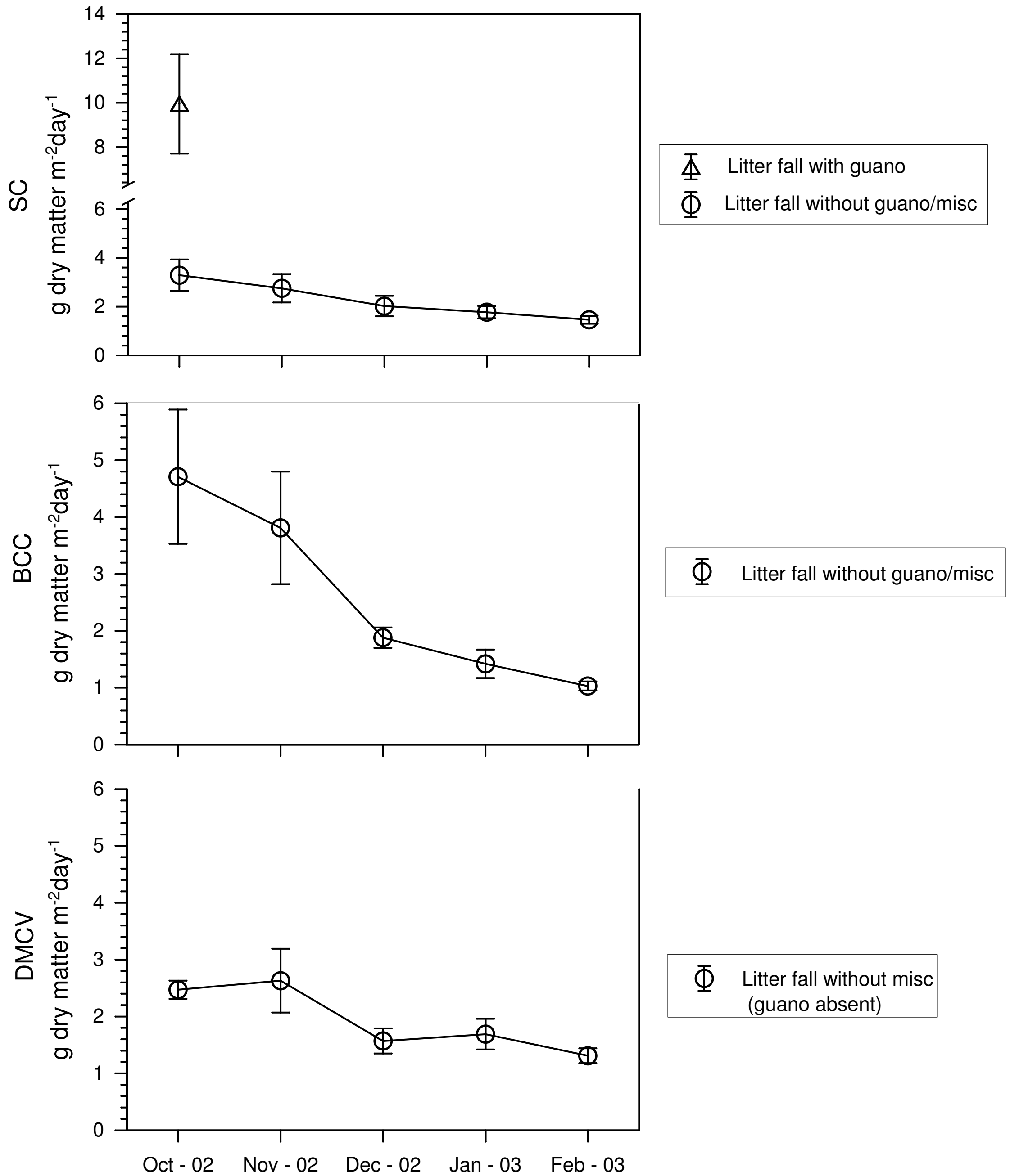

Figure 3.7. Mean (± standard deviation) litter fall with and without guano/miscellaneous per month for Soldier Cay (SC), and litter fall without guano/miscellaneous for Big Calabash Cay (BCC) and Dead Man Cay V (DMCV) for a 5-mo period between October 2002 to February 2003.

The data showed that October received the highest litter fall during the 5-mo sampling period, except for DMCV. These values are without bird guano and miscellaneous. In addition, October showed a high input of bird guano, especially the SC site (Fig 3.7). BCC also had input from bird guano, but it was much lower than SC. DMCV had no visible input from bird guano from the collected litter during the sampling period. For the SC site, guano contributed an average of 66% for October; compared to BCC, which had a mean guano contribution of 5% of dry weight litter fall for October. Calculations showed that for SC there was an average input of guano to the system of approximately 6.6 g · m^{-2} day^{-1} dry weight for October. Interestingly, the sites with highest guano input were the ones that also showed the highest presence of insects (e.g. ants, crickets, and weevils) and structural complexity. These insects were actually an underestimate since most of them escaped during the collection of litter.

The general tendencies for the three sites were a decrease in litter fall from October to February. The approximate maximum and minimum values of dry weight litter fall, excluding guano and miscellaneous, showed that SC produced 4.04 g · $m^2 day^{-1}$ in October to 1.28 g · $m^{-2} day^{-1}$ in February, respectively. For BCC, a maximum value of 6.06 · $m^{-2} day^{-1}$ and a minimum value of 0.96 g · $m^{-2} day^{-1}$ were calculated for October and February, respectively. DMCV produced the lowest litter fall values compared to SC and BCC, a November maximum of 3.14 g · $m^{-2} day^{-1}$ to a February minimum of 1.17 g · m^{-2} day^{-1}. DMCV showed an overall decrease in litter fall from October to February. However, for November and January, there was a slight increase compared to the previous month.

The yearly extrapolated values were necessary in order to make comparisons with reported data from the literature which is usually expressed in $g \cdot m^{-2}yr^{-1}$. Table 3.5 shows the results for the Turneffe sites for both mean yearly values.

Table3.5. Estimated litter fall without guano and miscellaneous for mean yearly values. Yearly values extrapolated from the 5-mo sampling period (October 2002 to February 2003).

Site	Mean yearly litter fall ($g \cdot m^{-2}yr^{-1}$)
SC	824.43
BCC	936.95
DMCV	705.20

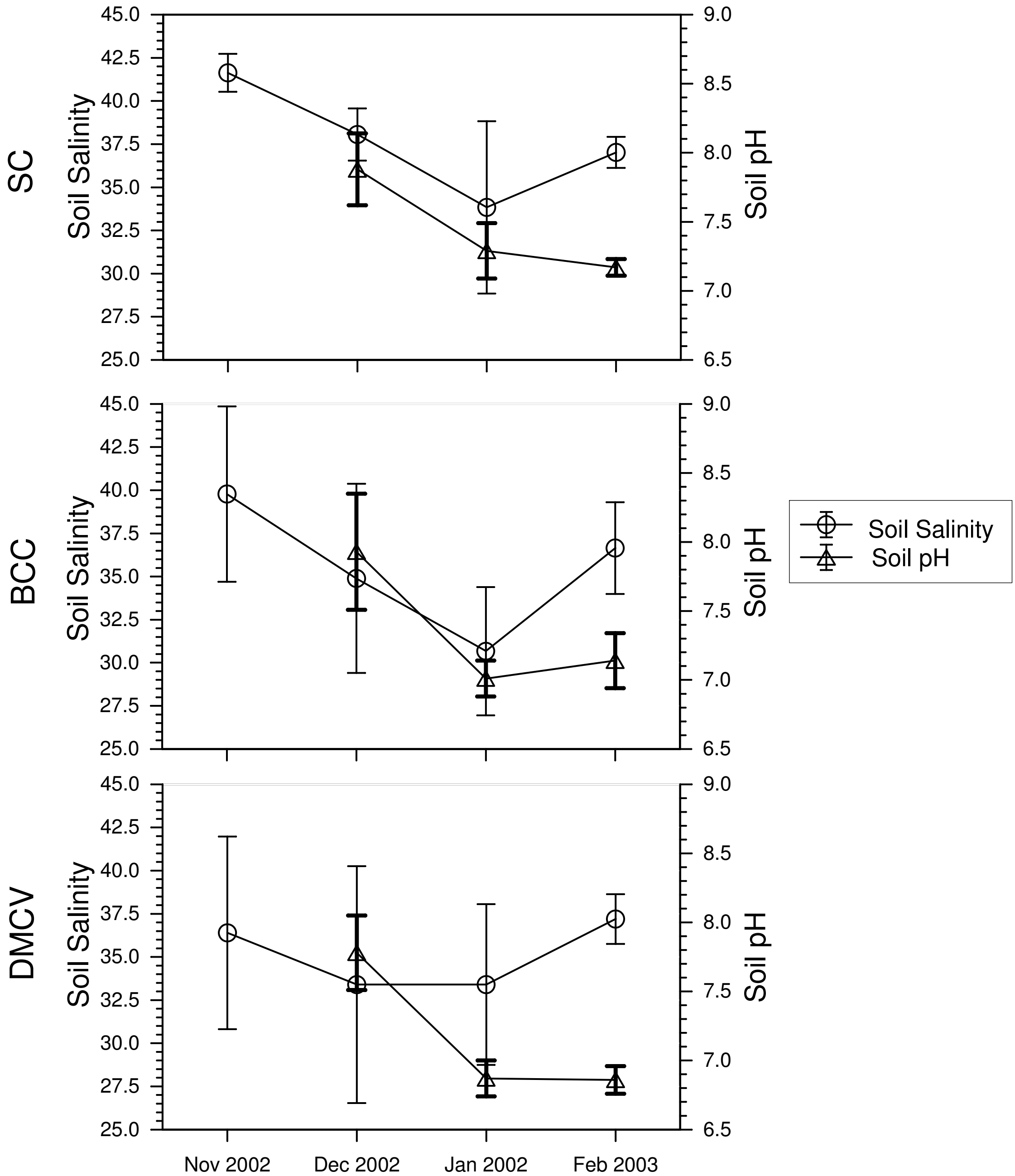

Figure 3.8. Monthly salinity and pH values (mean ± standard deviation) for Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay V (DMCV) at Turneffe.

Salinity and pH

Figure 3.8 shows the mean values for both pH and soil salinity. Due to lack of instrument availability at the beginning of the sampling period, salinity was not measured for October and pH values were obtained for the last three months for the Turneffe sites. The remoteness of the ESC site from the Turneffe sites proved impossible to sample salinity and pH in conjunction with the Turneffe sites. Values were obtained during a 1-wk field period.

3.4 Leaf Nutrient Analysis

Senescent and green leaves were analyzed for phosphorus nutrient content. The values were then transformed to RE_P and NUE_P. Figure 3.9 shows the mean values for the four sites. There was no significant difference among the four sites (ANOVA $P > 0.05$).

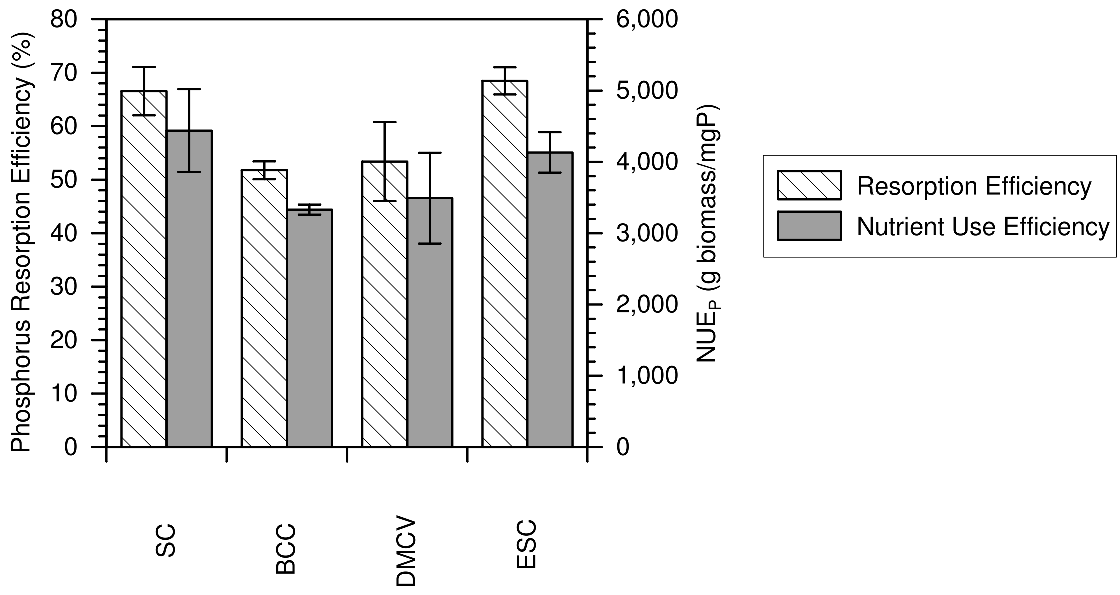

Figure 3.9. Phosphorus Resorption Efficiency and Nutrient Use Efficiency (mean ± standard error) for Soldier Cay (SC), Big Calabash Cay (BCC), Dead Man Cay V (DMCV), at Turneffe, and East Snake Cay (ESC) Toledo southern Belize.

4 Discussion

4.1 Dynamics of cay changes and estimates of vegetation coverage

Fringing mangrove forest typifies the Turneffe and ESC study sites. As defined by Lugo and Snedaker (1974), fringe mangrove forest develops along protected shores, over shoals or spits, often forming overwashed islands. As observed in the study sites, the leeward side of the cays had the highest canopy heights compared to the windward sides. At the water's edge, *R. mangle* dominated with other mangrove species distributed inland as soil elevations increased and flooding decreased. Canopy height ranged from 2–10 m. The width of the zones formed different mangrove and associated species was determined by the gradient of the shoreline at Turneffe and ESC. At these sites *R. mangle* commonly prograded into a littoral thicket in higher elevations. For example, at SC occasional *A. germinanas, L. recemosa*, and *C. erectus* occurred inland to a dense *R. mangle*-dominated fringe along the shoreline. The soil salinity gradient observed across these plots could help explain the zonation and distribution of mangrove species at my study sites.

Historical data showed that island vegetation for the eastern side of the Turneffe Atoll was heavily influenced by human habitation before Hurricane Hattie in October 1961. Stoddart (1962) gave an account of the vegetation types found before Hurricane Hattie. The most important introduced species was the coconut palm, *Cocus nucifera*. Several of the islands described by Stoddart (1962) were virtually unvegetated apart from coconut plantations. The ground vegetation was also subjected to repeated cutting, particularly at inhabited cays such as SC and BCC. Stoddart (1962) also pointed out that the mangrove vegetation was not well developed on these sand cays on the eastern side of Turneffe. His descriptions included observations of scattered mature mangrove trees around cay margins and innumerable *R. mangle*. seedlings in the shoal water around cays such as SC and BCC.

Boose et al. (1994) suggested that the interacting factors that influence the spatial distribution and severity of damage include meteorological, physiographic, and biotic features, along with the effects of previous natural and human disturbance on the area. Furthermore, factors controlling forest damage from storms at the landscape scale include: (1) wind velocity gradients resulting from hurricane size and intensity and proximity to the storm track, (2) variation in site exposure and other effects of local topography, and (3) differential response of individual stands to wind disturbance as a function of species composition and structure (Boose et. al. 1994). Evidently, the cocal forests was unable to withstanding or recover from storms even though vast numbers of coconut stands are still found on the bigger islands at Turneffe that was presumably less affected by Hurricane Hattie (Stoddart 1963). As Stoddart (1962) concluded, the cocal forest was not the best forest structure to withstand the devastating effects of a hurricane. Site factors such as structure type, tree age, tree height, tree health, rooting characteristics, and soil conditions have all been suggested to play important roles to wind susceptibility at the stand level (Foster 1988).

The scanned and georeferenced historic maps provided information on the physiographic changes that have occurred at the study sites since 1961. The estimated values indicate that the three Turneffe study sites (SC, BCC, and DMCV) have recovered entirely or close to their pre-hurricane dimensions. In fact, SC and DMCV have both increased in size compared to their pre-hurricane dimensions. Also, BCC was only 0.05 ha smaller than it was just before Hurricane Hattie. However, at BCC, piles of conch shells that marked the shoreline in Stoddart's (1960 and 1962) maps from before and after the hurricane, were well within the fringing *R. mangle,* approximately 5-6 m from the shoreline in 2003. In the case of ESC in southern Belize, my data indicated a decrease in cay size since Stoddart's surveys in 1961, especially on the southern side of the island. Stoddart's calculation for the area of ESC reported in 1982 of 1.94 ha comes within close approximation of 2 ha, when the area is recalculated from the scanned maps. The cay has lost substrate especially on the southeastern side of the island.

Aerial photographs were available for the Turneffe sites only. Georeferencing of these photographs showed that the Turneffe sites (SC, BCC, and DMCV) were dominated by *R. mangle.* These mangrove stands were 38, 57, and 46% of the total coverage, respectively. However, these percentages may be an underestimate for this species because it was not possible to differentiate different species in the Mixed Mangrove Vegetation zone where *R. mangle* also occurred. In addition, the mangroves *A. germinans*, and *L. recemosa*, and the mangrove associate *C. erectus* were found in all the study sites at Turneffe. I calculated percentage cover of each of these species for each study site except for *L. racemosa* at SC where it was included within the Mixed Mangrove Vegetation category. My results showed that these four mangrove species, which are the most common mangrove in the Caribbean, have managed to recolonize the devastated islands since Hurricane Hattie. Furthermore, the presence of non-mangrove species found at the study sites suggested an increase in the plant species diversity compared to an almost monoculture cocal forest before the storm.

It is believed that the dynamics of these systems are highly variable especially the physiographic changes that influence the physicochemical properties of the soil. These systems are highly susceptible to storm and wave energy, which erode and create land forms. For example, at SC, a narrow belt of 3 to 5 m width of *R. mangle* has emerged at the southern end of the cay. The elevated coral rubble created adequate conditions for the *R. mangle* to colonize this land form. It is likely that the coral rubble provided protection against wave action that would otherwise have hampered establishment of *R. mangle* propagules in this area. Apart from the general vegetation recovery since Hurricane Hattie, the existence of a *R. mangle* belt which was not described by Stoddart (1962, 1963), suggests that these mangroves have emerged over the last 40 years. At present this belt of mangrove contributes 13% to the total vegetation coverage. On the other hand DMCV had a category of Dead Mangrove patches of approximately 7.4% of the total cay coverage. These patches were found on the eastern side of the island and seemed to be a result of cay erosion due to wave action or more recent storms. Considerable amount of woody debris was also found almost in the middle of DMCV and patches of *R. mangle* had their prop roots buried in fine sand. Both of these features are indicative of recent storms. SC and DMCV had areas without vegetation, categorized as Unvegetated, that were 4.7% and 3.5% of the total cay area, respectively. Gaps found at DMCV were barren with no recruits within the fringing *R. mangle* stand or elsewhere on the island. It is not known why these areas of seemingly suitable habitat have not been colonized by mangroves. Certainly, this system has been through some stress as evidence of the low biomass, basal area, and litter fall values. The certainty that these have not been affected since Hurricane Hattie by a severe storm to cause catastrophic damage does not rule out the possibility that less destructive tropical storms and hurricanes could also change the island physiography, reflected at SC, DMCV and ESC.

4.2 Forest structure (dbh and height)

Calculations for forest structure were based on three permanent plots at each of the study sites (total of 0.03 ha per site) at Turneffe and ESC. For each plot, I measured tree density, a distinct attribute of forests that is commonly measured by foresters. Tree density or the number of stems per area, in a forest stand can describe how much a site is being used and the intensity of competition among trees for the site's resources (i.e., water, light, nutrients, and space). At higher densities, the growth rates of individual trees may slow down because there are more trees competing for a site's limited resources. Average tree densities for my plots at Turneffe ranged from 610, 850, and 1390 trees/0.1 ha, for SC, BCC, and DMCV, respectively. These tree densities were above most reported values for the Caribbean, which ranges from 100 to 500 trees/0.1 ha (Lugo and Snedaker 1974; Lugo 1980). Tree density for ESC was well within the lower range of reported values for the Caribbean with 236 trees/0.1 ha. Tree density in all my plots was greater than in the two established CARICOMP sites at Calabash Cay, Belize (CCB) and Twin Cays, Belize (TCB). CCB reported 205 trees/0.1 ha in a 2002 survey (E. Garcia, unpublished data), and TCB reported 137 trees/0.1 ha in a 2001 survey (I. Feller unpublished). ESC, which had the lowest tree density, also had the highest dbh and tree heights when compared to SC, BCC and DMCV. Within the Turneffe sites, maximum and mean values for dbh and height were variable, especially for SC and BCC. SC had higher mean values for dbh, but BCC has the maximum recorded dbh. Tree height exhibited the opposite pattern, i.e., BCC had higher mean values for height, but SC had the tallest tree. DMCV was the lowest for both measured parameters. Additionally, even though the maximum tree height and dbh were lowest in the DMCV plots (Figure 3.4), I observed trees outside the plots that were greater than these values. This suggests more developed and older trees than the ones found within the plots. In the case of SC, one *L. racemosa* tree was found which was 12 m tall with a 28.3 cm dbh. At BCC, one *L. racemosa* was 8 m tall with 24.1 cm dbh and two *C. erectus* trees that were 6 and 7.5 m tall with dbh's of 24.0 to 25.5 cm. For the DMCV, there was a relatively large *A. germinans* standing on its own with little vegetation nearby. The tallest tree at DMCV was 7.5 m with a dbh of 30.9 cm. ESC had a well developed and established mangrove forest. It was impossible to know the biggest mangrove tree within this site, but a couple of trees that were measured outside of the plots for comparison had heights > 19 m and dbh > 60 cm for both *L. racemosa* and *R. mangle.*

Doyle et al. (2002) reported similar findings in forest structure from the Dry Tortugas National Park in the USA. The published literature of the Dry Tortugas describes strikingly similar conditions to my study sites at Turneffe. The Dry Tortugas has not been affected by hurricanes since the mid-1960's; the relative calm has fostered mangrove colonization (Doyle et al. 2002). Additionally, the literature describes the conditions in which mangroves thrive in that particular island. Doyle et al. (2002) described the robust mangrove stands as anomalies because of the nature in which they thrive, i.e., mangroves growing on coral islands without organic matter. Furthermore, the presence of birds and the input of bird guano were also an important aspect of the Dry Tortugas mangrove stands. Doyle et al. (2002) reported values of 14 cm dbh and 7.5 m high for the largest canopy trees with an approximate age of 25 yrs, which are similar to the maximum values for SC and BCC.

The even agedness of many Caribbean mangrove stands as well as their small stature has been attributed to the effects of hurricanes. Typical maximum heights reported for mangroves in the Caribbean region range of 10 to 20 m (Wadsworth and Englerth 1959). However, estuarine forests are usually taller. Forest regeneration by few seeds or propagules could possibly give rise to uneven-aged stands. As observed at Turneffe (e.g. SC and BCC), older and taller trees were frequently surrounded by younger trees that were growing in the direction away from the parent plant. This could occur when an entire stand has been completely removed from the surrounding area, such as occurred at SC and BC following Hurricane Hattie. Both sites lost all its sparse mature mangrove trees and available seedlings during the storm. The *R. mangle* forest at DMCV resembled a typical even-aged stand that develops during regeneration (Roth 1992).

4.3 Aboveground biomass and basal area

The aboveground biomass of the Turneffe sites (SC, BCC, and DMCV); was within the ranges of 1 kg · m^{-2} to 27 kg · m^{-2} for the average values reported by CARICOMP (2002). ESC was well above these reported values with 32 kg · m^{-2}, whilst DMCV was at the lower level with 5.4 kg · m^{-2}. The combined total aboveground biomass of the three Turneffe sites was still lower than the ESC value. From the nine selected sites, only Barbados (GHSB) paralleled the ESC values. Values reported by Twilley et al. (1992), which included data from Asia, the Caribbean, and Florida, range from 9 – 29 kg · m^{-2}. Lugo and Snedaker (1974) reported values for Florida fringing mangroves in the range of 8.6 to 15.3 kg · m^{-2}, which was close to the values measured for SC and BCC. Again, DMCV was below this range. However, values from ESC were low when compared to the highest estimates of aboveground biomass of *Rhizophora*-dominated stands in Asia and the Pacific, which are 50 to 70 kg · m^{-2} (Clough 1992). When comparing global values, I found highly variable estimates of aboveground biomass. Saenger and Snedaker (1993) compiled biomass estimates from 43 comparable sites. There results showed a wide range of aboveground biomass estimates from as low as 7.9 to 436.4 t · ha^{-1}. This range places the Turneffe sites (SC, BCC, and DMCV) right at the lower quartile of this range (7.9 to 115.7 t · ha). However, ESC was well within the upper third quartile of this range (223.5 to 331.3 t · ha).

The mean values for the Turneffe sites were not significantly different. However, graphical representation of these sites showed that both SC and BCC share similarities in their structural parameters (Fig. 3.5). These observations suggest that it was necessary to know all the structural characteristics of a stand in order to make sound comparisons for their biomasses. Comparisons of the nine selected sites from CARICOMP (2002) reflect similar findings, and the Turneffe sites (SC, BCC and DMCV) were within reported ranges for both biomass and basal area. ESC and GHSB (Barbados) were exceptions and were significantly different from the remaining sites. It is important to note the existence of a time difference of 4 to 8 years when the CARICOMP values were obtained.

The basal area seemed to be an adequate parameter to use when comparing stands, and was easily computed from dbh measurements of individual trees. Generally, developed stands were characterized by tall canopies, high basal areas, and lower stem densities. These values become relative when speaking about the Caribbean region, which is affected by periodic hurricanes. It is possible that higher latitudes within the CARICOMP sites could be responsible for lower biomasses. In the wider region, Woodroffe (1982) suggested that higher latitudes were the cause of lower biomass stands. However, data are insufficient from the CARICOMP network to draw a firm conclusion. Within the Caribbean climatic region, such parameters as rainfall could also influence stand development. In the case of Belize, the northern part of the country receives less rainfall than the southern part. Furthermore, localized parameters such as soil salinity play an important role in determining the structural complexity of a given stand (Smith and Snedaker 1995). In Belize, it is also widely known from experimental studies at Twin Cays that primary production and forest development are nutrient limited (Feller et al. 2003). Development of a stand does not necessarily progresses with an increase in basal area or biomass because death of individual trees can drastically lower value even in the absence of major disturbances such as storms. The latter was observed at CCB which had basal area values of 30.43 $m^2 \cdot ha^{-1}$ during the 1996 survey, six years later the survey shows a decrease to 25.25 $m^2 \cdot ha^{-1}$ (E. Garcia, unpublished data). A total of 11 trees in the plots had died during the 6-yr period. The cause of death was not determined. In Clough (1992), Putz and Chan discuss long-term changes of forest structure in Malaysia. They reported wide fluctuations in aboveground biomass during 31 years, owing to the death of older trees and replacement by new trees. Like other forests mangrove forests undergo self-thinning, a process that involves density-dependent mortality of plants that are actively growing in crowded conditions in an even-aged stand (Weller 1987). In the case of CCB a plausible explanation could be disease. It is also known from Twin Cays, Belize, that wood-boring insects are responsible for most of the tree and branch death in the mangrove forest (Feller 2002). At Turneffe, SC, BCC and DMCV with a much higher tree density may be going through a process of self-thinning.

Roth (1997) conducted a study in Southern Lagoon, Belize, 30 years (353 months) after Hurricane Hattie struck the coast of Belize. Her findings show that a mixed fringe mangrove stand in the Southern Lagoon area had attained maximum heights of 17 m, average dbh of 7.4 cm, density values of 8280 trees/ha and basal area of 43.9 $m^2 \cdot ha^{-1}$. These values reflect some interesting results even though we do not know to what extent the Southern Lagoon area was destroyed by the storm. The maximum tree height reported by Roth (1997) was similar to the ESC site, but the average dbh at ESC is almost twice the value that she reported. The tree density value from Southern Lagoon was similar to the calculated value for BCC, but was much higher than the ESC tree density. Roth (1997) reported higher basal area values than the estimated values obtained for the Turneffe sites (SC, BCC, and DMCV) but lower than the values for ESC. It is possible that the Southern Lagoon site falls between BCC and ESC which showed the highest structural complexity of the sites under investigation. However, it is important to note that there was a time difference of 12 years since Roth's estimates when compared to the present study.

For the mangrove species in the Caribbean, failure to recover following a hurricane depends in part on species characteristics (Wadsworth and Englerth 1959), topographic situation (Craighead and Gilbert 1962) and proximity to the hurricane track (Stoddart 1963). Because mangrove forests are floristically simple compared with other forest types, many ecologists believe that complete recovery is almost assured. Records exist whereby mangrove forests, such as in Florida, have been completely devastated and the forests have appeared to grow back (Smith et. al. 1994). There is evidence, however, that mangroves do not always return to their former state following catastrophic disturbance. For Florida Craighead (1971) discussed a situation whereby an *A. germinans* forest was replaced by a *R. mangle* forest following the Labor Day storm of 1935. Species attributes and availability of propagules undoubtly interact with factors such as severity of storm and type of substrate in producing post hurricane regeneration patterns (Cintrón et. al. 1978).

Timing of observations is also very important to explain recovery patterns. Poorly refoliated individuals may die or continue sprouting while well refoliated trees may later succumb (Roth 1992). There are two sides of the story when it comes to the recovery or eventual death of mangroves especially *R. mangle*. Research has showed that hurricane related mortality can continue for months (Smith et. al. 1994), and even years (Craighead and Gilbert 1962; Dittus 1985). On the other hand, defoliation and subsequent refoliation have also been documented (Sherman et al. 2001). In fact, it is possible that defoliation could be an adaptation to reduce wind resistance and decrease stem breakage during hurricanes. If leaves of a mangrove are easily shed, wind throw and breakage may be less likely to happen. *Rhizophora mangle* has proven in some cases the most resistant to wind damage (Wadsworth and Englerth 1959), but its older branches are incapable of sprouting once broken, which could have happened at DMCV. The key to *R. mangle*'s survival during a storm might be the reduction of wind stress by defoliation to prevent heavy crown damage. *Rhizophora mangle's* inability to coppice and limited ability to resprout is obvious on the northwestern side of the Turneffe Atoll where Hurricane Keith caused severe damage in 2000 (personal observation). In the case of DMCV, the defoliated mangroves reported by Stoddart (1963) may have eventually died or else the stand would have had similar or higher structural complexity than SC and BCC.

4.4 Litter fall

It was most convenient to discuss mangrove productivity in terms of litter fall because of the dearth of literature available on this aspect of production. Litter fall rates vary with latitude (Saenger and Snedaker 1993), season (Williams et al. 1981), species (Slim et al. 1996), structural morphology of the forest (Woodroffe 1982), and sediment nutrient availability (Saenger and Snedaker 1993). The first measurements of litter fall in mangrove swamps were made by E.J. Heald and W.E. Odum in the North River estuary in south Florida in 1966-69 (Odum et al. 1985). The estimates produced for the riverine litter fall for *R. mangle* averaged 876 g · $m^{-2}yr^{-1}$. Subsequent studies show similar values although variations exist between different types of communities. Pool et al. (1975) found an average rate of about 2.7 g · $m^{-2}day^{-1}$ in the Caribbean and Florida, while Bunt (1982) reported an average of 2.3 g · $m^{-2}day^{-1}$ in Australia. High litter fall values have been obtained from fringing, overwash and reverine forests compared to basin (Lugo et al. 1988). Lugo et al. (1988) reported 250 – 970 g · $m^{-2}yr^{-1}$ for fringing forests. The most extensive study that has been conducted in the vicinity of Belize, is a 7-yr record of litter fall for a southeastern Mexican mangrove in the Gulf of Mexico state of Campeche (Day et al. 1996). The average litter fall rates obtained from this mixed mangrove fringing forest ranged from 1.09 (norte season – November to February) to 2.91 g · $m^{-2}day^{-1}$ (dry season – mid February to early June). The values obtained from the exptrapolation for the three sites at Turneffe show that SC and BCC fall within the upper range, while DMCV falls in the lower range of these values. Data reported from five CARICOMP sites that have data for a complete year show ranges from 500 to 2100 g dry matter · $m^{-2}yr^{-1}$ (CARICOMP 1997). The values obtained from SC, BCC, and DMCV fall within the lower range of the reported values for the CARICOMP sites as well. Similar to biomass estimates, litter fall also has a high variation globally. Saenger and Snedaker (1993) compiled litter fall estimates from 91 comparable sites. The values ranged from as low as 1.30 t · $ha^{-1}yr^{-1}$ in *R. mangle* stands in the USA to values as high as 16.31 t · $ha^{-1}yr^{-1}$ in *R. mangle* forests, also in the USA. These global estimates reported from the literature places the estimated values calculated for the Turneffe sites at the second quartile of this range 5.05 to 8.80 t · $ha^{-1}yr^{-1}$ for SC and DMCV whilst BCC falls within the third quartile of this range (8.80 to 12.55 t·$ha^{-1}yr^{-1}$).

The CARICOMP sites showed that during the winter, which translates to the "northerns" in Belize, produced the lowest values for litter fall. The maximum litter fall values recorded for Belize occur from August to October (Holtermann and Garcia 1998). Based on these data the 5-mo sampling period (October to February) for the Turneffe sites fell at the end of the highest litter fall period. The highest litter fall values could have been missed which could have occurred in August or September as well as the lowest values April or May. At Twin Cays, this pattern of high and low litter fall is consistent from year to year (I. Feller, unpublished data).

The proportion of leaves in total litter fall ranges between 60 and 90% (Pool et al. 1975; Bunt 1982). For all three Turneffe sites (SC, BCC and DMCV) the litter fall values accounted for the majority of the litter fall 63.9, 80.4 and 81.4% respectively. Because *R. mangle* is the dominant tree in the fringing forest, the majority of the leaf litter was from these species. Leaf fall occurs throughout the year but peaks are coincident with the rainy season, low temperature and extensive drought (Pool et al. 1975 and Lugo and Snedaker 1975). The rainfall pattern obtained from CCB which is the CARICOMP site in Turneffe, (1996-1997 data) clearly showed that mean rainfall peaks in October and November. These dates coincide with the peaks in litter fall obtained during the 5-mo sampling period. These values also conform to the previous finding from Holtermann and Garcia (1998). From these findings it can be assumed that peak litter fall for Belize is from August to October. From the outcome of these findings it can be assumed that the values obtained from the extrapolation of the litter fall data, should be a good estimation of the real values for the three sites at Turneffe because peak and low values were represented within the 5-mo sampling periods. Soil salinity and pH which were measured at the ending of each month during litter collections from SC, BCC, and DMCV and from a 4-day sampling period for ESC, also conformed to the values reported for other mangrove forests (Odum et al. 1985; Bava and Seralathan 1999; Kathiresan 2002;).

An important category identified within the litter fall for two sites in Turneffe (SC and BCC) was the input of bird guano. Bird guano was significantly high especially for the initial months during the sampling period (October and November) with a steep decrease during the following months. Bird guano input in mangrove stands has been described in the literature and could be a positive or negative influence on mangrove stands depending on the hydrologic properties of the system. Doyle et al. (2002) in his description of the Dry Tortugas, Florida, attributed the dieback of mangroves to beach erosion and excessive input of bird guano that lead to chlorotic stands. However, within the same island, bird guano provided fertile growing conditions for mangroves and has been correlated to an increased in internode elongation patterns within the mangrove nesting site of frigate birds (Doyle et al. 2002). Feller and Mathis (1997) described the effects of bird guano on a Belizean cay (Man-of-War cay, Southern Belize), to result in higher mangrove productivity and growth rates in comparison to nearby islands that supported no rookeries. Additionally, the insect fauna was more species-rich than on much larger nearby islands (Feller and Mathis 1997). Similar findings were reported by Onuf et al. (1977) whereby the most significant effect was in the amount of insect herbivory to the leaves of the plants.

Both SC and BCC, which are influenced by bird guano showed higher structural complexities compared to DMCV. The question that arises from these observations: when did birds start to use these cays for rookeries? Mangroves may need to achieve a certain stand development in order to sustain rookeries. On SC and BCC birds using the mangrove forest, included the Great-tailed Grackle (*Quiscalus mexicanus*), White Crowned Pigeon (*Columba leucocephala*) and the Brown Pelican (*Pelecanus occidentalis*). In particular the Great-tailed Grackle was responsible for high guano input in October, which coincided with fruiting by Sea Grape (*Coccoloba uvifera*) and Gumbo Limbo (*Bursera simaruba*). They used SC and BCC in great numbers in October, but there numbers drastically decreased with the end of the fruiting season for seagrape and gumbo limbo. Individual Brown Pelican were seen on several occasions feeding around SC and BCC and perching in mangrove trees. It is likely that the Great-tailed Grackle will continue to contribute significantly to the input of guano in both SC and BCC since these birds are also known to nest and feed around human habitation such as exists in these areas. In contrast, DMCV does not have human habitation close by. In addition, the bigger islands on its western side do not support a similar coastal forest and suitable fruit trees for the grackles.

4.5 Leaf nutrient analysis

Sites were tested and compared for RE_P and NUE_P. Resorption is one of the most important of all strategies employed by plants to conserve nutrients and consequently influences processes as varied as competition, nutrient uptake and productivity (Killingbeck 1996). Nutrient resorption from senescing leaves enables plants to conserve and reuse nutrients. As such, it could be expected that plants in infertile soils have a higher nutrient resorption efficiency (percentage reduction of nutrients between green and senesced leaves) and/or higher nutrient resorption proficiency (absolute reduction of nutrients in senesced leaves) than those growing in fertile soils (Distel et al. 2003).

The main purpose for measuring RE_P and NUE_P was to find differences among sites. ESC is <10 km from the mainland coast and potentially more under the influence of nutrient-rich sediments from fluvial discharge than SC, BCC and DMCV, which are oceanic >50 km offshore, and receives no terrigeneous inputs of sediment. Increased nutrient availability to ESC could impact its biomass apart from differences in its disturbance history. Fertilization experiments have shown that increase resource availability caused a decline in nutrient use efficiency (Shaver and Melillo 1984; Feller 1995, 1996,). Feller et al. (1999), showed that increased nutrient availability in mangrove ecosystems caused decrease in nutrient conservation at the individual, and ultimately at the ecosystem level. Kost and Boerner (1985) found that resorption efficiency in mangrove forests decreased along a natural gradient of increasing soil fertility and similar results have been found for other ecosystems (Shaver and Melillo 1984; Vitousek 1984). If sediment runoff from the mainland was higher in the vicinity of ESC, it might be possible to detect it from the RE_P and NUE_P values. RE_P and NUE_P values from ESC were not significantly different from SC, BCC and DMCV.

The results from ESC show no significant differences and the values obtained closely resemble the ones obtained for the sites at Turneffe (SC). In fact ESC had the highest mean value for RE_P followed by SC.

These findings, however, do not prove that soil fertility was uniform among all sites but merely sheds some light into the dynamic of this system. According to the literature phosphorus (P) concentrations in mangrove leaves varied with species (Sah et al. 1989; Feller et al. 1999), position to the forest relative to tidal inundation (Wong et al. 1995) and sediment nutrient status (Boto and Wellington 1983; Feller 1995; Feller et al. 2003,). Feller et al. (2003) showed that nitrogen (N) and P were not uniformly distributed within mangrove ecosystems and that soil fertility can switch from N to P limitation across a narrow tree-height gradient. Studies on biomass and soil have shown that in the wet tropical lowland forests, P deficiency was the major nutrient limiting plant growth (Vitousek 1984, Medina et al. 1995). Furthermore, the high carbonate environment typical of these offshore cays, $CaCO_3$ causes phosphate to precipitate out of the water further reducing the available P (Littler and Littler 1990).

The existence of coral patches around ESC supports the conclusion it might not be affected by fluvial discharge. ESC is located within the mid lagoon cays and is surrounded by fringing coral reefs that have the characteristic features of both inshore coastal and offshore barrier reef environments (Stoddart et al. 1982). In Heyman and Kjerfve (2001), A. Harborn observed the presence of 45 species and subspecies of hard corals within the Snake Cays including *Montastrea annularis* and *Diplora strigosa.* These species do not tolerate low salinity and high sediment of inshore environments (Heyman and Kjerfve 2001). Further studies are needed to determine if fluvial discharge has any effects on mangrove productivity at ESC.

4.6 Conclusions regarding the established hypotheses

In chapter 1, the established hypothesis "The mode of recovery is a function of the severity of the disturbance, the type of forest stand, prior to the impact, and extent of the area affected" was rejected. Patterns of recovery after hurricane damage are complex, and highly intertwined with factors of macro- and micro-topography, soil physicochemical parameters (e.g., salinity and nutrients). In addition, external factors to the system (e.g., input of bird guano, soil erosion and accretion) can have significant influences during recovery.

The second hypothesis which states "Mangrove forest biomass after a major hurricane, is still after 40 years, significantly lower than a relatively undisturbed mangrove forest" was accepted. There is a significant difference, in aboveground biomass between ESC (a relatively undisturbed mangrove forest) and the Turneffe sites (SC, BCC, and DMCV). The aboveground biomass estimates showed that ESC has three times more than the highest estimated biomass at Turneffe, which were obtained from BCC.

4.7 Methodological constraints and suggestions for improvements

During the course of the study, I am aware of certain constraints that need to be mentioned because of the extent of influence it had on the results presented could not be quantified.

For the georeferencing section, a hand-held GPS was used to log the coordinates of the sites. Coordinates were in the Universal Transverse Mercator (UTM) format. The GPS logged these coordinates and averaged each entry between 3 to 4 m accuracy. In principle, the accuracy of the GIS-data depends on the scale used and the same principle applies for TIFF-data (D. Kraft, per. comm.). Values reported for vegetation coverage and changes in island dimensions are only estimates. These estimates, however, were crosschecked with independent measurements that were made with other conventional methods. For example, I used a measuring tape to measure length and width of randomly selected vegetation stands (e.g., width of fringing *R. mangle*) and for the entire cays to get a rough estimate of the dimensions. Measurements obtained from historical maps depended on the accuracy of the maps and scale. However, the reported values given by Stoddart (1962, 1963, 1982) were also within close range of my estimates after his maps were scanned and digitized. Aerial photographs are powerful tools that can be used for documenting patterns of recovery. I know of the availability of historical aerial photographs (black and white) for SC, BCC, and DMCV, which can be requested through the Lands Department Office, Belmopan Belize. However, it was too late for me to have access to these resources when I learnt about it. The lack of aerial photograph from ESC at the time of the study prevented detailed comparison between the Turneffe sites and ESC in terms of vegetation coverage. I would suggest that an aerial photograph of ESC in the near future would be a good way to document the present status of this highly productive island.

The CARICOMP methodology was adapted for this study. This methodology of establishing permanent plots gives the advantage for future monitoring and obtaining detailed information. Even in the event of a hurricane disturbance, the location of plots can be found easily once the plot corners are properly marked. This method allows for comparisons within the Caribbean region where it is widely used. The method, however, is energy and time consuming, which is one of the reasons I believe many of the CARICOMP designated sites are inactive at the moment. Thus, little recent, comparable data are available. The data used for comparison in this study varied from as late as 1993 and as recently as 2002. From the available data posted on the CARICOMP web site, it is possible to note that some sites have incomplete yearly data for biomass and or litter fall.

Litter fall estimates for the Turneffe study sites are only available for five months, and it was not possible to collect them for ESC. It would be interesting to get the remaining litter fall values for the year in order to verify the seasonal tendencies for low and peak values as well as seed production periods of the Turneffe sites. For ESC, litter fall collections for the entire year to calculate productivity values for this system and determine how it compares to systems that have been affected by a catastrophic hurricane. Coincidental with litter fall collection, physical-chemical parameters such as soil salinity and pH should be measured along with meteorological data from the sites.

Soil fertility is a very important factor that plays a significant role in productivity of mangrove systems. Leaf nutrient analyses were conducted at one time for all sites and provided only an index of nutrient availability. It would be interesting to do leaf nutrient analysis of the sites during the time when these sites are receiving bird guano (SC and BCC). Direct soil nutrient analysis for all sites is also recommended for making sound comparisons between these systems. In addition, fertilization experiments across the disturbance gradient would be necessary to determine patterns of nutrient limitation.

4.8 Summary of key findings

- The vegetation of the Turneffe sites (SC, BCC, and DMCV) was dominated by *R. mangle.* However, the other two most common New World species, *L. racemosa* and *A. germinans*, and the mangrove associate, *C. erectus*, were found in all sites, including ESC.
- Most of the cays at Turneffe Atoll have not only recovered the area lost to erosion during Hurricane Hattie but have also increased in size. Of my three sites at Turneffe, only BCC was lower by 0.05 ha than its pre-hurricane dimension. In southern Belize where the effects of Hurricane Hattie were

minimal, ESC has decreased in size since 1961 with an estimated loss of 0.71 ha due to erosion. That erosion was unrelated to Hurricane Hattie damage.

- At the Turneffe sites, aboveground biomass estimates fell within the range of values reported by CARICOMP (2002); ESC's aboveground biomass estimate was higher than the values reported by CARICOMP. Basal areas from the sites produced similar results.

- Extrapolated litter fall data for SC and BCC was within the upper range of values reported for the CARICOMP region whilst DMCV fell within the lower range.

- Bird guano input, which seems to be seasonal, could be an important indirect factor for the recovery and ecosystem dynamics of SC and BCC. For the SC site, an average input of 6.6 $g \cdot m^{-2}day^{-1}$ of bird guano was estimated for October, which coincided with the end of the fruiting season observed on certain cay forest from the larger neighboring islands. Increased nutrients in guano may have enhanced mangrove growth and led to the increase in island size.

- Rookeries and the input of bird guano may have also affected recovery patterns of mangrove community structure. Specifically, cays with rookeries showed an increase in the occurrence of insects within the litter fall.

- Results from RE_P and NUE_P showed that the ESC plots are not significantly different from the plots of the Turneffe study sites. These data suggest that the differences in mangrove forest structure between the sites at Turneffe and ESC were not due to difference in soil fertility.

4.9 Conclusion

Hurricanes are among the most important factors determining the structure of ecosystems in the Caribbean (Waide 1991). Although they are a frequent and natural form of major disturbance, large hurricanes capable of causing catastrophic damage are less frequent. These rare, intense disturbances are thought to play a major role in the organization of Caribbean mangrove ecosystems (Lugo et al. 1976). However, prior to the present investigation, no studies had been conducted on the long-term effects of major hurricanes on vegetation coverage, biomass, and productivity.

High aboveground biomass is often a characteristic of undisturbed old-growth fringing and basin mangrove forests in the tropics. With disturbance and less favorable conditions, aboveground biomass is expected to be less than potential maximum. From this study, it is clear that we need a better understanding of the basic ecological factors affecting biomass and productivity, i.e. salinity, nutrients and climatic factors. The physical and chemical properties of the substrate and soil water can dramatically affect biomass and productivity in mangroves (Feller 1995). Thus, it is important to know the effects of salinity, tidal flushing, nutrients, temperature, rainfall and other variables on primary production and turnover rates for extended periods (at least one year). However, the interactions among disturbance, the hydrodynamics of mangrove ecosystems, climatic conditions, and soil factors on the one hand, and forest structure, growth, and productivity on the other, are complex. Thus, it is extremely difficult to identify the factors influencing the accumulation of biomass and rates of litter fall at any given site and determining how these factors are altered by the disturbance history of the site. Mangroves frequently show high within-region diversity of structural patterns and an equally high diversity of functional roles (Lugo and Snedaker 1974; Pool et al. 1977). To unravel these complex interactions, comparable long-term studies are needed at sites of known disturbance histories.

Hurricanes are just one of several types of disturbances in mangrove systems. Repeated measurements at relatively infrequent intervals are thus desirable for assessing the true impact of the hurricane on the structure and composition of an ecosystem. It remains unclear 1) how predictable damage and recovery are, 3) how successional trajectories are modified, and 3) whether and at what rate species composition, and nutrient cycles return to pre-hurricane conditions. The vast array of tightly intertwined parameters and much variation even within the same area complicate the predictability of recovery within mangrove systems. Only long-term observations coupled with well developed experimental studies will clarify certain tendencies, such as rates of litter fall and biomass accumulation in highly disturbed systems. Comparative, multidisciplinary studies using a series of permanent plots are needed to quantify the long-term effects of hurricanes on many ecological processes. For example, biomass and litter fall could be explained at the local or regional level if similar methodologies are used, thus, similar methodologies should be incorporated whenever possible for comparative reasons. These permanent plots would also provide the basis for studying and comparing susceptibility to and recovery from future hurricanes.

The coexistence of hurricanes, coral reefs, and mangroves in the Caribbean demonstrates that highly structured ecosystems with great diversity can flourish in spite of recurring exposure to intense destructive energy (Lugo et al. 2000). By understanding responses at the ecosystem level from hurricane disturbance, we would be in a better position to predict the damage and recovery from human-induced disturbances. While resistance and recovery have maintained these systems over the past, human impacts threaten their ability to survive. Hopefully findings from this paper will encourage future studies to complete the gaps within the same line of study.

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