

**LONG-TERM CHANGES IN MANGROVE FORESTS AND CAYS FOLLOWING
HURRICANES AT TURNEFFE ISLANDS, BELIZE**

by

Faustino Chi

M.Sc. (Aquatic Tropical Ecology)
The University of Bremen, 2003

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

(Forestry)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

June 2012

© Faustino Chi, 2012

Abstract

Fringing cays develop on the back-reef sediment apron in exposed reef environments. Long-term datasets that document disturbance and long-term recovery are rare. In this study, patterns of disturbance and recovery of the fringing cays on Turneffe Islands, Belize were examined focusing on the interaction between cay geomorphology and vegetation, and the role of mangroves. Historic aerial photos and field observations taken before and after catastrophic Hurricane Hattie in 1961 were combined with contemporary imagery and permanent and temporary plot data.

Some cays were devegetated during Hurricane Hattie and subsequently revegetated. However, there was a 26% loss of vegetated cays between 1945 and 2008. Devegetated cays have revegetated in the same general location, but have shifted an average of 18 m away from the reef toward the west-northwest. Cay vegetation has changed from dominance of *Cocos nucifera* L. before Hurricane Hattie to mangrove forest dominated by *Rhizophora mangle* L. However, much of the vegetated area in 2008 was inundated by tides.

Remeasurements of permanent sample plots indicated that there was significant increase in mangrove biomass on two of the three sampled cays between 2002 and 2008. Leaf litter was the dominant fraction in the litter fall with a mean residence time of 2.5 months.

Factors that played an important role on the distribution of vegetation on the fringing cays included: exposure to wave energy, tidal inundation, substrate elevation and distance to the

reef. I identified three distinct geomorphic-habitat zones on the fringing cays: sheltered leeward, ridge, and exposed reefward, each had distinctive substrates and plant communities. *Rhizophora mangle* dominated the leeward zone and has a competitor-stress tolerator plant strategy. It was also the most abundant species in the reefward zone, but typically did not reach large sizes.

In the absence of permanent human settlements, the vegetation on fringing cays has the capacity to recolonize in the same general location following a hurricane. Once vegetation was established on or adjacent to reforming fringing cays, these plants promoted further sediment accumulation and stabilization, indicating a self-reinforcing system. Given the exposure of these cays to recurrent hurricane damage, development of these cays seems unwise.

Table of Contents

Abstract.....	ii
Table of Contents	iv
List of Tables	xi
List of Figures.....	xvi
Glossary of Terms	xxvii
Acknowledgements	xxix
Dedication	xxxi
Chapter 1: Introduction	1
1.1 Focus and objectives	3
1.2 Approach to the problem and outcome	4
Chapter 2: Literature review	6
2.1 Disturbance	6
2.2 Wind, waves and tides	8
2.3 Hurricanes and tropical storms	10
2.4 Islands and cays	12
2.5 Mangrove forests	15
2.5.1 Economic importance of mangrove forests	18
2.5.2 Mangrove forest and shoreline protection	19
2.5.3 Mangrove forests as shelter and nursery grounds.....	22
2.5.4 Mangrove forests and sea level rise	23
2.5.5 Mangroves and hurricanes	26

2.5.6	Mangrove biomass, litter and bird guano	28
2.6	Turneffe geomorphology	30
2.7	Turneffe biodiversity	34
2.8	Turneffe and human settlement	37
2.9	Landfall of Hurricane Hattie of 1961 on Turneffe.....	42
2.10	Knowledge gaps and research questions.....	43
Chapter 3: Fringing cay dynamics and the impacts of hurricanes and humans		45
3.1	Introduction.....	45
3.1.1	Wind, waves, tides and coral reefs.....	45
3.1.2	Human activity, storms and cay vegetation on Turneffe	51
3.1.3	Landscape change, remote sensing and GIS.....	54
3.1.4	Study objectives and research questions.....	55
3.2	Data and methods.....	56
3.2.1	Study area.....	56
3.2.2	Satellite imagery and aerial photographs	59
3.2.2.1	Satellite imagery	59
3.2.2.2	Vertical aerial photographs.....	61
3.2.2.3	Oblique aerial photographs.....	65
3.2.3	Image analysis and ground truthing.....	67
3.2.3.1	Vegetation and cay map preparation – 2006 photo-mosaic.....	67
3.2.3.2	Vegetation and cay map preparation – comparison of 1945 and 2006 photo-mosaic.....	68
3.2.3.3	Location and orientation of fringing cay vegetation.....	70

3.2.4	Wind and tide from Carrie Bow Cay and Main Calabash Cay.....	72
3.2.5	Fringing cay vegetation under the influence of tides.....	75
3.2.6	Landfall of hurricanes and tropical storms on Belize’s coastline and Turneffe.....	76
3.2.7	Analysis of the effects of wind and hurricanes on cay shift	78
3.2.8	Effects of Hurricane Hattie on cay frequency, vegetation area and type.....	78
3.2.9	Short term effects of hurricanes – direct and indirect.....	80
3.3	Results.....	81
3.3.1.1	Cay frequency and size	81
3.3.1.2	Cay vegetation cover and type.....	81
3.3.1.3	Ground-truthing cay vegetation	83
3.3.2	Comparison of historic and contemporary remotely sensed data	84
3.3.2.1	Cay frequency and size in 1945.....	84
3.3.2.2	Location and orientation of cays: 1945 vs. 2006	84
3.3.2.3	Cay vegetation: 1945 vs. 2006.....	90
3.3.3	Causes of change to cays	93
3.3.3.1	Wind and tides	93
3.3.4	Hurricanes.....	97
3.3.5	Fringing cay shift in relation to storm track and mean wind direction.....	101
3.3.6	Effects of hurricanes on vegetation change	102
3.3.6.1	Case study 1: Direct effects of Hurricane Hattie (1961).....	102
3.3.6.2	Case study 2: Direct effects of Hurricane Keith (2000)	105
3.3.6.3	Case study 3: Indirect effects of Hurricane Ivan (2004).....	109

3.3.7	Human impacts	111
3.4	Discussion	115
3.4.1	Variability in number of fringing cays, vegetated area and size.....	115
3.4.2	Vegetation change from cocal to mangrove	118
3.4.3	Effects of waves and tides on vegetation above and below the spring high tide.....	123
3.4.4	Orientation of cay vegetation relative to reef crest.....	124
3.4.5	Land-falling hurricanes on Turneffe.....	126
3.4.6	Recovery and location of cay vegetation after storm damage	128
3.4.7	Some implications for the sale and development of fringing cays	132
3.5	Conclusion	134
Chapter 4: Stand-level growth in fringing mangrove		136
4.1	Introduction.....	136
4.1.1	Forest biomass	136
4.1.2	Forest litter	138
4.1.3	Nutrients in coastal areas	140
4.1.4	Rationale	141
4.2	Methods and data available.....	142
4.2.1	Approach.....	142
4.2.2	Plot set up.....	143
4.2.3	Field measurements	146
4.2.4	Above-ground litter and ground litter	148
4.2.5	Plots remeasurements.....	149

4.2.6	Sample and data processing and analysis	150
4.2.6.1	Stand-level measurements	150
4.2.6.2	Above-ground biomass	151
4.2.6.3	Above-ground litter and ground litter	152
4.2.7	Weather data	153
4.2.8	Statistical analysis	153
4.3	Results	154
4.4	Discussion	167
4.4.1	Mangrove above-ground biomass	167
4.4.2	Mangrove litter	172
4.5	Conclusion	177
Chapter 5: Spatial patterns in cay substrate and vegetation		179
5.1	Introduction	179
5.2	Methods	184
5.2.1	Selection of study sites	184
5.2.2	Image and map preparation	186
5.2.3	Identification of strata, transect layout and field plots	186
5.2.4	Field and plot level measurements	187
5.2.5	Data analysis	192
5.3	Results	194
5.1	Discussion	214
5.1.1	Ridge zone	216
5.1.2	Leeward zone	221

5.1.3	Reefward zone	223
5.1.4	Vegetation strategies	226
5.2	Conclusion	235
Chapter 6: Conclusion.....		237
6.1	Summary of principal findings and implications.....	238
6.1.1	Fringing cay dynamics and the impacts of hurricanes and humans (Chapter 3).....	238
6.1.2	Stand-level growth in fringing mangrove (Chapter 4).....	239
6.1.3	Spatial patterns in cay substrate and vegetation (Chapter 5)	239
6.1.4	Implications.....	240
6.2	Recommendations and future research	245
6.3	Concluding remarks on mangrove conservation.....	248
References.....		251
Appendices.....		300
	Appendix A. Fringing cay vegetated area for 2006.....	300
	Appendix B. Vegetated area of fringing cays before and after Hurricane Hattie.....	301
	Appendix C. Fringing cay coordinates from 1945 and 2006 photo-mosaic.....	303
	Appendix D. Fringing cay area above and below spring high tide.....	304
	Appendix E. List of hurricanes and tropical storms.....	306
	Appendix F. Aerial photographs of before and after Hurricane Hattie 1961.....	308
	Appendix G. List of fringing cays from eastern Turneffe.....	309
	Appendix H. Presence and absence of coconut palms relative to 1960 and 1961 cay area.	312

Appendix I. Presence and absence of coconut palms relative to 2006 cay area.	314
Appendix J. Fringing cay area damaged from Hurricane Keith 2000.	316
Appendix K. Permanent plot summary 2002.	317
Appendix L. Permanent plot summary 2008.	318
Appendix M. Fringing cays from eastern Turneffe.	319
Appendix N. Adapting the water-level method to measure substrate elevation.	320
Appendix O. Relationship between distance from the edge of reef crest, elevation, plot average stem diameter and plot average height of <i>Rhizophora mangle</i>	323
Appendix P. List of mangrove species from Proserpine, Australia and Turneffe, Belize.	324

List of Tables

Table 3.1. Summary of historical vertical aerial photographs taken by the Royal Air Force (RAF) and the US Air Force (USAF) of the eastern coast of Turneffe. Partial and no coverage means that in those cases the photos were not taken or could not be obtained or found.....	63
Table 3.2. List of aerial surveys conducted in collaboration with LightHawk, USA and Feller (Smithsonian Institution, USA). Oblique aerial photographs were taken of the eastern and western sides of Turneffe with focus on the fringing cays of the eastern side.....	66
Table 3.3. Net changes in number of eastern fringing cays on Turneffe since 1945.....	90
Table 3.4. List of vegetated cays identified from the 1945 and 2006 photo-mosaic. Each cay was given an ID number that can be used to interpret subsequent graphics.	92
Table 3.5. Cay area (vegetated and bare substrate) for group of eastern cays on Turneffe from 2008 survey.	97
Table 3.6. List of hurricanes and tropical storms with landfall on Turneffe based on center of lowest pressure. List based from NOAA database 1851 to 2008.....	100
Table 3.7. Mean angle and mean angular deviation for the directions of cay shift from a group of fringing cays on eastern Turneffe (1945 to 2006). Cay shift mean compared with hurricane and tropical storms mean directions (1851 to 2008) and 2 yr mean monthly wind direction based on readings from Carrie Bow Cay Marine Field Station (2007 to 2008). Results of Watson-Williams F-test for the two planned pair-wise comparisons.	101

Table 3.8. Group of eastern cays on Turneffe severely affected by Hurricane Hattie 1961..	102
Table 3.9. Estimated cay vegetated area in hectares for group of eastern cays on Turneffe. Cays identified from the 1945, 1961 (after Hurricane Hattie) and 2006 photo- mosaics.	104
Table 3.10. The proportion of cays with <i>Cocos nucifera</i> (Cn) as part of the vegetation before and after Hurricane Hattie (1961) and from the 2006 photo-mosaic and surveys; and the proportion of mangrove forest as a dominant vegetation type on the fringing cays.	105
Table 4.1. Summary of data collected within permanent plots between 2002 and 2008.....	149
Table 4.2. Mean percent species composition (by stems/ha) in permanent CARICOMP plots for 2002 and 2008 surveys on Soldier Cay, Big Calabash Cay and Dead Man Cay- 5; 9 plots, standard deviation in brackets.	155
Table 4.3. Plot characteristics of three Turneffe sites (Soldier Cay (SC)), Big Calabash Cay (BCC)), and Dead Man Cay-5 (DMC-5)) in 2002 and 2008. Means are from three plots.	157
Table 4.4. The results of the analysis of variance for above-ground biomass (kg/m^2) of 2002 and 2008, which were calculated using allometric equation from Cintrón and Shaeffer-Novelli (1984). Permanent plots from three sites were compared: Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5).....	158

Table 4.5. Results of pair-wise comparisons of above-ground biomass (kg/m^2). Interactions of Time (2002 and 2008) and Sites (Soldier Cay (SC)), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5)).	158
Table 4.6. Estimates of leaf litter turnover coefficients (k, per yr) and residence time (yr), based on estimates of leaf litter fall rates ($\text{g/m}^2/\text{yr}$) and leaf litter standing crop (g/m^2) for three sites: Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5).	167
Table 5.1. Plot summary of eight fringing cays (all tree species) on eastern Turneffe. Cays arranged from a north to south direction.	195
Table 5.2. Cay geomorphic habitat zones and levels of stress from soil salinity and tidal inundation and of disturbance from wave energy.	208
Table 5.3. Pearson correlation among dependent and potential predictor variables, correlation coefficients involving basal area and maximum tree height (all species); r values are given above p-values; significant correlations are in bold font.	209
Table 5.4. Multiple linear regressions for maximum height for all tree species.	210
Table 5.5. Multiple linear regressions for the square root basal area for all tree species.	210
Table 5.6. Logistic regression for the presence of one or more seedlings for four mangrove species (<i>R. mangle</i> , <i>A. germinans</i> , <i>L. racemosa</i> , and <i>C. erectus</i>).	211
Table 5.7. Logistic regression for the presence of one or more seedlings of <i>R. mangle</i> .	211
Table 5.8. Data from permanent CARICOMP plots, collected in 2002, used for ordination of four mangrove species found on fringing mangrove at three cays Turneffe, Belize	

(Soldier Cay, Big Calabash Cay and Dead Man Cay-5). Comparative data from circular plots show similar trend on dominance index of four mangrove species found on eight fringing cays of Turneffe, Belize (Cockroach Cay-20, -22, and -23, Soldier Cay, Big Calabash Cay, Dead Man Cay-3, -4, and -5)..... 213

Table B.1. List of fringing cays with estimated vegetated areas in hectares calculated from georectified photo-mosaics. 1960 photos were pre-Hurricane Hattie and 1961 photos were post-Hurricane Hattie..... 301

Table C.1. Coordinates (UTM Zone 16N) of centroids of the cay vegetated polygons from the 1945 and 2006 photo-mosaic..... 303

Table D.1. Cay area relative to spring high tide. Area measured in hectares. List of cays based on 2006 photo-mosaic and from survey work in 2007-2008. 304

Table E.1. List of hurricanes and tropical storms with landfall on the mainland coast of Belize based on center of lowest pressure. List based on the NOAA database 1851 to 2008 (Atlantic Oceanographic and Meteorological Laboratory - Hurricane Research Division). 306

Table G.1. List of fringing cays and vegetation status identified from 1945, 1960 (pre-Hurricane Hattie), 1961 and 1962 (post-Hurricane Hattie), and 2008 aerial photographs and ground surveys..... 309

Table H.1. Presence and absence of *Cocos nucifera* based on 1960 and 1962 oblique aerial photographs. Cay vegetated area based on photo-mosaics from before and after Hurricane Hattie 1961. 312

Table I.1. Presence and absence of *Cocos nucifera*, dominant vegetation type based on 2006 aerial photographs and 2007 – 2008 field surveys. 314

Table J.1. Estimated damage of cay vegetation area from Hurricane Keith 2000 (survey from 2003, 2006 and 2008).....	316
Table K.1. Summary of permanent plots established in 2002 at Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5) with 3 plots per site (A, B and C).	317
Table L.1. Summary of permanent plots re-measured in 2008 at Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5) with 3 plots per site (A, B and C).	318
Table P.1. List of mangrove species from Proserpine, Australia used by Saenger (2002) to illustrate Grime's model, and list of mangrove species from Turneffe, Belize which were superimposed on Saenger's triangular ordination.	324

List of Figures

- Figure 2.1. World distribution and diversity of mangroves species. (Adapted with permission Spalding et al. 2010). 17
- Figure 2.2. Aerial roots of red mangrove (*Rhizophora mangle*) during low tide at Big Calabash Cay, Turneffe, Belize. 21
- Figure 2.3. Location of Belize City, Carrie Bow Cay, Belize Barrier Reef and three offshore atolls: Turneffe, Lighthouse Reef and Glovers Reef. Inset map shows location of Belize within Central America and the Caribbean. (Adapted with permission Gischler 2003). 31
- Figure 2.4. Schematic sketches showing Holocene development for Turneffe. (A) 8000 YBP (years before the present), sea level ca. 15 m below present level. Turneffe was an emergent limestone islands; transgression of marine water, probably through the precursors of modern tidal channels; Pleistocene patch reefs probably still emergent as small cays in lagoon; (B) 7000 YBP, sea level about 10 m below present level. Parts of Turneffe flooded and mangrove-dominated; small Pleistocene areas probably still emergent at margin and in lagoon; (C) 6000 YBP, sea level about 7 m below present level. Mangrove-dominated parts of Turneffe increase in area; (D) 5000 YBP, sea level about 5 m below present level. Large areas in the east are still emergent, but a mangrove-encircled lagoon develops with *Halimeda*-dominated sediment; (E) 4000 YBP, sea level about 3.5 m below present level. Turneffes' main lagoon largely developed; seaward tidal channels open; parts of the north still emergent; carbonate sedimentation initiated on

northernmost part, probably still surrounded by mangroves. (F) Present situation. (Adapted with permission Gischler 2003).	33
Figure 2.5. Map of Turneffe showing the eastern fringing cays. (Redrawn from McGill 1996).	35
Figure 2.6. Photo of pig feeding between Big and Little Calabash Cay. The largest piggery was at the Calabash Cays. Photo taken during Stoddart’s survey of 1960-61. (Photo credit, Stoddart).	37
Figure 2.7. Aerial photograph of Soldier Cay showing the coconut palms (<i>Cocos nucifera</i>), as the dominant vegetation. Soldier Cay was also inhabited by humans. Photo taken during Stoddart’s survey of 1960-61 before Hurricane Hattie 1961. (Photo credit, Stoddart).	38
Figure 2.8. Track of Hurricane Hattie 1961. Eye of hurricane went across Turneffe and made landfall south of Belize City. (Modified after Stoddart 1963).	43
Figure 3.1. Diagram with typical characteristics of exposed and protected coral reef zonation. Note prominent spur and groove formation on the exposed-open reef. (Adapted with permission Blanchon et al. 1997).	46
Figure 3.2. Oblique aerial photograph showing spur and groove reef formation on the ocean- facing side of Cockroach Cay-22 and -23, Turneffe Atoll.	47
Figure 3.3. Aerial view of Turneffe’s northeastern cays (Cockroach Cay group). Photo- mosaic from 2006 showing coral reef zonation and location of fringing cays within the back-reef area.	49
Figure 3.4. Map of Turneffe. Highlighted names were part of survey and shows the grouping and number of cays. (Redrawn from McGill 1996).	58

Figure 3.5. Turneffe imagery: image to the left is area coverage of entire atoll by Landsat 2004; and image to the right is the extent of coverage from the QuickBird 2005 of the eastern side of the atoll. 60

Figure 3.6. Flowchart of the general working process used for the production of maps and aerial photograph interpretation. 69

Figure 3.7. Smithsonian’s Carrie Bow Cay Marine Field Station houses an Environmental Monitoring Systems which continually monitors real time meteorological and oceanographic conditions (aerial photograph from 2006). 74

Figure 3.8. A simplified fringing cay showing vegetation and substrate area above spring high tide and vegetation and substrate area above and below spring high tide. 76

Figure 3.9. Total areas for coccol, littoral and mangrove vegetation types. Areas calculated from a group of 35 fringing cays identified on the 2006 photo-mosaic. 82

Figure 3.10. Dead Man Cay-5 (southern group cay), 2006 photo-mosaic. Yellow outline shows periphery of 1945 cay vegetation, with yellow square as cay vegetation centroid. The red outline delimits the periphery of the 2006 cay vegetation with red star as the cay vegetation centroid. Black arrow indicates the direction of shift after 61 years (approximately 43 m predominantly west with a northerly component)..... 85

Figure 3.11. Orientation and magnitude (vector) of cay vegetation polygon centroid shift (light colored lines) based from 1945 to 2006 photo-mosaic (n = 31). Distance from center of chart measured in meters. Mean resultant length = 18 m (dark colored arrow), mean angle of the sample = 302.5° (dark colored arrow), ‘r’ =

0.6406, Rayleigh test, $p < 0.0001$, angular variance = 0.72, mean angular deviation = 48.5° 86

Figure 3.12. Orientation of reef crest directly in front of 46 vegetated fringing cays on Turneffe (light colored lines). Orientation identified from the 1945 and 2006 photo-mosaic. Distance from center of chart measured in meters. Mean length of the section of the protecting reef = 311 m (dark arrow), mean angle of the sample = 34° (dark arrow)..... 87

Figure 3.13. Cockroach Cay-28, yellow outline shows periphery of 1945 cay vegetation polygon, with its longest diagonal and the red outline shows the periphery of the 2006 cay vegetation polygon with its longest diagonal. 88

Figure 3.14. Orientation of longest axis of the vegetated fringing cays from Turneffe. Longest axis derived from the vegetation polygon of the 1945 photo-mosaic. $n = 42$ (light colored lines). Distance from center of chart measured in meters. Mean length = 116 m (dark arrow), mean angle of the sample = 24° (dark arrow)..... 88

Figure 3.15. Orientation of longest axis of the vegetated fringing cays from Turneffe. Longest axis derived from the vegetation polygon of the 2006 photo-mosaic. $n = 35$ (light colored lines). Distance from center of chart measured in meters. Mean length = 120m (dark arrow), mean angle of the sample = 20° (dark arrow)..... 89

Figure 3.16. Fringing cay vegetated area class by frequency of cays identified from the 1945 photo-mosaic and frequency of cays lost based on the 2006 photo-mosaic..... 91

Figure 3.17. Wind speed and direction at the Carrie Bow Cay Marine Field Station in 2007.
Distance from center of chart measured in km/h. The monthly mean wind speed and direction represented by the light colored lines. The yearly mean wind speed (19.6 km/h) and direction (51.5°) showed by angle and length of dark arrow..... 94

Figure 3.18. Wind speed and direction at the Carrie Bow Cay Marine Field Station in 2008.
Distance from center of chart measured in km/h. The monthly mean wind speed and direction represented by the light colored lines. The yearly mean wind speed (21.1 km/h) and direction (53.7°) showed by angle and length of dark arrow..... 95

Figure 3.19. Water depth from tide gauge at Main Calabash Cay (MCC) and Carrie Bow Cay (CBC) Marine Field Station. Data at MCC captured mostly diurnal sea level fluctuations (07 to 21 hrs). MCC data were taken mostly at hourly intervals and matched to the closest corresponding date and time from the CBC tide gauge data. No data were available from MCC for June 01, 2008..... 96

Figure 3.20. Number of hurricanes and tropical storms that have made landfall along the coast of Belize. Storm frequency based on the National Oceanic and Atmospheric Administration (NOAA) database from 1851 to 2008; including Tropical Storm Arthur (May 2008) which occurred outside of the hurricane season which runs from June to November..... 98

Figure 3.21. Number of hurricanes and tropical storms that have made landfall on Turneffe. Storm frequency based on the National Oceanic and Atmospheric Administration (NOAA) database from 1851 to 2008..... 98

Figure 3.22. Oblique aerial photos of Cockroach Cay-22 taken in April of 2003 (left) and April of 2008 (right). Center of cay shows zone of vegetation disturbance from Hurricane Keith of 2000. Recolonization had occurred and the disturbed zone had closed considerably in 2008. 107

Figure 3.23. Estimated damaged cay vegetation area from Hurricane Keith (2000) based on surveys from 2003, 2006 and 2008. Three cays from eastern Turneffe were surveyed (CRC = Cockroach Cay; Cay numbers 20, 22, and 23). 108

Figure 3.24. Mangrove trees on the ocean side of Soldier Cay, Turneffe, partially buried and scarred by corral rubble from the surge effects of Hurricane Ivan 2004. (Photo taken two weeks after Hurricane Ivan 2004). 110

Figure 3.25. Little Calabash Cay (center) and Main Calabash Cay (background), Turneffe. Photo taken during Stoddart's survey of 1960-61 prior to Hurricane Hattie 1961. (Photo credit, Stoddart). 111

Figure 3.26. Photo showing Little Calabash Cay (center) and Main Calabash Cay (background) after Hurricane Hattie of 1961. Little Calabash Cay served as the administrative center of the coccol industry before the hurricane on Turneffe. Photo taken during Stoddart's survey of 1962 after Hurricane Hattie 1961. (Photo credit, Stoddart). 113

Figure 4.1. Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5). 144

Figure 4.2. Orientation and layout of plots relative to the edge of vegetation. 145

Figure 4.3. Above-ground litter traps under the fringing mangrove canopy at Big Calabash Cay (BCC). 146

Figure 4.4. Percent plot surface substrate composition for Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5) an asterisk represents the percent of plot substrate below the spring high tide (SBHT). Mixture = combination of two or more substrate types (estimates from 2008). 155

Figure 4.5. Percent of stems within four height classes in meters for Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5) for 2002 and 2008. 160

Figure 4.6. Percent of stems within four diameter classes (DBH in cm) for Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5) for 2002 and 2008... 161

Figure 4.7. Above-ground litter from three Turneffe fringing cays stacked from north to south: Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5). Above-ground litter covers a 12 month period; litter was not collected between March 2003 and February 2004 (Data NA = Data Not Available). Total litter was calculated by summing all the litter fractions with the exception of guano and miscellaneous fractions. Leaves fraction was for all mangrove species combined. The bract, flower and fruit fractions were also combined. Error bars indicate standard error of the mean. 163

Figure 4.8. Top photo - algal bloom southwest of Soldier Cay (August 2002). Bottom photo - bird guano mixed with littoral forest seeds collected in November 2002. 164

Figure 4.9. A twelve month period of mean monthly weather data (air temperature, wind speed and rainfall) from Carrie Bow Cay Marine Field Station. Weather data

between March 2003 and April 2004 were omitted (broken line) in order to coincide with above-ground litter data from the Turneffe sites.....	165
Figure 4.10. Ground litter from Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5). Ground litter collected in 2002 from underneath above-ground litter traps from a 0.5 x 0.5 m quadrat. Error bars indicate standard error of the mean.	166
Figure 5.1. Map of Turneffe highlighting group of eight cays surveyed for this study. (Redrawn from McGill 1996).	185
Figure 5.2. A simplified fringing cay showing vegetation and substrate above and below spring high tide.....	190
Figure 5.3. Big Calabash Cay (BCC) and point locations used to produce an elevation surface from which plot elevations were obtained.	191
Figure 5.4. Group of eight cays located on the eastern side of Turneffe. Cay and substrate elevation relative to spring high tide (vertical axis) vs. distance from the edge of the reef crest. Profile based on mid-transect bisecting the cay from reef to leeward showing highest points of cay substrate.	196
Figure 5.5. Mean substrate area above the spring high tide for eight cays (Cockroach Cay-20, -22 and -23, Soldier Cay, Big Calabash Cay, Dead Man Cay-2, -4 and -5) located on the eastern side of Turneffe vs. distance from the edge of the reef crest with SE bars.	197
Figure 5.6. Relative density (stems/ha) of <i>C. nucifera</i> (Cn), Littoral (Lit), <i>A. germinans</i> , (Ag), <i>L. racemosa</i> (Lr), <i>C. erectus</i> (Ce), and <i>R. mangle</i> (Rm) for eight cays (Cockroach Cays (CRC-20, -22, and -23), Soldier Cay (SC), Big Calabash Cay (BCC), Dead	

Man Cays (DMC-5, -4 and -2) on eastern Turneffe, cays ordered from north to south.....	198
Figure 5.7. Average number of tree stems/ha (all species) vs. exposure from reef, relative to spring high tide with SE bars. Ridge represents the group of plots that were located on substrate above the spring high tide.	199
Figure 5.8. Average tree basal area (all species) vs. exposure from reef, relative to spring high tide with SE bars. Ridge represents the group of plots that were located on substrate above the spring high tide.	200
Figure 5.9. Average basal area by vegetation type and exposure from reef, relative to spring high tide with SE bars. Ridge represents the group of plots that were located on substrate above the spring high tide. (Rm = <i>R. mangle</i> , Lr = <i>L. racemosa</i> , Ag = <i>A. germinans</i> , Ce = <i>C. erectus</i> , Cn = <i>C. nucifera</i> , Lit = littoral).	201
Figure 5.10. Average stem diameter (DBH) and height for all tree species and substrate elevation with SE bars vs. distance from the edge of reef crest. Line across the zero value (y-axis) represents the spring high tide.	202
Figure 5.11. Relationship between substrate elevation and basal area (BA) vs. distance from the edge of reef crest with SE bars. Average basal area for <i>R. mangle</i> (Rm), combined basal area for <i>A. germinans</i> (Ag), <i>L. racemosa</i> (Lr), <i>C. erectus</i> (Ce), and combined basal area of Littoral forest (Lit) with <i>C. nucifera</i> (Cn). Dashed line across the zero value (y-axis) represents the spring high tide.....	203
Figure 5.12. Number of live seedlings per ha of <i>R. mangle</i> (Rm seedling) and substrate elevation with SE bars vs. distance from the edge of reef crest. Line across the zero value (y-axis) represents the spring high tide.	204

Figure 5.13. Extreme maximum and minimum substrate elevation where seedlings were found. Line across the zero value (y-axis) represents the spring high tide. Rm = *R. mangle*, Lr = *L. racemosa*, Ag = *A. germinans*, Ce = *C. erectus*, Lit = Littoral forest, Cn = *C. nucifera*..... 205

Figure 5.14. Substrate elevation and salinity vs. distance from the edge of the reef crest with SE bars. Dashed line across the zero value (y-axis) represents the spring high tide..... 205

Figure 5.15. Mean percent substrate composition and elevation vs. distance from the edge of reef crest with SE bars. Dashed line across the zero value (y-axis) represents the spring high tide..... 206

Figure 5.16. Substrate cores from Cockroach Cay-23 showing accumulation of mangrove peat on sand, and buried peat layers. Core-A taken 187 m from the reef crest and Core-B taken 284 m from the reef crest..... 207

Figure 5.17. Triangular ordination of mangrove species. Distribution of species (squared symbol) were from Proserpine, Australia (data from Saenger 1985); species with asterisk were from Turneffe, Belize. Dominance index derived from the product of maximum height and tree density. Maximum rate of litterfall (Proserpine) derived from *in situ* monthly leaf counts, while maximum rate of litterfall (Turneffe) derived from oven dried litterfall ($\text{g}/\text{m}^2/\text{mo}$). The full and abbreviated names of the mangrove species from Proserpine, Australian and from Turneffe, Belize, used in this graphic are listed in Appendix P. (Redrawn with permission Saenger 2002). 214

Figure 6.1. Conceptual model for vegetated fringing cay formation and the effect of storm energy on reef sediments and vegetation. 241

Figure A.1. Cay vegetated area based on 2006 photo-mosaic. Cays arranged from a north to south direction..... 300

Figure F.1. Oblique aerial photographs of fringing cays before and after Hurricane Hattie 1961. Photos to the left taken in 1960 those to the right in 1962. Photo A = Cockroach Cay-20, B = Pelican Cay, C = Soldier Cay, D = Big Calabash Cay, E = Little Calabash Cay. Photo taken during Stoddart’s survey of 1960-62 before and after Hurricane Hattie 1961. (Photo credit, Stoddart). 308

Figure M.1. Eight fringing cays on eastern Turneffe selected for temporary plot establishment..... 319

Figure N.1. A 15 m length clear tube with a 1 cm inside diameter was used along with two graduated telescoping poles, and GPS, to measure substrate elevation..... 320

Figure O.1. Elevation, average height and average stem diameter vs. distance from the edge of the reef crest for *R. mangle* trees with SE error bars. Dashed line across the zero value (y-axis) represents the spring high tide. 323

Glossary of Terms

1. **Back-reef** - area behind, or to the landward of a reef. This zone usually includes a lagoon between the reef and the land (Allaby and Allaby 1999).
2. **Cay areas:**
 - a. **Vegetated area** - area of vegetation which has colonized above and below the spring high tide, excluding bare substrate above the spring high tide.
 - b. **Vegetated and bare substrate** - area of vegetation which has colonized above and below the spring high tide including those areas without vegetation (bare substrate) which are also above the spring high tide.
 - c. **Vegetation and substrate above spring high tide** - area of vegetation and bare substrate which are above the spring high tide only.
3. **Cay vegetated centroid** - a centroid calculated from the polygon of the cay vegetated area.
4. **Cay vegetated polygon** - a digitized polygon created around the periphery of the cay vegetated area.
5. **Fore reef** - the portion of a reef seaward of reef crest. A synonym of reef slope (NOAA CoRIS 2009).
6. **Fringing cay** - a cay that forms on the sediment apron of the back-reef on Turneffe. This type of cay is predominantly found on the eastern side of Turneffe and in close proximity to the coral reefs that surrounds the atoll.
7. **Lagoon** - a lagoon that forms in the back-reef area. For the eastern side of Turneffe the lagoon is between the large islands and the fringing cays.

- 8. Large islands** - islands located on the leeward side of the fringing cays (e.g., Black Bird Cay which is on the leeward of Soldier Cay).
- 9. Leeward zone** - zone found on the fringing cays to the lee of the ridge zone.
- 10. Littoral forest** - a widely adopted forest type in Belize to mean coastal forest without coral and mangrove (Wood et al. 1988).
- 11. Motu cays** - sand cays with shingle ridges.
- 12. Rampart (of coral rubble)** - a narrow ridge built by waves along the seaward edge of a reef flat. It consists of boulders, shingle, gravel or reef rubble (NOAA CoRIS 2009).
- 13. Reef crest** - the sharp break in slope at seaward margin or edge of reef flat (NOAA CoRIS 2009).
- 14. Reefward zone** - zone found on the fringing cays between the reef crest and the ocean facing edge of the ridge zone.
- 15. Ridge zone** - zone which develops on the fringing cays at a certain distance away from the reef crest and is above the spring high tide.
- 16. Spur and groove** - a system of shallow ridges (spurs) separated by deep channels (grooves) oriented perpendicular to the reef crest and extending down the upper seaward slope (NOAA CoRIS 2009).

Acknowledgements

First and foremost I offer my sincerest gratitude to my supervisor, Dr. Steve Mitchell, who has supported me throughout my thesis with his patience and knowledge whilst allowing me the room to work in my own way. Thank you for the encouragement and effort to be along with me in the field and office, one simply could not wish for a better or friendlier supervisor. I also thank the members of my graduate committee for their timely comments on the thesis, Dr. Ilka Feller, Dr. Lori Daniels, and Dr. Roland Stull.

I acknowledge the Canadian Commonwealth Scholarship Program (CBIE fellowship), UBC Forestry (NSERC discovery research grant), UBC International Tuition Award, Belize Protected Areas Conservation Trust (research grant), Smithsonian Marine Science Network, USA (research equipment grant), Russell E. Train Education for Nature, USA (WWF fellowship), and Friends of Turneffe, Belize (research grant) for their financial support for this project. I am very grateful to the University of Belize, Institute of Marine Studies, for allowing me to use the Calabash Cay Research Station as a base during my stay at Turneffe. I am also grateful to our island neighbors who allowed us to ride with them in their boats when we were heading to the mainland, thank you Turneffe Flats, Oceanic Society at Blackbird Cay and Blackbird Cay Resort.

My deepest gratitude to Dr. David and June Stoddart for opening their private library and allowing me to use photographs from before and after Hurricane Hattie. Their invaluable collection of photos was important for this project. I am also grateful to LightHawk, Jamie

Heath, and Dr. Ilka Feller for their assistance in photographing the stunning beauty of Turneffe from above. A special thank you to Naa Language-Opoku, Jerry Maedel, Norman Hodges and Chris Bater for the assistance with the GIS and software and Dr. Tony Kozak for assisting with statistical analysis and SAS code. A thank you to Dr. Peter Saenger for his timely comments on content from Chapter 5. I am grateful to the staff at the UBC, Forest Sciences, for the support they provided during my time as a UBC graduate student. For the wonderful friendship, a thank you, to my windthrow lab colleagues at UBC, Forest Sciences.

I am indebted to the field volunteers who were consistently high spirited even when we were being attacked by mosquitoes, sand flies and jelly fish or during our rough-water boat rides in and out of the Turneffe reef channels. Mrs. Teresa Catzim deserves a special mention for preparing wonderful food and wonderful lunches for the field. We were all very fond of your “Progresso style baked bread”.

I am extremely grateful to Michael Armstrong, Andrea Griffiths, Dr. Alan and Beryl Mitchell, Janet Mitchell, Dr. Andrew Cameron, Jessica Beaubier, Victor and Alicia Ku, Evaristo Montejo, Renira Velloso, Pejman Rasouli, Maryam Ansari, Forest Li, and Suzanne Perry for making us feel part of the family. I owe my deepest gratitude to all my family. A special thank you to my mom, Otilia Chi and those who were directly involved in taking the time to help me sort my personal affairs when I could not do it from Turneffe or from Vancouver, thank you Heidi Tejada, Rick Chi, Teresa Tejada, Ernesto Chi, and Julian Chi Sr. My deepest gratitude to my wife Ulrike, for supporting and encouraging me to pursue this degree. I am grateful for God’s provision of joys, challenges, and grace for growth.

This thesis is dedicated to all the Belizeans who lost their lives during Hurricane Hattie of 1961 and especially those who were at Turneffe Islands during the storm.

Chapter 1: Introduction

Mangrove forests, seagrass beds and coral reefs are ecologically rich and are economically important throughout the tropics, but their connectivity is poorly understood (Pittman and McAlpine 2003). Each of these ecosystems can thrive in isolation (Parrish 1989). Where they occur together, such as at Turneffe Islands in Belize, considerable interactions occur (e.g., Sheaves 2005; Valentine et al. 2008; Mumby and Hastings 2008).

Because of their offshore locations, atoll ecosystems are exposed to and reflect the effects of gradients of wave and wind energy, including periodic tropical storms and hurricanes (Díaz et al. 1996). Periodic hurricanes are part of the natural disturbance regime in Belize's coastal landscapes. Due to their geographic location, offshore cays (adjacent to the coast of the mainland) receive the brunt of tropical storms. These offshore cays also experience episodes of human development.

There is a general lack of knowledge on long-term recovery after catastrophic disturbance in atoll ecosystems, and in particular, in mangrove-dominated atolls. Additionally, anthropogenic impacts on mangrove forests are increasing worldwide and this merits attention. Documenting change over time is crucial, especially since events such as hurricanes and human development can substantively alter the landscape, sometimes rendering it unrecognizable from its previous state. Long-term observations are essential to understanding the natural variability and resiliency of, these coastal ecosystems. Baselines are important for assessing the effects of humans on disturbance and recovery processes. The

documentation of past ecosystem response to environmental change is particularly relevant in a time of global warming.

Turneffe Islands, also referred as Turneffe Atoll (hereafter “Turneffe”), is the largest atoll in Belize, and is 12 km outside the Belize Barrier Reef, due east of Belize City. Turneffe is sufficiently far offshore that it is not directly influenced by water pollution and sediment runoff from the mainland, making this atoll an interesting site to study recovery from natural disturbance and in the absence of permanent human settlements. The vegetation at Turneffe is composed mainly of flooded mangrove islands and higher elevation sandy cays that support coral and littoral forest. Murray et al. (1999) estimated that 70% of the vegetation of Turneffe was dominated by mangrove forest.

A group of vegetated cays can be found on the eastern seaboard of Turneffe which are in close proximity to the reef that surrounds the atoll. Stoddart (1965) distinguished eight cay-types in Belize defined by topography, sediment and vegetation. For the eastern seaboard of Turneffe, he identified three types: vegetated sand cay, vegetated and shingle cay, and vegetated shingle cay. In this thesis, cays in close proximity to the Turneffe reef, are termed “fringing cays”, (see Glossary), while the Turneffe islands west of these fringing cays are referred as “large islands”.

Cays on Turneffe have long been affected by human use as indicated by pottery remains of the Maya civilization (Stoddart 1963). In the 20th century, Turneffe had cays with and without human settlements, which were affected by Hurricane Hattie. This hurricane in

October 1961 caused catastrophic damage to human settlements, cocal forest, mangrove forests, littoral forest, and cay substrates. After the hurricane, the surviving human population left the atoll, although they continued to use it as fishing grounds.

Around the mid 1980's tourism grew from being a moderate contributor to the Belizean economy to the fastest growing industry. Tourism is now Belize's largest industry. With tourism came development, particularly coastal development and resorts were built primarily on the eastern side of Turneffe. In addition, Turneffe is experiencing a demand for coastal real estate. Several cays are currently for sale. In order to balance development and push for conservation, both the Turneffe Islands Coastal Advisory Committee (TICAC) and the Turneffe Atoll Sustainability Council (TASC) play crucial roles in overseeing revisions of the Turneffe Islands Development Guidelines, and they are pressing for better management practices.

This research project examines the dynamics of mangroves and cays of Turneffe and yields valuable information on the disturbance and recovery processes in these ecologically sensitive and hurricane prone landscapes. This in turn can provide insights for guidelines for resort or suburban developments, and for reforestation projects in disturbed habitats.

1.1 Focus and objectives

The focus of this thesis is on the fringing cays found on the eastern seaboard of Turneffe. The goal of this research is to map and describe the characteristics of these cays and to estimate

change over time based on historic and contemporary data with a focus on mangrove forest distribution and the effects of hurricanes. The objectives of this thesis are to: 1) quantify patterns and test for causal agents that contributed to changes on cays and cay vegetation; 2) investigate tree and stand-level growth in mangrove-dominated stands on fringing cays; and, 3) document and analyze spatial patterns in cay geomorphology and in mangrove structure and composition.

1.2 Approach to the problem and outcome

Information sources for this research program includes historical records and aerial photographs, contemporary aerial photographs and satellite images, surveys of permanent sample plots, and temporary plots. Dr. David Stoddart, a retired geographer and Professor Emeritus from the University of California, Berkeley, graciously provided his original photographic slides from on-the-ground and aerial photographs of Turneffe and related scientific material from Belize. These photos were valuable to assess the effects of before and after Hurricane Hattie of October 1961.

The thesis has the following structure: Chapter 2 commences with a review of the literature on disturbance, islands and cays, and mangrove ecology, then focuses on the geomorphology, biodiversity, and human use of Turneffe and the effects of Hurricane Hattie. Chapter 3 commences with a review of the processes that affect the fringing cays, and then presents data on spatial patterns and possible causal agents that explain the observed patterns. Chapter 4 investigates the above-ground biomass, basal area and litterfall in red mangrove-dominated

fringing stands based on permanent plots remeasured over a period of 6 years. Chapter 5 investigates the substrate composition of eight cays and the effects of substrate condition and exposure on vegetation structure and composition, and examines the plant strategies of local mangrove species. Chapter 6 contains an integrative discussion of disturbance dynamics in fringing cays and concludes with remarks concerning conservation policy and planning, and suggestions for future research.

Chapter 2: Literature review

In light of the rapid global loss of mangrove forests (Spalding et al. 2010), it is important to consider patterns of recovery from natural and anthropogenic disturbances. The following review identifies some of the factors that shape mangrove disturbance and recovery, and then provides a detailed summary of what is known about disturbance and recovery dynamics on Turneffe.

2.1 Disturbance

Ecologists define disturbance as any relatively discrete event in time that removes organisms and opens up space that can be colonized by individuals of the same or different species (Pickett and White 1985; Begon et al. 1990). Disturbance, once considered an anomaly disrupting stability in ecological field studies (Gerritsen and Patten 1985), is now recognized as a key process that maintains diversity in communities, promotes secondary succession, contributes to nutrient cycling and drives evolution (Harper 1977; Connell 1978; Bormann and Likens 1979; Paine and Levin 1981). Ecologists now recognize that natural systems are largely structured by disturbance (e.g., Pickett and White 1985; Waide and Lugo 1992; Huggett 1995). Large, infrequent disturbances play an important role in many forested landscapes, in part because the resulting landscape pattern influences the rate and pattern of energy flow, nutrient cycling, wildlife and human responses, and susceptibility to subsequent disturbance (Turner and Dale 1998).

Forest ecosystems are subject to a variety of disturbances, which can be differentiated along scales of severity, spatial extent, frequency, and duration (Karr and Freemark 1985; White and Pickett 1985; Jordan 1985; Lugo et al. 1986; Foster 1988a and 1988b). The main agents of natural disturbances in forests are fire, weather (extreme events vs. general weather), soil disturbance (geomorphic processes), and insects and pathogens (herbivory) (Gibson 2002; Feller 2002). Anthropogenic disturbances include fire, livestock husbandry, logging, fuelwood cutting, and clearance for agriculture, aquaculture, road building, urban development, and resort development.

Island ecosystems can be structured by disturbance events and differences exist between tropical and temperate islands in that tropical islands are exposed to extreme weather events that are rare in temperate latitudes (Whittaker 1995). An extreme weather event can impact both island and mainland systems; however, because of the geographical and geologic attributes of islands (e.g., offshore islands are surrounded by water), the disturbances are not typical of the mainland regimes when scaled to island size (Whittaker 1995).

Analysis of the disturbance regime of a landscape can be of great value for understanding community and landscape structure and composition, and for developing appropriate management plans. The subject of disturbance interactions is a growing field in science and there is much work still to be done, particularly in tropical forests. For example, Grove et al. (2000) observed that any study that attempts to quantify interactions between past human disturbance and cyclone damage in rain forests will provide valuable insights to ecologists, and will be of importance to decision makers, developers, and resource managers.

2.2 Wind, waves and tides

The breakage or uprooting of trees by rare events such as wind storms is referred to as windthrow or blowdown. However, the disturbance caused by wind storms results from interactions among regional climate, local soil, topographic, and stand characteristics, and the growth and form of individual trees (Newton 2007). Damage can be in the form of defoliation, debranching, stem failure, root failure or uprooting (Mergen 1954). The amount of damage caused by wind is a function of wind speed, duration, and the direction from which the winds originate (Newton 2007). In the Caribbean, some areas experience intense and slow-moving weather systems with such frequency that hurricanes may be considered essentially a chronic disturbance and the vegetation is continually recovering from wind damage (Foster et al. 1998).

Boose et al. (1994) examined the impacts of severe hurricanes on forested landscapes in the northeastern United States and Puerto Rico and concluded that wind damage served as an important source of landscape-scale (~ 10 km) patterning in forests and was a major factor in vegetation dynamics at that scale. At the stand-scale (~ 1 km), extensive blowdown was considered to be an important factor regulating hydrological, energy and nutrient regimes (Boose et al. 1994). The stand-level impact was also highly dependent on the local history of natural disturbances and human activity (Foster et al. 1999; Chazdon 2003). The survival, releafing, and sprouting of windthrown and damaged trees may provide important biotic control on subsequent ecosystem development (Scatena et al. 1996; Zimmerman et al. 1996). Even on relatively small islands such as Puerto Rico, at the landscape scale, the decline in

wind intensity inland has produced historical gradients of hurricane impacts that control canopy structure and forest composition (Scatena and Larsen 1991; Boose et al. 1994).

In the aftermath of hurricanes, a considerable amount of biomass remains in redistributed accumulations and contributes to the process of ecosystem recovery (Peterson and Pickett 1991; Cooper-Ellis et al. 1999). The probability of fire and other disturbances increases with an increasing load of fine woody debris and leaves (Patterson and Foster 1990; Lynch 1991; Paine et al. 1998). It has been observed that despite the effects of hurricanes, forests exhibited a remarkable resilience to a visually catastrophic event and maintained tight biotic control over ecosystem processes, despite major structural damage (Bowden et al. 1993; Foster et al. 1997). However, the infrequent, unanticipated, and often substantial impacts of intense storms make it difficult to undertake integrated and long-term assessments of environmental, vegetation, and ecosystem responses (Cooper-Ellis et al. 1999).

Coastlines are transition zones between land and sea. They have distinctive biophysical conditions and are continually modified by erosion and accretion. Exposed intertidal zones can receive high energy input from incoming waves, which deliver their energy as they break on the shore. Davis and Hayes (1984) argued that the relative effects of waves and tides rather than the absolute values were more important in shaping the coast. Dronkers (2005) described a nonlinear mutual dependence between water motion and coastal geomorphology.

Wind forces on the ocean surface accumulate and propagate in the wave field. The wave that has the most influence along coastlines is the progressive, surface wave produced by wind

(Davis 1996). Wave energy depends on wind speed and fetch. The longer the area exposed to wind and the stronger the wind blows for an extended time, the greater the fetch and the greater the resultant waves. The emerging collection of waves is known as the wave train. As the wave train propagates into shallow water, a change in wave height and wavelength can be observed. This process is referred to as shoaling. When a wave breaks, the energy stored in the bending of the ocean's surface is transferred, first into potential energy, since the wave height increases then into sound, heat, and momentum transfer.

Tides in the Caribbean are described as microtidal. A microtidal environment experiences small changes in sea level from low to high tide. For example, a mean range of 15 cm has been reported for Carrie Bow Cay, Belize (Kjerfve et al. 1982) and a range of 30 cm for the country of Belize (Gischler 2003).

2.3 Hurricanes and tropical storms

Hurricanes are described as heat engines that convert the heat energy of the tropical ocean (26 °C or warmer) into wind and waves (Emanuel 2005). The formation of a hurricane begins with a low pressure zone created by poorly organized clusters of thunderstorms with weak surface winds. At this point it is called a tropical disturbance. As the low strengthens and the thunderstorms become more organized, it becomes a tropical depression and is given an identifying number. When sustained surface winds exceed 63 km/hr, it has become a tropical storm, at which point it is given a name. A tropical storm can mature into a hurricane when the surface winds exceed 119 km/hr. A mature hurricane is a cyclone, or vortex, revolving

counterclockwise, in the Northern Hemisphere. This vortex can extend upward 10 to 15 km above the sea or land surface and outward to a radius of 1000 km around the eye. The central eye is characterized by low pressure and low wind speeds, and is surrounded at a radius of approximately 30 km by the eyewall, an area of intense convection where the highest wind speeds and precipitation occur (Foster and Boose 1995). Past the hurricane eyewall, wind speeds and precipitation normally decline exponentially, such that severe wind damage seldom extends beyond 100 km from the eyewall (Frank 1977). The removal of warm moist sea air upon landfall causes hurricanes to weaken, although tropical storms are known to regain their intensity if they move back out to sea, but colder oceans diminish their power (Foster et al. 1998). The parabolic path which is often followed by hurricanes in the Northern Hemisphere is influenced by the tropical winds and the prevailing westerlies at higher latitudes (Simpson and Riehl 1981). In the Atlantic, the hurricane season extends from June to November when ocean temperatures are warmest.

To make the predicted hazards of approaching hurricanes clearer to emergency forces, hurricane forecasters use a disaster-potential scale, the Saffir-Simpson Hurricane Wind Scale, based on the hurricane's intensity. Based on the United States Department of Commerce, National Oceanographic and Atmospheric Administration's website for its National Hurricane Center (Schott et al. 2009), a Category 1 hurricane has sustained winds of 119-153 km/hr. This category has very dangerous winds and will produce some damage to trees. Large branches of trees will snap and shallow rooted trees can be toppled and extensive damage to power lines and poles can result. In contrast, the highest category, a Category 5 hurricane, can have sustained winds greater than 249 km/hr and will produce catastrophic

damage to vegetation. Nearly all trees will be snapped or uprooted, and power poles will be downed. Fallen trees and power poles will isolate residential areas and cause power outages that can last for weeks to possibly months. Most of the affected area will be uninhabitable from weeks to months.

2.4 Islands and cays

An island is certainly an intrinsically appealing object of study. It is simpler than a continent or an ocean, and a visibly discreet object that can be labeled with a name and its resident populations identified (MacArthur and Wilson 1967). There is good evidence that humans have extinguished island endemics. Wherever we have colonized islands, whether in the Pacific, Caribbean, Atlantic Ocean, Indian Ocean, or the Mediterranean, we have impacted adversely the native biota, often diminishing the ecosystem services on which we rely (Diamond 2005).

Islands exist in various shapes and sizes, are extremely variable in their arrangement in space, geology, environments, and biotic characteristics (Whittaker and Fernández-Palacios 2007). Islands can be divided into two broad categories: 1) true islands, being land wholly surrounded by water; and 2) habitat islands, being other forms of insular habitat, i.e. discreet patches of habitat surrounded by strongly contrasting habitats (Whittaker and Fernández-Palacios 2007). Throughout much of the Caribbean, the word 'island' is widely interchangeable with the word 'cay'. Cays are usually a low insular bank of sand, peat, mud,

rock, coral, etc. The fringing cays found on the eastern side of Turneffe, Belize, which are the focus of this study, fall under the latter definition.

A great deal of research on island dynamics has been conducted on barrier islands, particularly concerning their formation and migration (Rosati 2009). Barrier islands are considered a coastal landform formed by relatively narrow strips of sand parallel to the mainland coast (Bird 2000). Three different explanations for the formation of barrier islands have been proposed: 1) upbuilding of offshore bars; 2) cutting of inlets through spits; and 3) submergence of ridge-like coastal features (Schwartz 1971). Barrier islands may consist of organic debris. However, their common materials are sand and gravel (Hoyt 1967). As described by Hoyt (1967), barrier islands are generally elongate islands, which are parallel to the shore and separated from the mainland by a bay, lagoon, or marsh area. Individual barrier islands range from a few kilometers to over 100 km long. Width is commonly only a few kilometers. Because coastal environments are affected by similar phenomena (e.g., tide, wind, and storm), observations on barrier islands can provide interesting insights for fringing cays, which are deposits of coral sand and rubble that form on the inside of back-reef. The fringing cays of Turneffe are much smaller in size than many barrier islands found globally, which are in the average length of over 1 km (Stutz and Pilkey 2011). The coral reef directly seaward of the fringing cays is believed to produce much of the substrate found on these cays from coarse coral rubble to fine sand. They may have also organic soils from littoral forest and organic peat from mangroves as components of their substrate.

Islands are exposed to wind, wave and current energy. Globally periodic intense disturbance is considered a natural feature of many islands (Whittaker 1995). According to Lugo (1999), while hurricanes have the highest frequency of recurrence among major 'stressors', the susceptibility of Caribbean islands to hurricanes is intermediate. According to Whittaker (1995) species and ecosystems of storm-prone regions have evolved and are evolutionarily conditioned by storms and the relatively short recurrence intervals of hurricanes should not threaten these ecosystems. He contends that the threat may be greatly increased, however, when humans are added into the equation. The impact of hurricanes on small islands may be very different from large islands, as it is likely that the entire area of a small island may be affected (Whittaker 1995).

Abbot and Black (1980) conducted a study of vascular plant species on 76 sandy cays in Western Australia, over a period of three years and identified some of the distinctive features of these small islands. Their study attributed slight changes in the turnover patterns to an increase in rainfall and to the passage of a cyclone. Furthermore, they pointed out that for small islands the species number does change with time because: 1) these cays do not have a constant area or shape, because they consist wholly of sand and coral debris deposited by wave action; 2) sandy cays have extensive, gently sloping beaches that receive large numbers of propagules in flotsam stranded by wave action; and, 3) most sandy cays occur in tropical regions, and are subject to frequent cyclonic or hurricane disturbances that often cause waves temporarily to inundate cays and wash vegetation away. Also on small islands, wave action may prevent establishment of plants or the limited area of soil present may be a small target for propagules to reach and the continual deposition of seaspray may limit the available

niches to only the most salt-tolerant species (Whitehead and Jones 1969; Buckley 1981 and 1982).

2.5 Mangrove forests

Mangroves are woody plants and grow in tropical and sub-tropical latitudes along the land-sea interface. Mangroves can exist in conditions of high salinity, extreme tides, strong winds, high temperatures and muddy, anaerobic soils. There may be no other group of plants with such highly developed morphological and physiological adaptations to extreme conditions (Kathiresan and Bingham 2001). The word “mangrove” has been used to refer either to the constituent plants of tropical intertidal forest communities and to the community itself (Tomlinson 1986). The term “mangal” is also used to describe mangrove communities. Duke (1992) defined a mangrove plant as, “...a tree, shrub, palm or ground fern, generally exceeding one half meter in height, and which normally grows above mean sea level in the intertidal zone of marine coastal environments, or estuarine margins.” Mangroves can be categorized based on certain features. Tomlinson (1986) developed five criteria for “true mangroves”. They: 1) have complete fidelity to the mangrove environment, occur only in mangal, and do not extend into terrestrial communities, 2) play a major role in the community and have the ability to form pure stands, 3) have morphological specializations that adapt them to their environment, for example, aerial roots and vivipary, 4) possess physiological mechanisms for salt exclusion, and 5) are in taxonomic isolation from terrestrial relatives at least at the generic level. Criterion number one is the most significant. Tomlinson (1986) recognized three groups of mangroves: major mangrove species, minor

mangrove species and mangrove associates. The major species are the strict or true mangroves. Minor species of mangroves are distinguished by their inability to form a conspicuous element of the vegetation; thus occurring in peripheral habitats and only rarely in pure communities. The mangrove associates usually form part of a transitional community and are usually members of the beach community.

Mangrove distributions are strongly affected by temperature (Duke 1992) and moisture (Saenger and Snedaker 1993). Large-scale currents have the potential to influence distributions of propagules by preventing them from reaching some areas (De Lange and De Lange 1994). The combined effects of these factors which appear to be consistent around the world produce characteristic distributional ranges for most species (Duke et al. 1998; Fig. 2.1).

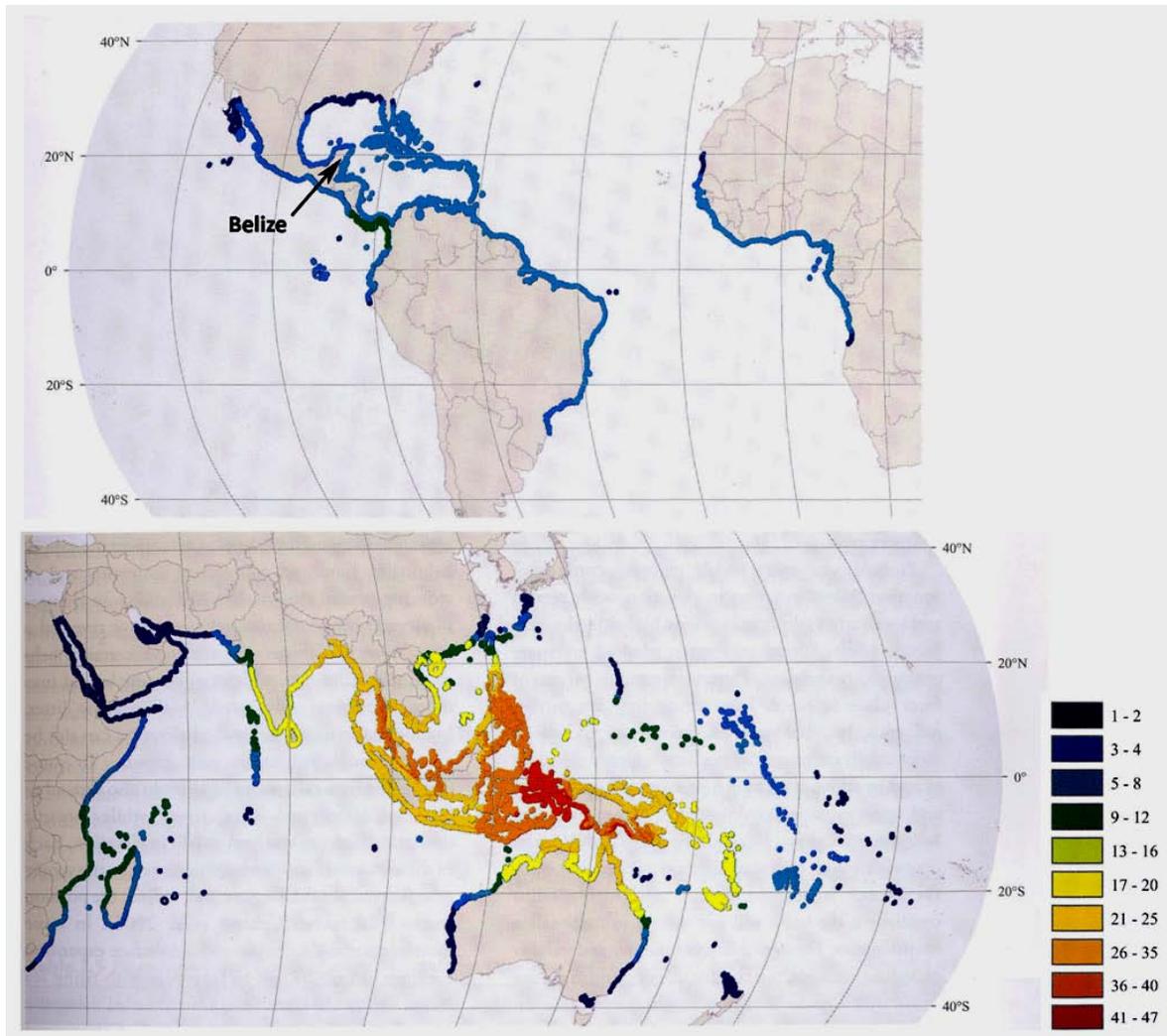


Figure 2.1. World distribution and diversity of mangroves species. (Adapted with permission Spalding et al. 2010).

Belize is home to three true mangroves, *Rhizophora mangle* L., *Avicennia germinans* L., and *Laguncularia racemosa* Gaertn., and the mangrove associate *Conocarpus erectus* L. All of the above species are widely distributed on Turneffe. Murray et al. (2003) estimated that mangroves are found in 60 to 80% of Belizean offshore cays. Mangrove forest cover in Belize has been recently estimated at 75 000 ha (Cherrington et al. 2010). The distribution of

mangroves in Belize is largely controlled by three factors: the barrier reef, the shallow gradient of the coastline and the narrow tidal range (Murray et al. 2003).

2.5.1 Economic importance of mangrove forests

The basic building blocks of human welfare can be attributed to the goods provided by natural ecosystems. All ecological functions of forests are also economic functions (Pearce 2001). Costanza et al. (1997) identified 17 specific goods and services provided by ecosystems: gas regulation, climate regulation, disturbance regulation, water regulation, water supply, erosion control and sediment retention, soil formation, nutrient cycling, waste treatment, pollination, biological control, refugia, food production, raw materials, genetic resources, recreation and cultural services.

Mangrove ecosystems provide goods and services. Spaninks and van Beukering (1997) have elaborated on these services and have pointed to the often neglected value of mangrove products that result in the conversion of mangrove forests to marketable products, such as aquaculture. Various studies have been undertaken that have identified the economic importance of mangrove forests. The Food and Agriculture Organization of the United Nations (Christensen 1982) described quantitatively the various uses of mangrove resources in the area and thus provided comparative data for land-use planning in Thailand. Hodgson and Dixon (1988) demonstrated the benefits from tourism coupled with fishery production substantially outweighed the short-term benefits that may accrue from increased logging in Palawan. Lal (1990) compared the net benefits of converting mangrove lands to rice and

sugar cultivation by estimating the benefits of mangrove-related products that would be lost after conversion in Fiji. Bennet and Reynolds (1993) estimated the benefits to fisheries and tourism of mangroves in Malaysia. Gammage (1997) explored the different commercial and community uses of mangrove ecosystems in El Salvador.

A study conducted along the Mesoamerican reef system of Belize and Mexico showed that extensive mangrove habitats enhance the biomass of fishes on Caribbean reefs (Mumby et al. 2004). Cooper et al. (2009) found that in total, the value of reef and mangrove-related fisheries, tourism, and shoreline protection services in Belize was estimated to be US\$395 to \$559 million per year and that mangroves provided an estimated US\$174 to \$249 million of this total, some independently, and some through their supporting role for nearby coral reefs.

2.5.2 Mangrove forest and shoreline protection

Mangroves are tightly bound to the coastal environments in which they occur (Kathiresan and Bingham 2001). The chemical and physical conditions found in mangrove environments both affects and is created by the plants themselves, as a result perturbations to the system can have long-term effects (Kathiresan and Bingham 2001). In this coastal position, mangroves bear the full brunt of hurricanes and tropical storms (Piou et al. 2006). Damage to the mangroves affects sediment budgets and promotes coastal erosion (Kamaludin 1993). The eroded sediments may then cause further damage to the adjacent mangroves by smothering prop roots. It has long been reported that mangroves protect and stabilize coastlines. In the aftermath of the Indian Ocean tsunami, Dahdouh-Guebas et al. (2005) and

Danielsen et al. (2005) found that mangroves played a critical role in storm protection. More recently in Mexico, after the passage of Hurricane Dean 2007, the UNDP (2010) reported that the damage to houses was 6% in areas protected by mangroves, while it was 16% in areas where mangroves had been destroyed. However, the degree of protection depends on the condition of the mangrove forest.

With their intricately entangled above-ground root systems (Fig. 2.2), mangrove communities protect shorelines during storm events; the root barrier is capable of absorbing wave energy and reducing the velocity of water (Mazda et al. 1997). Measurements of wave forces and modeling of fluid dynamics suggested that mangrove vegetation protects coastlines by reducing wave amplitude and energy (Massel et al. 1999). Analytical models performed by Hiraishi and Harada (2003) showed that 30 mangrove trees per 100 m² in a 100 m wide belt can reduce the maximum tsunami flow pressure by more than 90% . Mangrove roots tend to retain sediment and consolidate the soil thereby facilitating accretion. Erosion in mangrove-covered shorelines is less likely or will erode significantly more slowly than unvegetated shorelines during periods of high wave energy (Saenger 2002).



Figure 2.2. Aerial roots of red mangrove (*Rhizophora mangle*) during low tide at Big Calabash Cay, Turneffe, Belize.

During storm events, a mangrove shoreline can also act as an effective windbreak (Oliver 1982). A mangrove canopy produces frictional drag which causes a rapid decrease in wind speed immediately inland of the mangrove community (Saenger 2002). This windbreak, or “bioshield” serves as a protection to leeward areas. When mangroves are damaged during storm events, the mangrove community usually, but not always, recovers in the absence of human-induced stress (Chi 2003; Piou et al. 2006). Coastal areas affected by storms usually suffer loss of substrate, which makes it problematic for mangroves to colonize eroded areas. Field (1998) identified several site characteristics to consider when planting mangroves. They were: insolation, gradient of site, stability of the site, exposure to wind, exposure to

waves, rate of siltation, nature of the soil, absence of debris, salinity of the soil water, tidal currents, depth of tidal inundation, availability of fresh water, height of water table, availability of propagules or seeds, and presence of pests.

2.5.3 Mangrove forests as shelter and nursery grounds

Coral atolls and their terrestrial and marine ecosystems are a key component of tropical biodiversity, are rich in marine resources, and provide opportunities for recreation and tourism (Peckol et al. 2003). Mangroves are an integral component of these ecosystems and are unique amongst vegetation communities in that they span the marine and terrestrial environment. The health of coastal and ocean ecosystems is dependent on coastal wetlands which also supports commercial and recreational fisheries (Gosselink 1984). Mangrove communities have been shown to be important in serving as an intermediate nursery habitat that may increase the survivorship of young fish (Mumby et al. 2004). The research conducted by Mumby and colleagues included Turneffe as one of their research sites. Some fish species moved from mangroves into their adult habitat in stages.

The Turneffe mangroves are closely connected with seagrass beds, patch reefs, and coral reefs. The intricate relationship between these adjacent ecosystems is particularly important in the inner lagoons of the atoll. Mangroves enhance fish biomass in two ways: 1) efflux of detritus and nutrients may enrich primary production in neighboring ecosystems; 2) mangrove may provide a refuge from predators and/or plentiful food that increases the survivorship of juveniles (Mumby et al. 2004). As a result, mangroves are considered nursery

ground for fish. It is very common to find larval and juvenile fish among the mangroves of Turneffe. Studies done in Belize by Sedberry and Carter (1993) found that most of the fish collected from mangrove waters are juveniles of species that live on the reefs as adults. The abundance of fish can be very high in mangrove systems where fish biomass can be from 10 to 66 g/m² (Flores-Verdugo et al. 1990). There may be a diurnal pattern to use of mangroves by fish. In southwestern Puerto Rico, fish found in the mangroves during the day may completely disappear at night, probably migrating to sand flats and seagrass beds (Rooker and Dennis 1991).

2.5.4 Mangrove forests and sea level rise

There are many anthropogenic reasons for coastal wetland loss, ranging from development by humans to subsidence/sea level rise (Orson et al. 1985). Coastal wetlands are both highly vulnerable to sea level change, but are also adaptable under certain circumstances. The capacity of mangroves to maintain soil elevations near to sea level will ultimately determine their stability (McKee et al. 2007a). Coastal wetlands have the ability to aggrade (grow vertically) (Nielsen and Nielsen 2002) when sediment is available. However, in the absence of substantive sediment inputs to counter sea level rise, large areas can be lost because of the low overall elevation of the marsh surface. Mangrove forest will be able to cope with sea-level rise where the rate of sedimentation approximates or exceeds the rate of local sea-level rise (McKee et al. 2007a; Ellison and Stoddart 1991). In some locations, mangrove communities survive by migration inland during periods of sea-level rise. Indeed, Hendry and Digerfeldt (1989) have shown that mangrove communities in western Jamaica were able

to keep pace with mid-Holocene sea-level rise (ca. 3.8 mm/yr). Torrescano and Islebe (2006) working at El Palmar, a swamp along the Rio Hondo River south of the Yucatan Peninsula, near the Belizean border, found that there have been changes within the last 500 years from a tropical forest type to a mangrove-dominated forest due to changes in sea level. Mangroves develop in a range of environments from autochthonous (e.g., mangrove litter dominated) to allochthonous (e.g., river run-off, anthropogenic discharges). According to some ecologists, macrotidal sediment-rich environments, such as northern Australia, is more promising for the survival of mangrove communities where strong tidal currents redistribute sediment (Semeniuk 1994; Woodroffe 1995), than in microtidal, sediment-starved environments like in many small islands (Parkinson et al. 1994). It has been suggested that where the rate of shoreline recession increases, mangrove stands will become spatially compressed and suffer reductions in species diversity (Bijlsma et al. 1996). Turneffe being of an autochthonous system, it is likely that mangroves will have a much more difficult time dealing with sea level rise if the rate of mangrove peat accumulation is less than the rate of sea level rise.

Some species of mangroves appear to be more robust and resilient than others to the effects of human disturbance, climate change, and sea-level rise (Ellison and Stoddart 1991; Aksornkhae and Paphavasit 1993). The capacity of mangroves and other coastal wetlands to respond to sea-level rise by landward migration is now severely limited in many localities by agricultural clearing or other human land uses. The mangroves of Turneffe have very limited or no space for migration. The eastern fringing cays, which are the focus of this study, are at sea level, and there is limited space between the reef and the larger islands. Most of the mangrove cays within the inner lagoons of Turneffe are permanently flooded and so are

already below sea level. Based on sediment cores analysis, Gischler (2003) found that sea level has risen 3.5 m over the past 4000 years at Turneffe and therefore mangrove areas were lost. Human-induced global warming may accelerate this process.

Mangrove forests usually create thick, organically rich sediments as their substrata.

Mangroves also produce peat which is primarily organic matter in composition and dominated by fine roots; as a result mangrove plants contribute directly to soil formation.

Loss on ignition experiments done by McKee et al. (2007a) showed that the organic content of peat deposits from different sites in Central American mangroves averaged 65%. This shows that mangrove forests have great below-ground productivity and play a significant role in carbon sequestration, not only above but also below ground (Fujimoto 2004). According to McKee et al. (2007a), the Caribbean region is an important reservoir of mangrove peat. Peat cores from Twin Cays, Belize indicate deposits up to 10 m thick (Macintyre et al. 2004).

These types of offshore peat-forming mangroves are particularly vulnerable to human disturbance. McKee et al. (2007a) has clearly shown that the removal of mangrove vegetation stops soil accretion, while decomposition, physical compaction and erosion processes continue, leading to submergence and land loss.

Because of their location at the interface between land and sea, mangroves are likely to be one of the first forest ecosystems to be affected by sea-level rise and therefore act as a 'canary in the coal mine' for climate change impacts. Ellison and Farnsworth (1997) studied the response of *R. mangle* to increased inundation, mimicking the sea-level changes expected in the Caribbean in the next 50 to 100 years. After 2.5 years of higher water, (with

approximated field conditions in Belize, the source locale for the seedlings), plants had significantly lower rates of photosynthesis and growth, were shorter and narrower, and had fewer branches and leaves, and more acid-sulfide in their soils. The study suggested that increased mangrove growth rates predicted for increasing atmospheric CO₂ may be offset by decreased growth resulting from changes in tidal regimes.

Snedaker (1993) argued that mangroves in the Caribbean are more likely to be affected by changes in precipitation than by rising sea levels. He contended that mangroves require large amounts of fresh water to reach full growth potential. He hypothesized that a decrease in rainfall in the Caribbean would reduce mangroves' productive potential and increase their exposure to full-strength seawater. In this scenario, peat substrates would subside as a result of anaerobic decomposition by sulfate-reducing microorganisms, leading to the elimination of mangroves in affected areas (Snedaker 1993).

2.5.5 Mangroves and hurricanes

Stand-replacing hurricanes are a fundamental, evolutionarily significant component of mangrove forests fringing the Caribbean Sea (Ross et al. 2006). Return intervals for major hurricanes in this region was 20-30 years (Lugo and Snedaker 1974). Although there was little evidence that hurricanes produce “long-term detrimental impacts to unmodified coastal systems” (Conner et al. 1989), such storms were capable of accelerating, disrupting, and reversing numerous geomorphic events and ecological processes, and devastating human settlements in coastal areas (Tanner 1961; Lugo et al. 1983; Conner et al. 1989). In addition

to hurricane characteristics, the damage to coastal forest from hurricanes was also influenced by species composition, age structure, and geomorphic characteristics (Michener et al. 1997). Oceanic storm surges that carry high-ionic-strength water and organic-rich sediments several kilometers inland, can also damage coastal environments (Chabreck and Palmisano 1973; Cablk et al. 1994). Salt spray together with winds can have local effects on vegetation through desiccation and salt stress (Hook et al. 1991). Hurricanes can also affect the long-term sustainability of mangroves with primarily organic (e.g., peat) soils such as those occurring on Caribbean islands located far from terrigenous sources of sediment (e.g., continental landmasses) (Cahoon et al. 2002). In these environments, continual production and addition of new organic matter (e.g., roots) is necessary to maintain mangrove sediment elevation because the peat is constantly decomposing (Middleton and McKee 2001). Hurricane Mitch buried mangroves in Honduras under 15 cm of sediment. However, these mangroves suffered no mortality (Cahoon et al. 2002). The same hurricane caused massive sedimentation on mangrove surfaces in the Gulf of Fonseca and destroyed extensive areas of mangrove forests. Recovery, especially of *L. racemosa*, was apparent despite high sediment elevation (Hensel and Proffitt 2002).

Hurricanes may act as major selective forces governing coastal ecosystem structure and are capable in the broad-scale conversion of one ecosystem state into another state, e.g., forest into marsh, and mangrove into open water (Michener et al. 1997). Studies on the long-term effects of disturbances are rare. Ferwerda et al. (2007) compared recovery in clear-cut mangroves with hurricane-affected mangroves in Darwin, Australia, 25 years after disturbance. They attributed the difference primarily to the absence of shade in the clear-cut

area which could have affected the settlement and growth of different species, and favoring *Avicennia marina* in the clear-cut area. Knowledge of the long-term effects of clearing, and the factors involved in the regeneration process can make an essential difference for the success of restoration and management of mangrove areas. With the increased attention for restoration issues (King 1991; Ellison 2000), this knowledge becomes even more important.

2.5.6 Mangrove biomass, litter and bird guano

The interaction and degree of environmental gradients define a constraint envelope for determining the structure and productivity of mangrove communities (Twilley and Rivera-Monroy 2005). Distinct mangrove community types include riverine, fringe, basin, scrub, and overwash communities. These distinct communities reflect local variations in topography and hydrology within a coastal landform that influences the distribution of soil resources and abiotic regulators along with hydroperiod gradients (Lugo and Snedaker 1974). The importance of these environmental gradients, resources, regulators and hydroperiod in controlling vegetation patterns and productivity of mangrove ecosystems is well documented in the literature (Lugo and Snedaker 1974; Boto and Wellington 1984; McKee 1993; Chen and Twilley 1999; Feller et al. 2002 and 2003; Krauss et al. 2006). Salinity and nutrient availability have also been recognized as one of the main factors in controlling mangrove forest structure and productivity (Lugo and Snedaker 1974; Cintrón et al. 1978; Chen and Twilley 1999; Feller et al. 2002 and 2003; Castañeda-Moya et al. 2006). Mangrove species respond to low nutrient availability with morphological and physiological plasticity (Feller et al. 2002 and 2003; Lovelock et al. 2004). Long-term fertilization experiments of *R. mangle* in

Belize (Feller 1995; Feller et al. 2002; Lovelock et al. 2006), Florida (Koch and Snedaker 1997) and Panama (Lovelock et al. 2004; ; Feller et al. 2009) have suggested that scrub forests respond positively to phosphorus additions increasing above-ground net primary productivity (NPP_A) and shifting resource allocation from roots to shoots. These experiments have also shown that fringe mangrove trees in Belize respond positively to nitrogen addition but not to phosphorus. Understanding the allocation of carbon to above- and below-ground biomass and productivity is significant for the global carbon budget of mangrove ecosystems (Bouillon et al. 2008). Recent estimates for mangrove forests indicate that litterfall (NPP_L), wood (NPP_W), and root production (NPP_B) account for ~31%, 31%, and 38% of the global NPP_T , respectively (Bouillon et al. 2008). Mangrove forests produce organic carbon well in excess of the ecosystem requirements and are considered important sources of carbon export (~40%) to adjacent coastal waters and local carbon burial (~10%) (Twilley et al. 1992; Duarte and Cebrian 1996; Jennerjahn and Ittekkot 2002; Bouillon et al. 2008).

A key source of nutrients for plants that colonize nutrient-poor environments can be from bird guano deposition, and, as discussed in Chapter 4 in this thesis, this seems to be a factor on the fringing cays at Turneffe. Birds are an integral part of most freshwater ecosystems (lakes, rivers, wetlands) but their function in the trophic dynamics of these water bodies has often been ignored (Kerekes 1994). Bird colonies increase nutrient concentrations and phytoplankton productivity in the Barents Sea (Golovkin 1967), mangrove productivity in Florida (Onuf et al. 1977), and benthic macroalgal production in the Baltic Sea and South Africa (Bosman et al. 1986). Piscivorous seabird colonies also can affect terrestrial habitats. Lindeboom (1984) concluded that penguin excrement was the primary source of nitrogen for

the Marion Island ecosystem, located east in the Southern Indian Ocean. Allaway and Ashford (1984) reported that seabirds were responsible for depositing about 0.7 kg dry weight/m²/year of nutrient-rich excrement onto coral islands on the Great Barrier Reef, Australia, maintaining the forest that provides nesting sites for the colony. Bosman and Hockey (1986) noticed that the presence of guano-producing seabirds changed significantly the structures of the algal, and invertebrate communities. Leaf grazing of mangrove trees that support bird colonies was higher than nearby unenriched mangroves, presumably in response to greater nutritive value in the leaves from enriched areas (Onuf et al. 1977). Bird perch experiments by Powell et al. (1991) demonstrated that the presence of a single bird roosting consistently at the same location can alter the species composition and increase the biomass of a small patch of the surrounding seagrass bed.

2.6 Turneffe geomorphology

Turneffe rests on an isolated carbonate platform (Gischler and Hudson 1998), and these offshore islands have never been connected to the mainland. This makes it an autochthonous system. The continental margin of Belize is structured by a series of five north-northeast-striking fault-blocks that form the basement of the 250 km long barrier reef and the three isolated oceanic platforms, Turneffe, Lighthouse Reef and Glovers Reef (Gischler and Lomando 1997; Fig. 2.3). All three platforms are surrounded by deep water and have breakwater reefs encircling lagoons (Stoddart 1962).

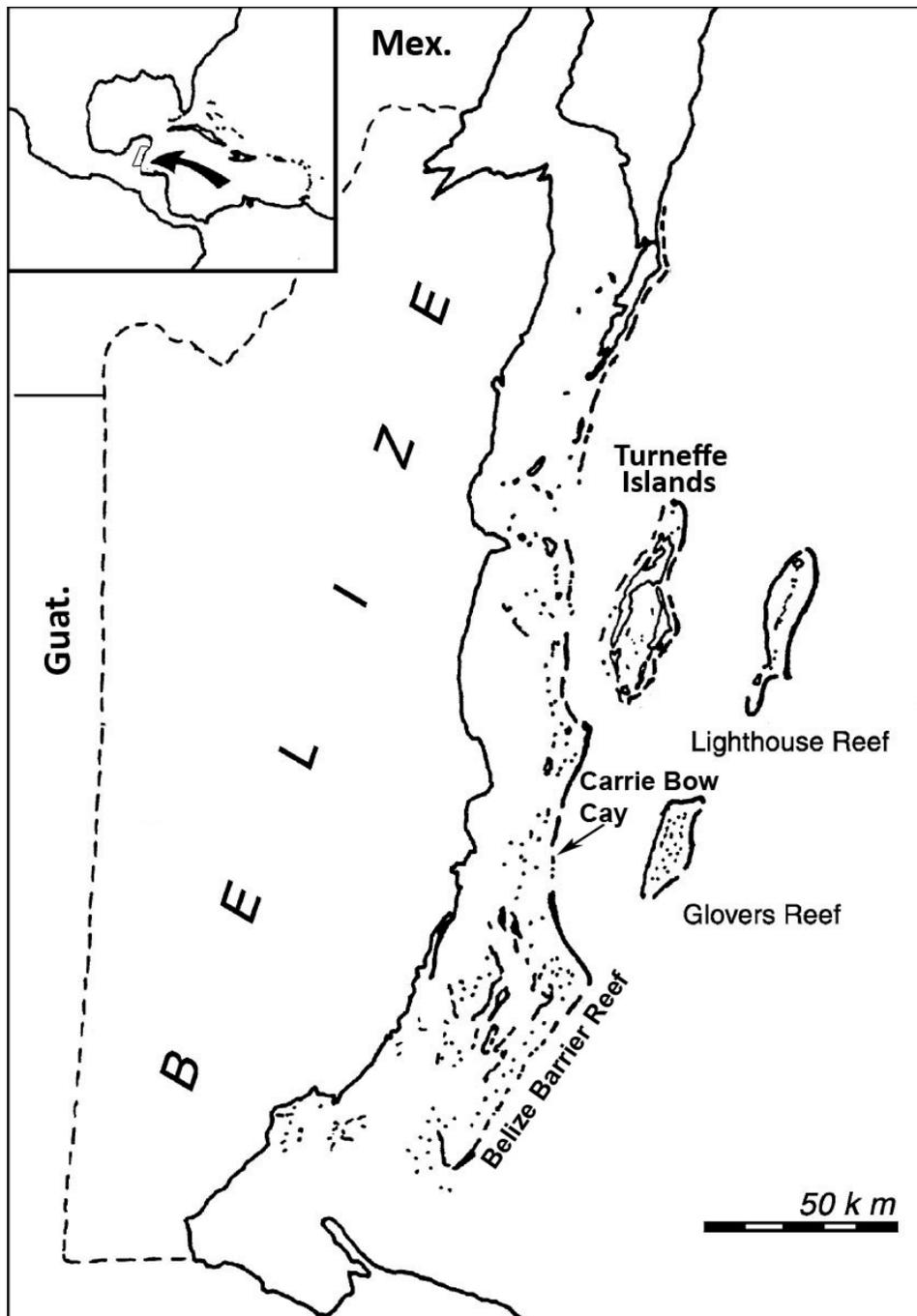


Figure 2.3. Location of Belize City, Carrie Bow Cay, Belize Barrier Reef and three offshore atolls: Turneffe, Lighthouse Reef and Glovers Reef. Inset map shows location of Belize within Central America and the Caribbean. (Adapted with permission Gischler 2003).

According to Gischler and Hudson (1998), plate tectonics produced the morphology of ridges and valleys that control the distribution of modern reefs in southern Belize. Winds and storms controlled most of the sediments that developed on these platforms, and subsequent reefs often developed due to the build-up of sediments, especially on windward margins (Wood 1999). A shallow reef grows around the platform when the rate of carbonate production at the margins was high, combined with a steady rate of subsidence (Wood 1999). A lagoon with patch reefs formed within the perimeter reef.

The following account of the Holocene flooding scenario for Turneffe was provided by Gischler (2003; Fig. 2.4).

“During the late Pleistocene, Turneffe Islands were dish-shaped limestone islands that were probably fringed by coral reefs. As the rising Holocene sea level approached the level of the bedrock surface, rising groundwater enhanced soil development. Subsequently marine waters breached the peripheral bedrock rim (perhaps through relic tidal channels in the elevated Pleistocene reef margin) and entered the central depressions, allowing mangroves to colonize the inner parts of the islands, this happened between 7000 and 2700 years BP. As sea level continued to rise, mangrove-rimmed lagoons with extensive Halimeda [seagrass] growth formed, comparable to the present situation in Turneffe Islands. At even higher sea levels, mangrove areas diminished in size and reefs colonized or retrograded onto the peripheral rim of the Pleistocene islands. In Turneffe Islands, this stage of peripheral reef development started around 4800 years BP reflecting the different bedrock elevation (Gischler and Hudson 1998; Gischler and Lomando 2000). Open marine conditions

eventually developed in the lagoons on the northernmost part of Turneffe Islands. In the main lagoonal part of Turneffe Islands, open marine conditions did not develop due to the high bedrock elevation and the protected position of Turneffe behind another platform. Flooding of the Turneffe platform at relatively low rates of sea level rise as well as protection and lack of open marine conditions has led to extensive mangrove development.” (Gischler 2003, pp. 127-128).

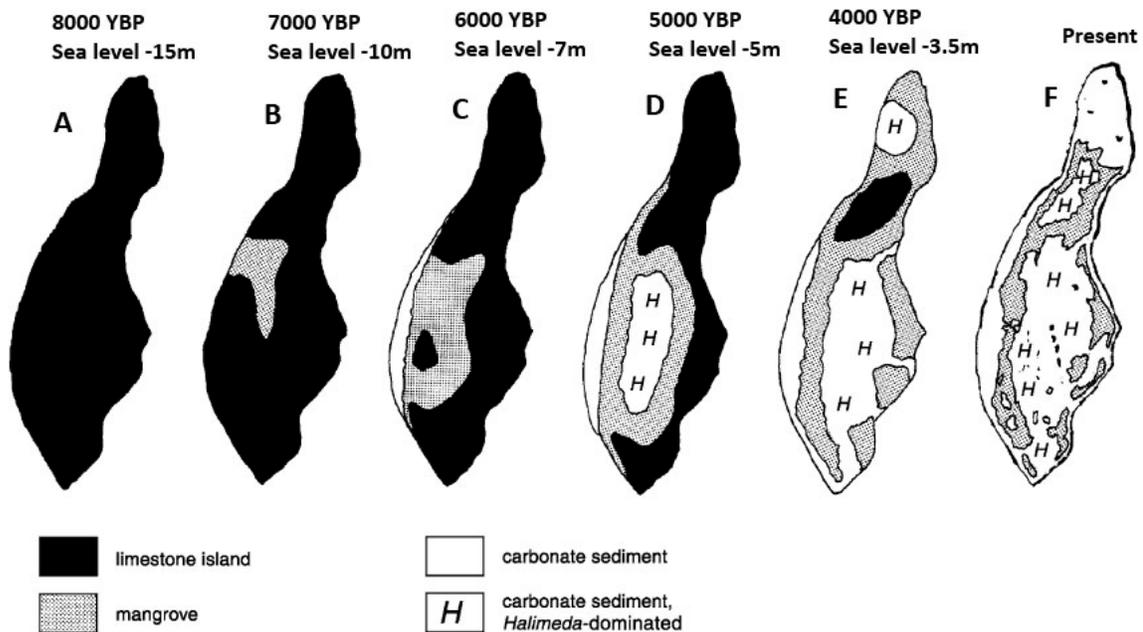


Figure 2.4. Schematic sketches showing Holocene development for Turneffe. (A) 8000 YBP (years before the present), sea level ca. 15 m below present level. Turneffe was an emergent limestone islands; transgression of marine water, probably through the precursors of modern tidal channels; Pleistocene patch reefs probably still emergent as small cays in lagoon; (B) 7000 YBP, sea level about 10 m below present level. Parts of Turneffe flooded and mangrove-dominated; small Pleistocene areas probably still emergent at margin and in lagoon; (C) 6000 YBP, sea level about 7 m below present level. Mangrove-dominated parts of Turneffe increase in area; (D) 5000 YBP, sea level about 5 m below present level. Large areas in the east are still emergent, but a mangrove-encircled lagoon develops with *Halimeda*-dominated sediment; (E) 4000 YBP, sea level about 3.5 m below present level. Turneffes’ main lagoon largely developed; seaward tidal channels open; parts of the north still emergent; carbonate sedimentation initiated on northernmost part, probably still surrounded by mangroves. (F) Present situation. (Adapted with permission Gischler 2003).

2.7 Turneffe biodiversity

Although there may be as many as 15 atolls or atoll-like structures in the Caribbean, the Mesoamerican Caribbean Reef contains four of the best developed atolls, including Turneffe (Kramer and Kramer 2002). Turneffe is composed of a group of cays with an encircling coral reef structure. The windward and leeward mangrove rims encircle up to 8 m deep lagoons with restricted circulation. The lagoon in the northernmost part of Turneffe is well-circulated and has abundant patch reefs of coral with no extensive mangrove development (Gischler and Hudson 1998). The eastern seaboard of this atoll has a distinct group of fringing cays not seen on the other Belizean atolls (Fig. 2.5). In spite of these distinctive features, Turneffe lacks the conservation status of the other atolls, with the exception of two spawning aggregation sites and the declaration of a public reserve at Cockroach Bay (northern Turneffe).

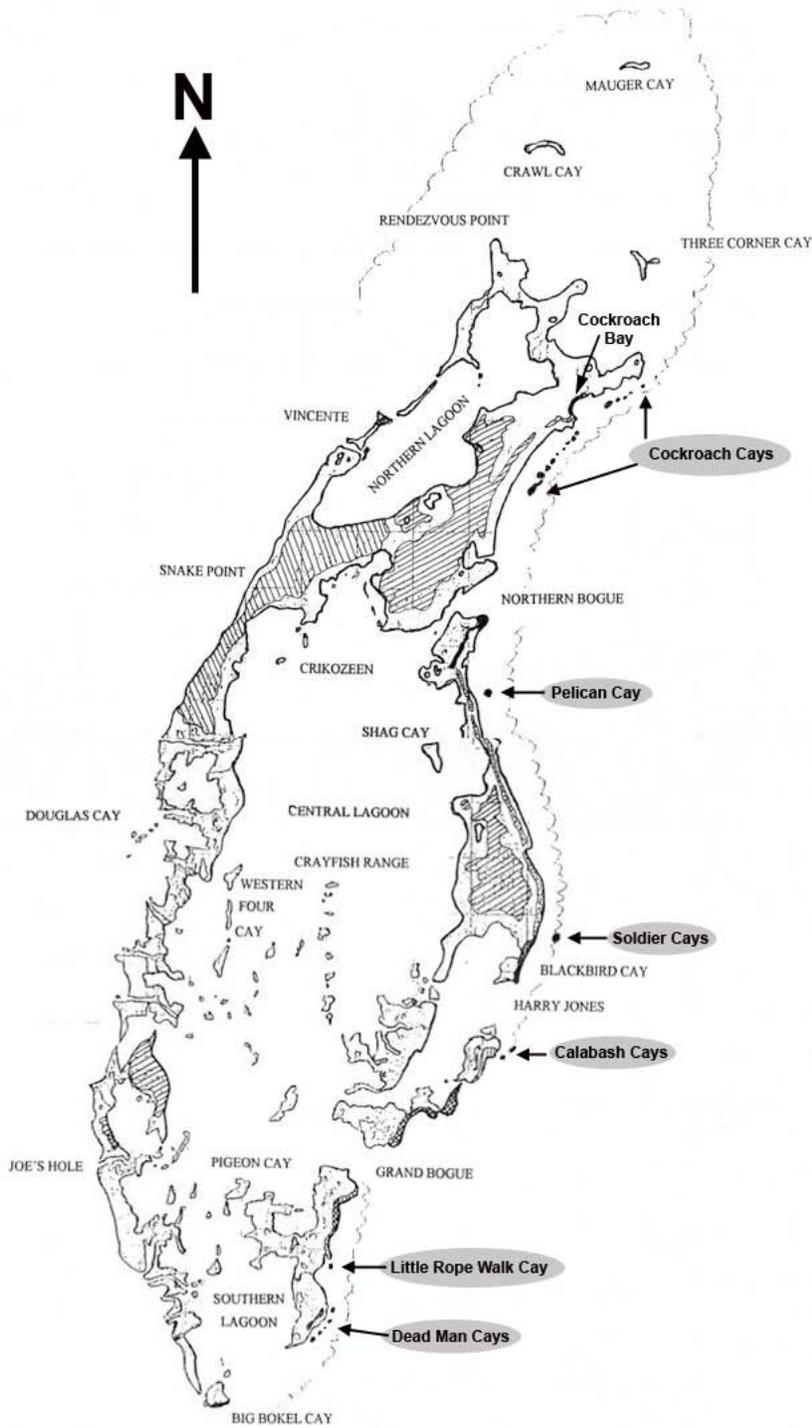


Figure 2.5. Map of Turneffe showing the eastern fringing cays. (Redrawn from McGill 1996).

Turneffe encompassed an area of 525 km², with 125 km² dominated by mangroves. The individual cays were characterized by a variety of mainly wetland vegetation types dominated by mangrove forests, which reflected the low topography of the land. The higher elevation cays were generally colonized by littoral forest, (e.g., *Coccoloba uvifera* L., *Bursera simaruba* L. and *Thrinax radiata* Lodd. ex J. A. and J. H. Schult) and *Cocos nucifera* L. A number of bird species were observed to roost on the littoral and mangrove cays of Turneffe, amongst them, the great-tailed grackle (*Quiscalus mexicanus* G. F. Gmelin), white crowned pigeon (*Columba leucocephala* L.), brown pelican (*Pelecanus occidentalis* L.), mangrove warbler (*Dendroica petechia* L.), and green heron (*Butorides virescens* L.). An observation made by Stoddart (1962), was that introduced rats (*Rattus rattus* L.) were a major pest on the large islands and smaller cays along the eastern side of Turneffe. However, at the time of this study no rats were encountered on any of the fringing cays visited during field work.

Turneffe's reefs, mangrove and seagrass habitats provide important habitat for diverse assemblage of reef fish, lobster, conch, and sportfish. Fish spawning aggregation sites are also known to exist off both the northern and southern tips of Turneffe (Kramer and Kramer 2002), and it is believed that some sites have been lost (Kobara and Heyman 2010). Meerman (2006) concluded that there is ample reason for declaring much of the Northern Turneffe a conservation zone. Turneffe is the only atoll in Belize with extensive mangrove forests in close proximity to seagrass beds and coral reefs and provides a unique opportunity to study mangroves and their interaction with adjacent ecosystems.

2.8 Turneffe and human settlement

Historically, the atoll was used by humans during the Maya era (Stoddart 1963). At the Calabash Cays on the eastern side of Turneffe, a freshwater lens can be accessed via surface wells. It is very likely that settlements were established especially around those areas, and it was around these areas that broken Maya pottery has been recovered. During the modern era, Stoddart's 1960 survey documented that in addition to the larger sandy cays several of the small eastern fringing cays were inhabited by humans. The inhabitants had domesticated animals, mainly chickens, dogs, and pigs (Fig. 2.6). The largest piggery was located on the Calabash Cays. These animals were seen wandering between Big and Little Calabash Cay across the reef flat (Stoddart 1962).



Figure 2.6. Photo of pig feeding between Big and Little Calabash Cay. The largest piggery was at the Calabash Cays. Photo taken during Stoddart's survey of 1960-61. (Photo credit, Stoddart).

The settlers on Turneffe were also engaged in the planting and harvesting of coconuts. The dominant vegetation of the higher elevation eastern cays at the time of Stoddart's survey in 1960 was the coconut palm (Stoddart 1962). Large areas were cleared and planted to coconuts (Fig. 2.7). Little Calabash Cay was the center of the Turneffe copra (the dried endosperm of the coconut), industry (Stoddart 1969). Large buildings and wharves had been erected on these cays to cater for the industry. Records obtained from the Belize Archives and Records Service, showed that around the 1950's the growing and harvesting of sponge was also thriving. Special stipulations were included in approved leases for coccol plantations, whereby lease holders were not to undertake any land development of the mangrove swamps or any development that would affect or interfere with the sponge industry without the consent of the director of agriculture. Both the coccol and sponge industries were affected by subsequent hurricanes.



Figure 2.7. Aerial photograph of Soldier Cay showing the coconut palms (*Cocos nucifera*), as the dominant vegetation. Soldier Cay was also inhabited by humans. Photo taken during Stoddart's survey of 1960-61 before Hurricane Hattie 1961. (Photo credit, Stoddart).

Goodban (1952) reported that coconut trees were already in the settlement of Belize by 1809 and that large plantations had been established in coastal areas and the cays by 1883. Based on available export figures, by 1870 the cocal industry had achieved an important status, and plantations had been progressively extended until nearly all the suitable coastal and cay areas had been planted to coconuts by 1920 (Goodban 1952). A decline of the industry occurred in the 1930's after Belize was struck by the Hurricane of 1931 (Goodban 1952). This hurricane created havoc in the cocal plantations on the cays and coastal areas. Later, the storms of 1942 and 1944 struck the northern and southern areas of Belize, respectively, so that all the plantations were subject to storm disturbance over a relatively short period of time (Goodban 1952). Coconuts are particularly vulnerable to hurricanes. Damage to plantations from the Hurricane of 1931 was approximately 80% of bearing trees and, since the cost of rehabilitation was high, most of the plantations were left on their own to recover. At the time of Goodban's report (1952), the plantations had failed to recover on their own, and no extensive rehabilitation had been carried out. Some of these cocal forests were considered to be breeding grounds for pests and diseases. The cocal forest of Turneffe was among the areas affected by the earlier storms but seemed to have been rehabilitated by 1952. In this year, it was estimated to contain 1000 acres of coconuts (Goodban 1952). The Turneffe plantations were on government land that was leased to private interests.

In 1955, Hurricane Janet made landfall on the northern part of Belize and greatly affected the cocal plantations in that area. Efforts were made to revive the industry by the introduction of the Coconut Industry Board established in 1958 (Mertley et al. 1987). However, in 1961, Hurricane Hattie made landfall south of Belize City, passing directly through Turneffe.

Aerial photographs taken by Stoddart in 1962 show the devastation caused to the coccol forest on the atoll. Entire cays, which had been planted to coconuts, were stripped of vegetation and had their substrate eroded. According to retired fisher folk from Belize City, the coccol industry was abandoned on Turneffe after the passage of Hurricane Hattie with the exception of a few cays where coconuts were reintroduced. Indeed, by 1962, Belize only exported around 17500 coconuts while importing 275400 coconuts from Mexico and Honduras (Mertley et al. 1987). A decline on the industry was seen afterwards. By comparison, during its peak in 1914, Belize exported an estimated 6 million coconuts (Goodban 1952).

Lethal yellowing, a disease associated with phytoplasmas (Beakbane et al. 1972), affects at least 30 species of palm (Harrison et al. 1999) and has killed millions of coconut palm trees throughout the Caribbean, Florida, and Mexico, and currently threatens the Central American region (Maust et al. 2003). Phytoplasmas are minute cell wall-less prokaryotes that are generally confined to the phloem of plants (Maust et al. 2003). Phytoplasmas have been identified as the probable cause of diseases in several hundred plant species (Agrios 1978). Lethal yellowing was confirmed in Belize in December of 1992. This disease affects coconut trees, causing them to die within 3 to 6 months after the appearance of the first symptom (Ashburner and Quiroz 1996). By the late 1990's, there was an outbreak of lethal yellowing on the coccol forest of Turneffe (Platt et al. 1999). There was a concentration of the disease on Main Calabash Cay (Berlin 1996). At the time of my field research (2006-2008), the smaller cays east of Calabash Cay (Big Calabash Cay and Little Calabash Cay) had no signs of lethal yellowing, even though these cays are in close proximity to Main Calabash Cay.

Coconuts are still an important part of the vegetation along the mainland coast of Belize and on the cays. Even though it is not a thriving industry in Belize at the moment, coconuts have become an integral part of the Belizean culture through food. Belizeans consume coconut milk in the popular coconut rice and rice and beans dish. The coconut trees themselves are important economically to the tourism industry. Resort owners spent a considerable amount of resources in trying to keep their coconut palms healthy. As in other tropical locations around the world, the selling point of many tourist destinations in Belize is the iconic (but non-native) coconut palms, white sandy beaches and clear waters.

Humans are having other impacts on the Turneffe cays. A study conducted by Minty et al. (1995) found that the youthful nature of the soils in many of the eastern cays makes them extremely susceptible to erosion when vegetation cover was removed. Meerman (2006) reported that the eastern side of the atoll, including the small cays, was being affected by human activities (fishing, development and land speculation). Land on the atoll is owned by the Government of Belize, but there has been leasing and development of land parcels on the east coast (McGill 1996). This development is of concern to conservationists because it is taking place in the most sensitive sites of the entire island mass. The fringing cays have potential for turtle and sea bird nesting sites, and this area encompasses critical habitats for the endemic species like Turneffe parrotsnake and habitat for the American crocodile.

Human activities on the atoll are increasing. At the time of this study, three operational resorts catered to scuba divers, sport fishermen and tourists and there were two research centers. In 2005, the first airstrip was constructed on Blackbird Cay. On March 2010, the

Belize National Coast Guard inaugurated a multi-million dollar Forward Operating Base located on Main Calabash Cay. Other human presence at Turneffe consists of numerous small fishing camps scattered throughout the atoll. Small-scale commercial fishers collect spiny lobster and conch and fish for snapper and grouper. A substantive amount of the catch from Turneffe goes to the cooperatives in Belize, primarily from the conch and lobster fishery.

2.9 Landfall of Hurricane Hattie of 1961 on Turneffe

Hurricane Hattie was the most recent storm to cause catastrophic damage to the vegetation and cays of Turneffe. In 1960, Stoddart surveyed the cays along the Belizean Barrier Reef system, including Turneffe. In October 1961, Hurricane Hattie hit Turneffe, and destroyed entire cays, as well as most of the vegetation and human habitation (Vermeer 1963).

Hurricane Hattie was a Category 5 hurricane (Saffir-Simpson Hurricane Wind Scale) in which the eye swept along a 40 km wide track. When plotted on hurricane charts, Hurricane Hattie's path went right across Turneffe (Fig. 2.8). This intense storm had winds near the center that exceeded 240 km/hr and gusts of more than 320 km/hr (Stoddart 1963). The fringing cays on the eastern side of Turneffe with their fringing mangrove communities, littoral and cocal forest were severely damaged. Most of the settlers perished during Hurricane Hattie, and Turneffe was largely abandoned as a place of permanent settlement until recently. Hurricane Hattie completely transformed some of the cays that Stoddart had surveyed the previous year. Within a few months after the storm, Stoddart revisited and remapped the areas that he had surveyed in 1960 (Stoddart 1963).

research on damage and recovery from hurricanes in atoll ecosystems. Historic aerial photography and Dr. David Stoddart's field work of the 1960's enabled the investigation of disturbance and recovery over several decades.

Chapter 3: Fringing cay dynamics and the impacts of hurricanes and humans

3.1 Introduction

In the most hurricane-prone parts of the Caribbean, the average return time of hurricanes ranged from 9.4 years in Florida to 12 years in the U.S. Virgin Islands and Puerto Rico between 1851 and 2001 (Gardner et al. 2005). Due to their geographic location, offshore cays receive the brunt of these tropical storms. These offshore cays also experience episodes of human development. In this chapter, I describe the structure of reefs in general with a focus on the back-reef sediment apron upon which fringing cays form on Turneffe. I then present historic and contemporary data on the human use, geomorphology and vegetation of the fringing cays at Turneffe, followed by a spatial analysis of the changes that have occurred since 1945.

3.1.1 Wind, waves, tides and coral reefs

In reef-bound tropical coastlines, a substantial amount of surface wave energy is dissipated through wave breaking and bottom friction processes on coral reefs (Lowe et al. 2005). Coral reefs that surround Turneffe were the primary wave dissipaters and, by extension, affected the conditions of the fringing cays that formed behind the reef crest. The coral reefs were bisected by well drained channels. In most areas, the fore reef was structured with spurs and grooves (Fig. 3.1). These channels allowed for the reworking of sediments on the fore reef.

Planimetrically, the orientation of spurs and grooves are typically at right angles to the direction of refracted waves, and spacing is related to wave energy (Munk and Sargent 1948; Emery et al. 1949; Blanchon and Jones 1995). Aerial surveys showed that the eastern side of Turneffe had a more well-developed spur and groove formation (Fig. 3.2), than the protected leeward side of the atoll.

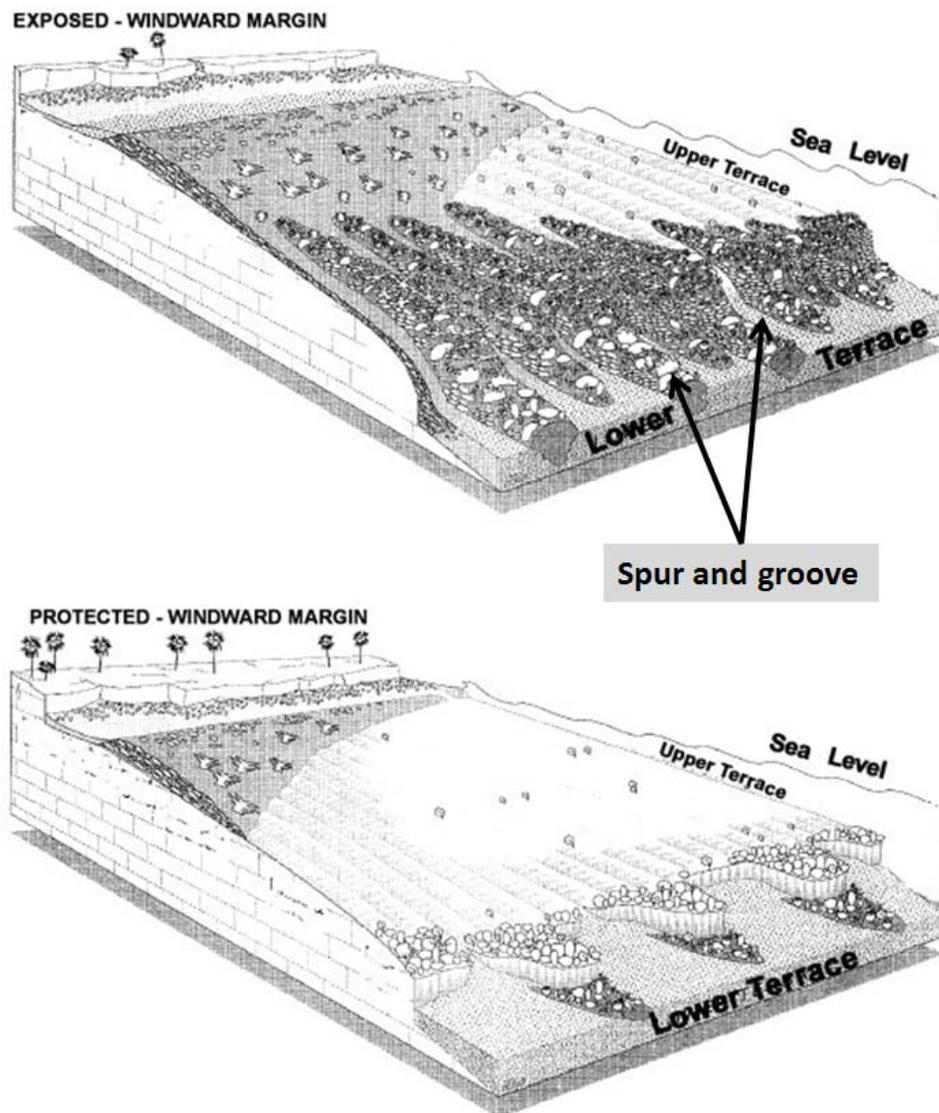


Figure 3.1. Diagram with typical characteristics of exposed and protected coral reef zonation. Note prominent spur and groove formation on the exposed-open reef. (Adapted with permission Blanchon et al. 1997).

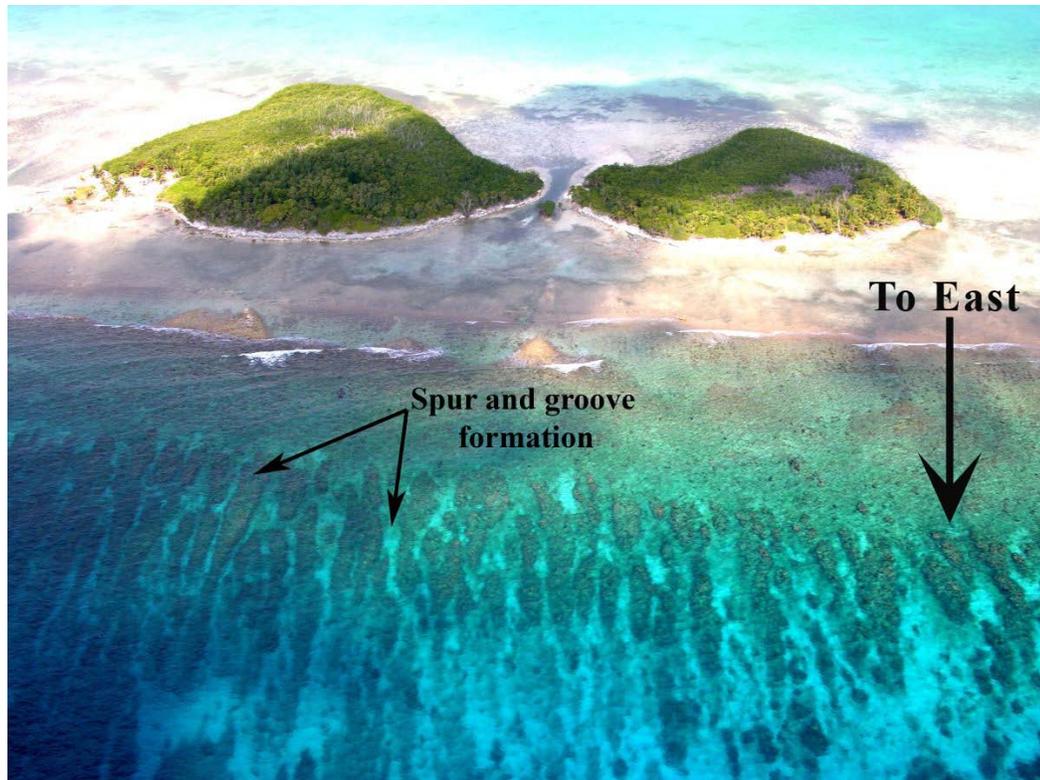


Figure 3.2. Oblique aerial photograph showing spur and groove reef formation on the ocean-facing side of Cockroach Cay-22 and -23, Turneffe Atoll.

A pressure gradient that drives reef circulation is created when a wave breaks on a reef and produces an increase in the mean water surface elevation (Longuet-Higgins and Stewart 1962). These wave-driven currents are responsible for the cross-reef transport of nutrients, sediment, plankton, larvae, etc. (Lowe et al. 2005). Reef sediments in the form of sand and coral rubble accumulated behind the reef crest on the back-reef sediment apron on Turneffe's eastern seaboard. In addition to routine wave energy, offshore cays and atolls bear the brunt of incoming storms. Larcombe and Carter (2004) explained that cyclonic activity on tropical reef shelves acted as a sediment pump. They explained that tropical cyclones contributed sediment to the shelf system in three discrete ways: 1) by direct breakage of reef material

during cyclone passage across the outer shelf reef tract, which means carbonate gravel and sand were added to the back-reef sediment aprons; 2) by erosion of Pleistocene clay and breakage of shells and other biogenic material at the seabed within the middle shelf cyclone corridor; and 3) by rainfall-induced input of terrigenous detritus at river-mouth point-sources. On Turneffe, the first of these mechanisms appeared to dominate formation of fringing cays.

The zonation pattern found on the eastern side of Turneffe was clearly visible from the air (Fig. 3.3; Cockroach Cays). This planimetric view of a section of the 2006 photo-mosaic shows the cays in relation to the larger islands and the reef system. The horizontal reef zones found within the high wave energy environment included the fore reef and reef crest. Behind the reef crest and with less wave energy was the reef flat zone. The reef flat zone included the back-reef sediment apron, where sediment can accumulate above the spring high tide, and a lagoon. Different types of vegetation can occupy various areas depending on different parameters (e.g., tide, salinity, and elevation, type of substrate and wave energy). A unique feature of Turneffe that differed from the other Belizean atolls was the chain of small fringing cays with vegetation that occurred especially on the eastern seaboard of the atoll. These small cays link mangrove, seagrass and coral reef ecosystems. These cays are under pressure for development and have already suffered from heavy human impacts prior to Hurricane Hattie 1961. As such, these offshore cays are worth protecting for scientific and conservation reasons and can hold answers to the interplay of seagrass beds, mangrove forests and coral reefs, without the effects of fluvial discharge.

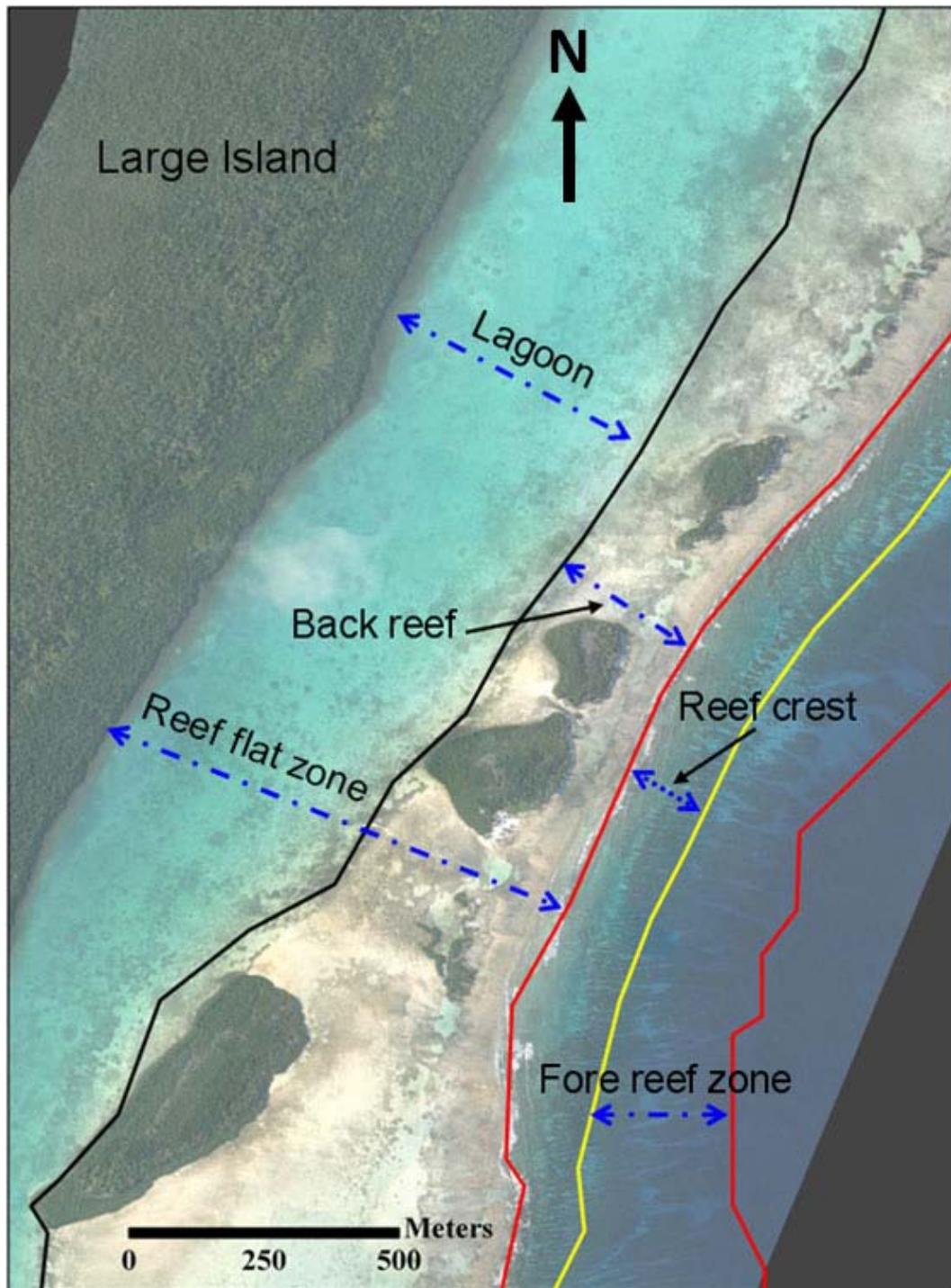


Figure 3.3. Aerial view of Turneffe's northeastern cays (Cockroach Cay group). Photo-mosaic from 2006 showing coral reef zonation and location of fringing cays within the back-reef area.

In the semi-protected environment of the back-reef sediment apron, seagrass, mangrove, littoral and coral forest colonized sediments, depending on their elevation relative to high and low tide levels. Vegetation established behind the reef crest was continually affected by routine and periodic peak wave action and tidal inundations. In the case of seagrass and mangroves, both were well-adapted to inundation, and their survival depended on the movement of water for the dispersion of seeds and propagules. In these environments, seagrass can survive periodic exposure from low tides. However, unlike mangroves, they do not have the ability to colonize above the high tide line. The episodic inundation and enhanced wave energy during storms were important disturbance processes in these low-relief ecosystems.

Recurrent tropical storms have a profound effect on Belize's coastline. Because of their significant economic and ecological impacts, Caribbean hurricanes are now well documented. The online hurricane database maintained by NOAA provides information on specific hurricanes from 1851 forward. The best track data provide information on storm direction, wind speed, translation speed and storm category. The effects of early hurricanes are not well documented, except for the effects of Hurricane Hattie of 1961 on coastal Belize, and specifically Turneffe, that were documented by Stoddart (1963). During this hurricane, Cay Caulker, an offshore Belizean island to the north of the track of Hurricane Hattie experienced 4.5 m of storm surge above mean sea level (Stoddart 1963) while Mullins River, where Hurricane Hattie made landfall along the Belizean coast, experienced 6 m of storm surge above sea level (Stoddart 1963).

3.1.2 Human activity, storms and cay vegetation on Turneffe

Human activities on Turneffe date back to the Late Classic to early Post-Classic Mayan periods based on dated pottery fragments (Wright et al. 1959; MacKie 1963). Wright et al. (1959) believed that these settlements were permanent and that the Mayas engaged in fishing and subsistence farming. There is no doubt about the potential for long-term habitation since there were at least on three sites on the eastern side of the atoll where fresh water can be obtained from hand-dug wells. Access to fresh water on an offshore island is essential and the discovery of water sources can lead to prolong settlement of these areas. Settlement by fishers and the rise of importance of the cocal industry in the late 1800's were also influenced by the availability of fresh water on Turneffe. Well-established settlements like the one at the Calabash Cays had substantive buildings before Hurricane Hattie destroyed the site in 1961 (Stoddart 1963).

For many years prior to Hurricane Hattie, the vegetation on the eastern cays of Turneffe had been modified by human activities, primarily by the cutting of littoral forest and mangroves and planting to coconuts. Stoddart (1962) documented some of the vegetation types that were found on the cays during his survey in 1960 and 1961. The dominant vegetation was the coconut (Stoddart 1962). According to Henderson (in Stoddart 1962), coconuts were widespread on the sand cays of British Honduras by 1810 and were established on the atolls as early as 1720. In addition to the cocal industry, a sponge industry was also initiated on Turneffe in the early 19th century but had failed by the 1930's due to disease and hurricane damage (Stoddart 1962). According to retired fishers from Turneffe, most of the sponge

aquaculture was conducted on the protected areas of the inner lagoons. The interplay between the large scale historic effects of humans on the fringing cays and subsequent storms makes the fringing cays on Turneffe a good site to study long-term changes at the landscape level.

Like mangrove forests around the world, mangroves in Belize are frequently disturbed. Storm damage ranges from defoliation and crown damage to windthrow of complete areas (Hutchings and Saenger 1987). Human disturbances on Turneffe vary from selective logging to clearance of all vegetation for temporary or permanent developments, placing an ever increasing pressure on coastal resources and habitats. Turneffe provided an ideal place to study these impacts and processes of recovery. Knowledge of the long-term effects of vegetation clearing, and the factors involved in ecosystem recovery following storms are important for coastal planning and management on Turneffe as well as the rest of Belize. With the increased attention on restoration issues (King 1991; Ellison 2000), this knowledge becomes even more important.

The establishment and first stages of regeneration of mangroves has been addressed by various studies (Sukardjo 1987; Clarke and Allaway 1993; Roth 1992). Factors such as fruit dispersal (Clarke and Allaway 1993; Sengupta et al. 2005), predation by crab (Osborne and Smith 1990) and soil properties (Duarte et al. 1998) influence the initial stage of colonization. Anecdotal research on the dispersal of mangrove propagules emphasized long-distance dispersal in high-energy oceanic environments where ocean currents were thought to carry *R. mangle* propagules at least 100 km (Davis 1940; Murray 1986). However, more recent studies indicate that dispersal was more limited for most species (Nathan 2001).

Clarke and Allaway (1993) gave a mean dispersal range of a few hundred meters for *A. marina*, the mean settlement of propagules of the *R. mangle* takes place within a few meters from the adult tree (Blanchard and Prado 1995). This indicated that nearby presence of well-developed mangroves may be an essential influence on the rate of re-establishment of mangroves in human and naturally cleared areas. Krauss et al. (2008) conducted a review of the literature on the environmental drivers of mangrove establishment and early development.

Susceptibility to and recovery from hurricane damage also varied between Caribbean mangrove species. Ross et al. (2006) studied recovery of fringing mangroves in Florida nine years after the passage of Hurricane Andrew 1992. Mortality and damage were concentrated in canopy individuals, and the changes in the relative abundance of the two dominant mangrove species following the hurricane varied strongly along the productivity gradient. Ross et al. (2006) found that the shade-tolerant *R. mangle* generally became the dominant canopy in the competitive environment of the recovering coastal fringe forest following Hurricane Andrew, but the shade-intolerant *L. racemosa* was better represented in less productive interior fringe sites where canopy closure was delayed. *Rhizophora mangle* dominated the mangrove forest of Turneffe and seems better adapted at colonizing even the higher energy areas like the fringing cays on the eastern side of Turneffe. However, differences in storm susceptibility depend on mangrove structure as well as species. Bardsley (1985) determined that dwarf mangroves sustained little impact in contrast to tall emergent mangroves from the Australian cyclone Kathy. Roth (1992) also observed higher susceptibility of emergent mangroves to windthrow under hurricane conditions on the

Nicaraguan coast. Patterns of mangrove mortality relative to hurricane intensity suggested that it depends in part on local site conditions. Forest damage is greatest about the eyepath, damage is known to decrease with increasing distance from the storm's track (Stoddart 1963; Doyle et al. 1995) and sites adjacent to open water in the direct windpath can sustain higher impacts than interior sites with a higher degree of wind sheltering (Doyle et al. 1995).

3.1.3 Landscape change, remote sensing and GIS

Historical reports and maps are an important source of information on hurricane damage; aerial photographs and satellite images are another. Historical aerial photographs are recognized as an important source of information for studies of vegetation dynamics (Green et al. 1993). Data from remote sensing satellites enables efficient monitoring of land use and land cover change because of repetitive coverage at short intervals and consistent image quality. With the rapid growth of technology and software development for geographic information systems (GIS), the use of historical aerial photographs has opened new possibilities for the analysis of vegetation changes. For example, with digital image processing and GIS techniques, it is possible to detect and quantitatively analyze vegetation changes along ecosystem boundaries over time (Aronoff 2005). These changes can then be linked to anthropogenic or natural disturbance processes.

In Belize, historical vertical aerial photographs come from the reconnaissance work conducted by the Royal Air Force, UK (RAF) and United States Air Force (UAF). A large number of historical photos are now declassified and are available in libraries, archives and

government institutions. A substantive number of RAF photo prints was housed at the Ministry of Natural Resources in Belmopan, Belize. The collection in Belmopan has some coverage for Turneffe. In the UK, The British Empire and Commonwealth Museum has additional coverage for Belize. The oldest set of photographs available for my study was from 1945, and I used this for comparative analysis of landscape change over the last six decades.

3.1.4 Study objectives and research questions

The broad objective of this study is to examine local and landscape-scale long-term changes in cays and vegetation patterns and process along the east coast of Turneffe before and after a major hurricane. The specific objectives are to: 1) document changes in cay location and vegetation composition and cover over time; 2) explore causal agents responsible for cay changes. I tested the following hypotheses: 1) there has been a significant reduction in the number and vegetated area of fringing cays on the eastern seaboard of Turneffe since 1945; 2) the coconut palm has not returned to the before-Hurricane Hattie coverage but instead mangrove coverage (mainly *R. mangle*) has expanded on the fringing cays; 3) the majority of the fringing cay vegetation is under the influence of tides; 4) severely eroded cays revegetate in the same general area following storm damage; 5) the orientation of the longest axis of the cay vegetated area is parallel to the reef crest in front; 6) there is a directionality to routine wind and episodic storm track directions; and 7) fringing cays have shifted away (due west north-west) from the reef crest between 1945 and 2006.

3.2 Data and methods

3.2.1 Study area

Turneffe is approximately 30 km from Belize City and 12 km outside the Belize Barrier Reef. It is the largest of the three atolls located in Belize and has an area of approximately 525 km². The autochthonous nature of this atoll provides an ideal working environment for biogeographical studies and dynamics of coastal ecosystems (mangrove forests, seagrass beds and coral reefs) in the absence of fluvial discharge. The Turneffe platform is surrounded by deep water (Stoddart 1962) and has a surface-breaking reef rim with a windward spur and groove system (Stoddart 1962; James et al. 1976; Gischler 1994). Turneffe has an extensive mangrove forest primarily dominated by *R. mangle*. This forest grows on a variety of substrates and ranges from open canopied dwarf forests (≤ 1.5 m in height), to closed canopied forests that reach a height of ≥ 15 m. The lagoon floors are extensively covered with the seagrass *Thalassia testudinum* Banks and Sol. ex K.D. Koenig and the alga *Halimeda* spp. (Gischler and Hudson 1998); these species can also be found along the back-reef zone.

The fringing cays on the eastern seaboard of Turneffe (Cockroach Cays to Dead Man Cays) extend for approximately 40 km in a north to south direction (Fig. 3.4). Access to the fringing cays was by boat through the various channels, inner lagoons and reef breaks. The University of Belize Institute of Marine Studies, research station, located on Main Calabash Cay, was used as the base station during field work. Remote sensing and field work during

2006, 2007 and 2008 was conducting in the early months of each year (February to July) to avoid field work during hurricane season.

The fringing cays found on the eastern seaboard of Turneffe can be grouped into three geographically separate groups (Fig. 3.4): the Northern Group (Cockroach Cay group), the Central Group (from Pelican to Little Calabash Cay), and the Southern Group (from Little Rope Walk to Dead Man Cay-1). In some maps, the Cockroach Cays are divided into two groups, the Cockroach Cays and the Grassy Cays Range. To avoid confusion and to be consistent with Stoddart's naming and numbering of Turneffe cays, I will use the term Cockroach Cays to describe the group of northeastern fringing cays. Stoddart produced detailed maps of selected eastern cays based on oblique and vertical aerial photographs from 1960 and 1962 that covered cays from Dog Flea Cay to Dead Man Cays (Stoddart 1962). When Stoddart assigned the names and numbers for the fringing cays during his investigation, he did not include two of the cays from this group that were present during his survey. He did mention Rope Walk Cay (also known as Lindsay Cay) and that he was unable to visit due to its inaccessibility. The other cay was between Cockroach Cay-2 and -3. This cay was missed and was not included in his map, but this cay was visible from aerial photographs from 1945 and those taken before and after Hurricane Hattie. Both cays were incorporated in this study.

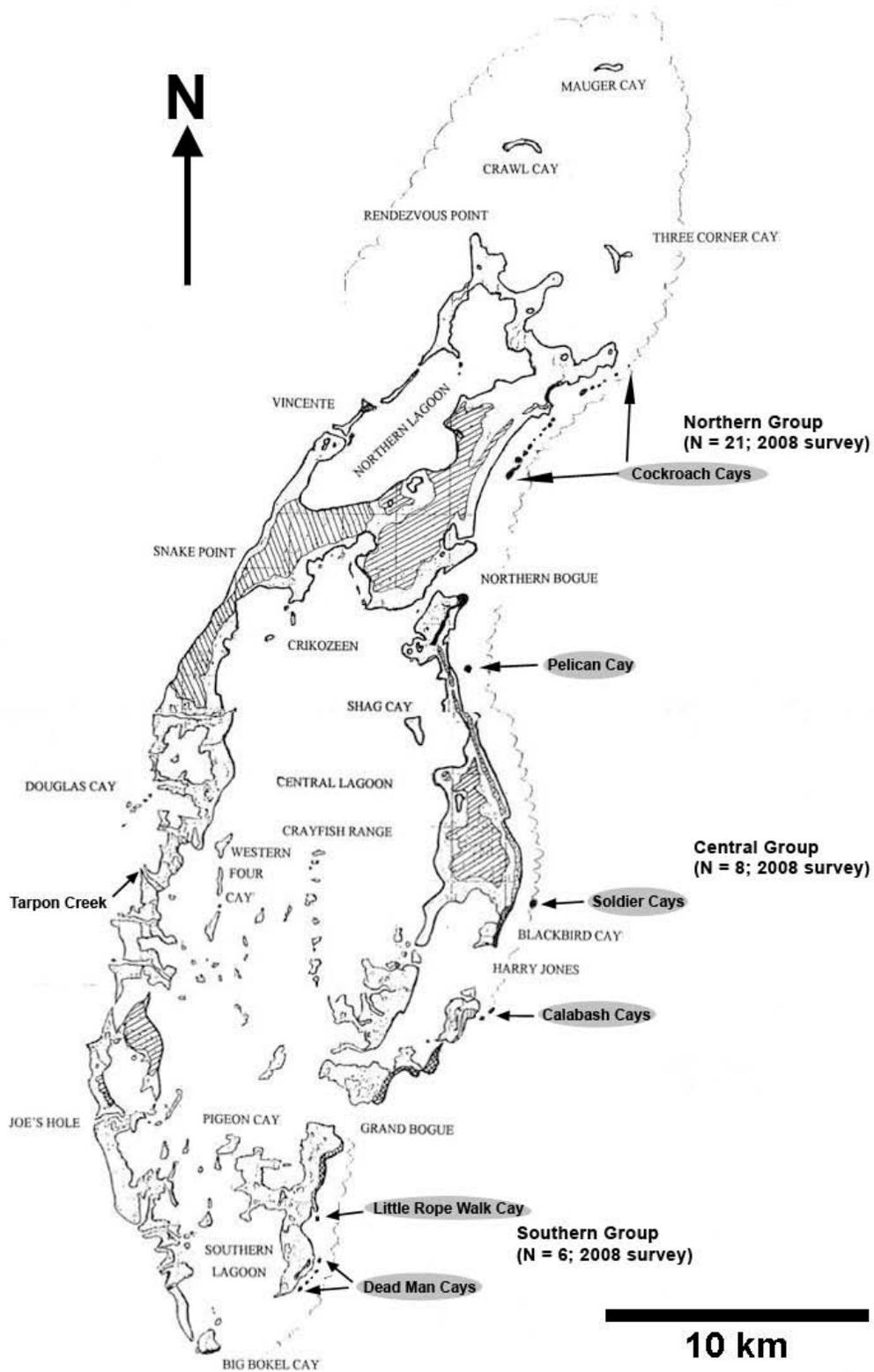


Figure 3.4. Map of Turneffe. Highlighted names were part of survey and shows the grouping and number of cays. (Redrawn from McGill 1996).

3.2.2 Satellite imagery and aerial photographs

3.2.2.1 Satellite imagery

I obtained QuickBird satellite images for the eastern seaboard of Turneffe, taken in August 2005 (Pacific Geomatics Ltd. Canada). In 2006, Pacific Geomatics Ltd. Canada custom orthorectified and radiometrically-corrected tiled QuickBird imagery. Two image swaths for the Turneffe area were delivered: image T001, the south-eastern image, and image T002, the northeastern image (QuickBird image on the right of Fig. 3.5). Each image was independently ortho-corrected (Projection: UTM Zone 16N; Datum: WGS 1984). Both multispectral and panchromatic images were acquired, with 2.4 m and 0.61 m spatial resolution at nadir, respectively. The imagery covered the eastern cays of Turneffe (Cockroach Cays to Dead Man Cays). The QuickBird multispectral and panchromatic images were pansharpened with ENVI software version 4.5 to produce a high resolution color image to be used as the base layer for subsequent image rectification. The QuickBird image was used for initial mapping and as a base for rectification of the low elevation aerial photographs. A Landsat image from 2004, which covers the extent of the entire atoll, was acquired from Dr. Ed Boles, University of Belize in 2006 (image to the left on Fig. 3.5). The image was used mostly for field work and navigation during ground-truthing and to access study sites.

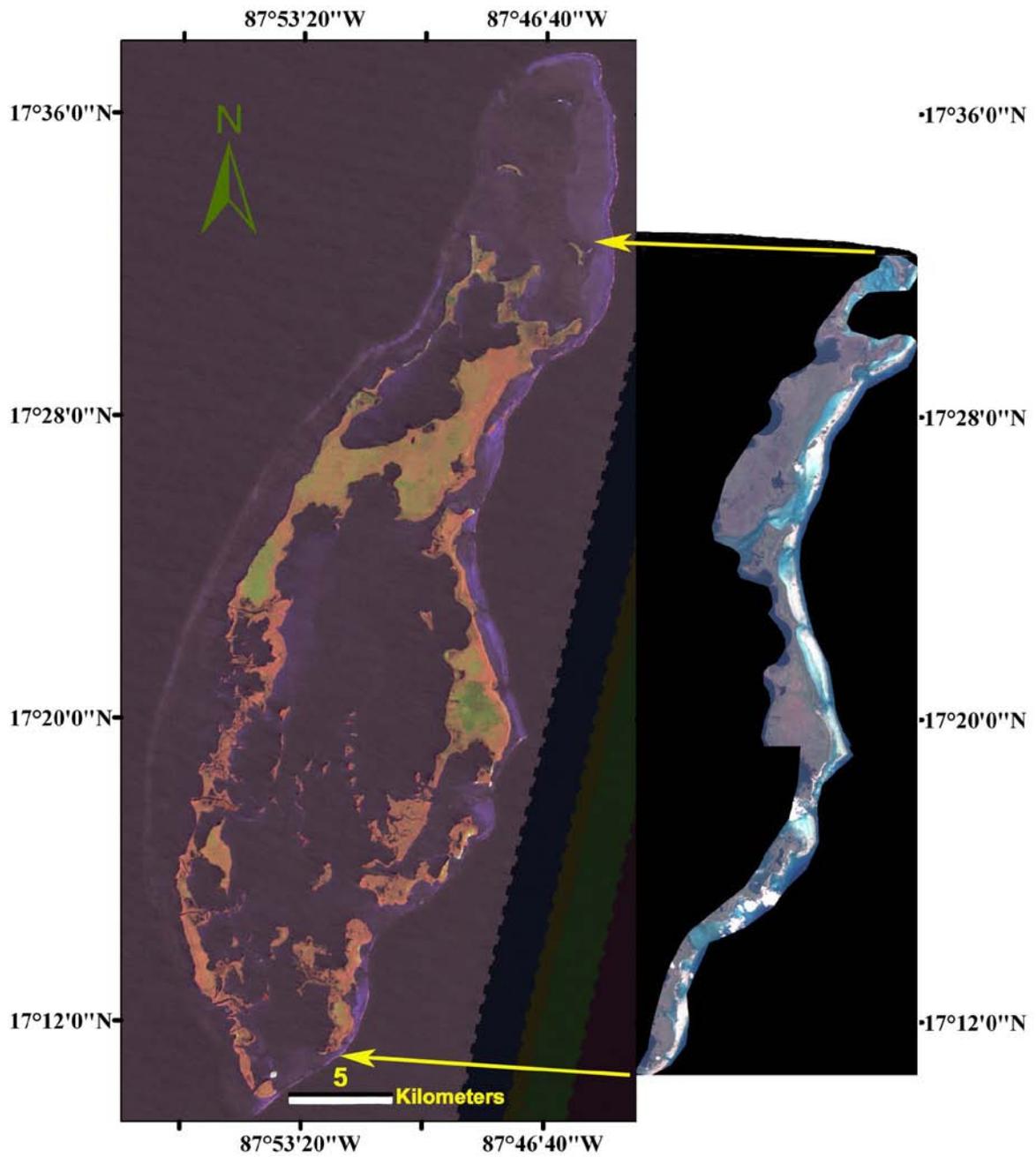


Figure 3.5. Turneffe imagery: image to the left is area coverage of entire atoll by Landsat 2004; and image to the right is the extent of coverage from the QuickBird 2005 of the eastern side of the atoll.

3.2.2.2 Vertical aerial photographs

In April 2006, digital vertical aerial photographs were taken of the eastern side of Turneffe. Photos were taken in collaboration with Terrasaurus Aerial Photography Ltd., Canada and LightHawk, USA. These photographs were taken using dual Canon EOS-1Ds MarkII with a 16.7 megapixel capacity. The flight lines were oriented to ensure efficient coverage of the eastern fringing cays, with pre-selected GPS coordinates for the flight path. Photographs were taken at an altitude of 2500 m and objects as small as 10 cm were visible in the images. Adobe Photoshop version 8.0 was used to organize these aerial photographs by flight-path and for the selection process. A digital elevation model (DEM) for the coast of Belize with a 2 km pixel resolution was used for the ortho-rectification. While coarse, this DEM was adequate for this project on Turneffe because the atoll has a very low relief and all ground control points were at sea level (Jamie Heath, owner of Terrasaurus Aerial Photography Ltd, personal communication). A minimum of eight GCPs were used per photo to create the orthographic projections, two of the eight GCPs were stereopaired to match precisely to the corresponding image data on the second photo of the pair. The GCPs included coral rocks, and edge of narrow channels. In addition, since the QuickBird base image and aerial photograph dates were close in time, distinctive seagrass patches, individual trees and human-made structures were added as GCPs. It was necessary to use these additional points because the high resolution aerial photographs each covered small areas (~ 15 ha). GCPs were distributed as evenly as possible throughout the entire photograph. The total root mean squared error for the 2006 georectified images was kept at an average of 0.1 m.

Orthorectification is the process of removing geometric error, radial displacement and tilt and relief distortions from aerial photographs so that orthophotos are of consistent scale and derived measurements are planimetrically accurate (Morgan et al. 2010). The resulting 2006 orthophoto mosaic does not cover the entire area of the QuickBird imagery base layer. However, all fringing cays of interest are covered on this photo-mosaic. The adjacent reef system and proximal portions of the larger islands were included in this coverage. The orthophotos were combined to form an orthoimage mosaic that allowed the study area to be viewed as a single composite image. The mosaics were initially in geotiff format rendering large file sizes. The geotiff mosaics were joined and compressed into three separate images with ECW output format in order to be more manageable within the ArcGIS platform. The seamless digital photo-mosaic, including color balancing and compression, was prepared by Terrasaurus Aerial Photography Ltd. with a 10 cm resolution, using PCI Geomatics (version 10.1.3, Ontario Canada) digital image processing software (www.pcigeomatics.com).

Historic aerial photos were obtained from the Land Management Program Physical Planning Valuation Office located in Belmopan, Belize between 2006 and 2007. The following sets of photos were taken by the Royal Air Force (RAF) in 1945, 1962 and 1975, see Table 3.1 for the extent of coverage. The scales of these aerial photographs were not available. However, based on recognizable features (e.g., distinct channels ≥ 3 m wide), the scale was estimated at 1:30,000. Permission was granted by the Defense Procurement Agency, Bristol, UK for the scanning of the RAF photos located in Belmopan, Belize. An additional set of historic photos taken by the RAF after Hurricane Hattie of October 1961 was obtained from the British Empire and Commonwealth Museum, UK. This set has complete coverage of the eastern part

of Turneffe. An incomplete set of historic photos taken in 1960 by the US Air Force (USAF) were provided by D. R. Stoddart (Emeritus Professor of Geography, University of California, Berkeley, CA).

Table 3.1. Summary of historical vertical aerial photographs taken by the Royal Air Force (RAF) and the US Air Force (USAF) of the eastern coast of Turneffe. Partial and no coverage means that in those cases the photos were not taken or could not be obtained or found.

Group of Cays	Year and extent of coverage				
	1945 (RAF)	1960 before Hurricane Hattie (USAF)	1961 after Hurricane Hattie (RAF)	1962 (RAF)	1975 (RAF)
Cockroach Cays	complete	partial coverage	complete	no coverage	no coverage
Pelican Cay	complete	no coverage	complete	no coverage	no coverage
Soldier Cays	complete	no coverage	complete	complete	complete
Calabash Cays	complete	no coverage	complete	complete	complete
Little Rope Walk Cay	complete	complete	complete	complete	no coverage
Dead Man Cays	complete	complete	complete	complete	no coverage

The historic photo prints located in Belmopan, Belize were scanned with an HP PrecisionScan Pro 3.02 at 1200 dpi. The 1960 USAF photos and the after Hurricane Hattie photos were scanned with an Epson Expression 1640XL scanner at 1200 dpi. All scanned photo prints were saved in tagged image file format (tiff) and Adobe Photoshop version 8.0 was used to organize and pre-process the digital copies (flipping and cropping) before georectification. After scanning photographic prints to create a digital file, polynomial

georectification was performed in three steps: 1) matching of ground-control points (GCPs) on the scanned photo image with the base layer, 2) transformation of the GCP coordinates on the scanned image from a generic raster set to a geographical projection and coordinate system, and 3) pixel resampling.

All photos from the RAF and USAF were georectified with Environment for Visualizing Images (ENVI version 4.7, Research Systems, 2008), image processing system. The QuickBird 2006 image was used as the base layer for all the image-to-image registrations. The same ground control points (GCPs) were used for all image dates. A minimum of eight GCPs were selected on each photo (Hughes et al. 2006). Each frame was then georectified using a polynomial transformation with image-to-image control points taken from 2006 QuickBird satellite imagery. All the photographs were warped with a second-order polynomial transformation. Images were resampled using nearest-neighbor interpolation. The 1945 photos, which were the oldest, were georectified first. Extra effort was made to georectify the subsequent batches of photos where coverage overlapped using the same GCPs used with the 1945 photos. This ensured that for the coverage within the overlap the same GCPs were used for the georectification process. The selection of GCPs on the photograph was spread as widely as possible across the image to improve accuracy throughout the photograph. However, it was also noted that better accuracy can be obtained by concentrating GCPs near the features of interest (e.g., Hughes et al. 2006). To improve and enhance the image-to-image registration precision, pairs of control points with large errors were removed. The total root mean squared error for all the historic georectified images was kept at an average of 5 m. Fortunately, in most of the historical photos, a number of coral reef rocks and

narrow channels were visible. These features are stable over long time periods and proved to be the best GCPs. The georectified historical photos were then combined using ENVI producing a photo-mosaic with a 0.60 m pixel resolution. All mosaics from the historic photos in addition to the pansharpened QuickBird imagery were loaded into ArcGIS. The mosaics were overlaid onto the QuickBird imagery. Each individual mosaic layer was activated one at a time, and the swipe layer tool within ArcGIS was used to make sure that the GCPs used during rectification matched with the corresponding QuickBird layer, particularly those GCPs close to the fringing cays. Corrections were made in the event that corresponding GCPs between layers were more than 5 m off from the QuickBird base layer. As a final check to confirm consistency between the 1945 and 2006 photo-mosaics, eight features were selected which were presumed to be stable over time and which were not previously used as GCP's. These map features were coral patches identified on both the 1945 and 2006 photo-mosaics located close to the reef crest and on the back-reef sediment apron. The approximate centers of the coral patches were digitized within ArcGIS and the x and y coordinates were calculated within ArcGIS. The average difference between the x and y coordinates for the 1945 and 2006 images was 0.9 m (0-1.3 m) and 1.3 m (0 to 2.1 m) respectively.

3.2.2.3 Oblique aerial photographs

To provide additional information on year-to-year changes, oblique aerial photographs were taken of the eastern cays yearly in April from 2003 to 2008 (Table 3.2). Oblique aerial

photographs of the fringing cays were taken by Dr. I.C. Feller (Smithsonian Institution, USA) and me in collaboration with LightHawk, USA.

Table 3.2. List of aerial surveys conducted in collaboration with LightHawk, USA and Feller (Smithsonian Institution, USA). Oblique aerial photographs were taken of the eastern and western sides of Turneffe with focus on the fringing cays of the eastern side.

Year	Extent of coverage
2003	Eastern Turneffe from Dog Flea Cay to Dead Man Cays
2004	Eastern Turneffe from Dog Flea Cay to Dead Man Cays
2005	Eastern and western Turneffe from Dog Flea Cay to Big Cay Bokel
2006	Eastern and western Turneffe from Dog Flea Cay to Big Cay Bokel
2007	Eastern and western Turneffe from Dog Flea Cay to Big Cay Bokel
2008	Eastern and western Turneffe from Dog Flea Cay to Big Cay Bokel

A very valuable set of historic photo slides was provided by Dr. D.R. Stoddart in 2006. The set of 1961 color transparencies (taken before Hurricane Hattie 1961), partially covers the fringing cays of eastern Turneffe (Cockroach Cays to Dead Man Cays). Dr. Stoddart also provided aerial-oblique and on-the-ground photo slides that he took from 1962 and 1965 with partial coverage of these eastern cays. These color transparencies were scanned using a Minolta Dimage Scan Elite 5400 with input dpi of 2000 and output dpi of 300. Each photo was renamed and organized using Adobe Photoshop 8.0 and saved in JPEG file format in order to embed additional information on its metadata. ArcGIS 9.3.1 was used to extract approximate x and y coordinates from the QuickBird imagery of the locations where the photo slides were taken. The software RoboGEO 5.6.4 was used to manually geotag these photos with the estimated coordinates and to name photos according to location. Geotagged

photos were organized by year, and ESRI™ shape files were created to make these photos available via a specific path to be viewed on GIS.

The oblique photos were organized by year and area of coverage for comparison purposes only and were not used for aerial coverage calculations. These photos assisted with the identification and number of cays within a given year, vegetation type and identified the effects of human and natural disturbance over time (presence or absence of either coconut trees or mangrove vegetation, presence or absence of human-made structures, and effects of storm damage on cay vegetation).

3.2.3 Image analysis and ground truthing

3.2.3.1 Vegetation and cay map preparation – 2006 photo-mosaic

For all the photo-mosaics, including the satellite imagery, the UTM map projection was used. This permitted metric distance measurements of multi-temporal changes. The 2006 aerial photo-mosaic was the most recent vertical image and provided coverage of the eastern fringing cays. The high resolution images allowed a more detailed analysis of the vegetation and it was therefore a good baseline against which to compare the subsequent photo-mosaics. From this 2006 photo-mosaic, all visible fringing cays with vegetation along the eastern side of Turneffe were mapped in ArcGIS. Polygons representing the various perimeters were digitized for all fringing cays. Two cay areas were calculated from the 2006 photo-mosaic: 1) vegetated area and 2) vegetated area and bare substrate (refer to Glossary). The area of the

following vegetation classes was also calculated: cocal, littoral and mangrove. A vegetation type that is widely found in coastal environments is littoral forest. The definition for littoral forest has been widely adopted in Belize to mean coastal forest without cocal and mangrove forest (see Glossary).

The aerial photographs from 2006 were high resolution (10 cm pixel resolution). The ground truthing process involved identifying the group of 35 vegetated fringing cays which were identified from the 2006 photo-mosaic. Hard copy maps were produced with map keys and coordinates to show location. The laminated maps were used in conjunction with a GPS (Garmin 76CSx) to verify specific positions on the cays (e.g., distinctive vegetation canopy like coconut palms and vegetation boundaries). All 35 vegetated fringing cays were found on-the-ground and the periphery of the vegetation was confirmed. The following field notes were taken of each vegetated fringing cay: 1) dominant vegetation type (e.g., cocal- or mangrove-dominated); 2) presence of *C. nucifera* on the cay; 3) photos were taken of the periphery vegetation and/or substrate; and 4) the presence/absence of any human-made structure(s) (e.g., sheds, shacks, houses, and docks).

3.2.3.2 Vegetation and cay map preparation – comparison of 1945 and 2006 photo-mosaic

Upon completion of the ground truthing process for the 2006 photo-mosaic, polygons representing the cay vegetation perimeters were digitized for all fringing cays on the 1945 photo-mosaics using ArcGIS. Each cay vegetated area was calculated using ArcGIS. These

photo-mosaics also showed the reef system and considerable areas of the large islands. The 1945 photo-mosaic revealed information on the location and size of the fringing cays relative to the reef crest and large islands and presence/absence of cay vegetation. The resolution of the image enabled classification of landscape features (i.e. vegetation, reef, channels, open water and pond areas). Figure 3.6 shows a flow chart of the general working process adopted for the production of maps.

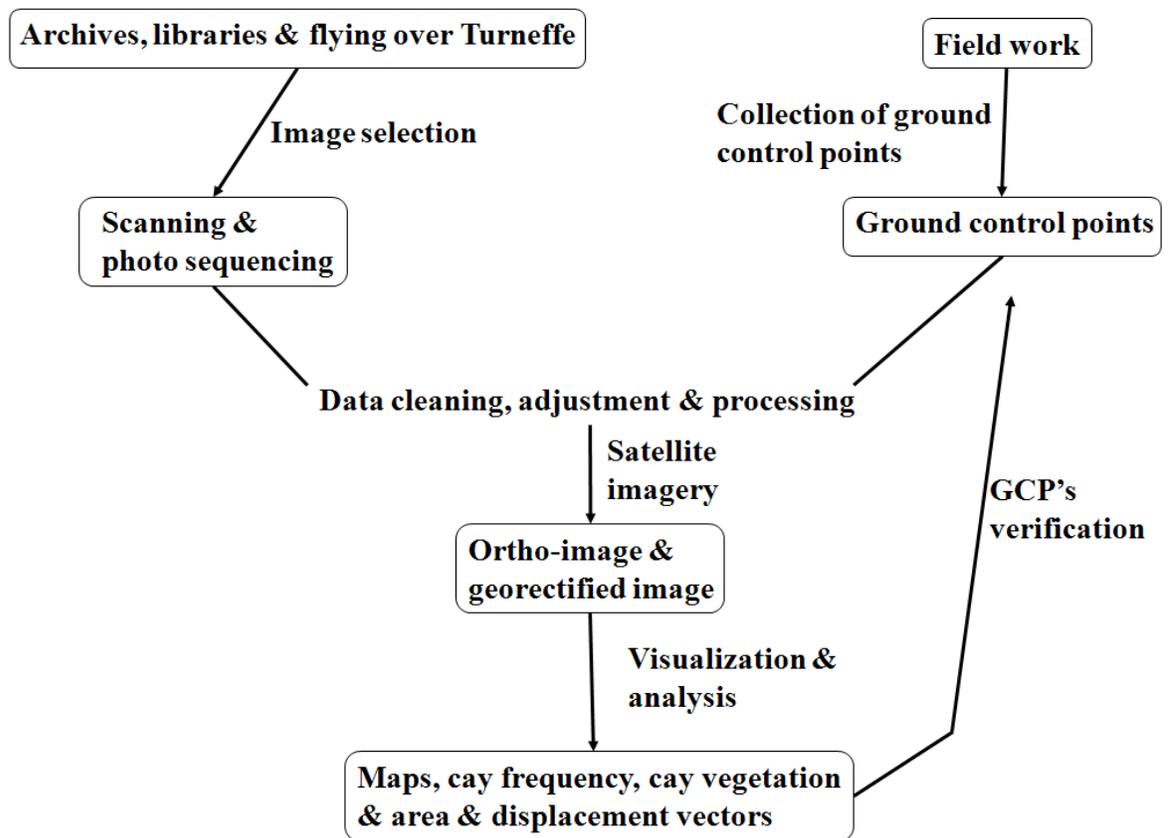


Figure 3.6. Flowchart of the general working process used for the production of maps and aerial photograph interpretation.

3.2.3.3 Location and orientation of fringing cay vegetation

The geometric center of the 1945 and 2006 vegetation polygons created within ArcGIS was calculated and represented by a centroid. The centroids were taken to represent the geometric location of the vegetation polygons and were used in distance calculations. The centroid for each of the cay vegetation polygons of the 2006 and 1945 photo-mosaic was created through the XTools Pro 5.3 extension for ArcGIS. These coordinates were then added to the table of cay information, along with cay area. In preparation for the field work, the 2006 vegetation polygons and centroids were superimposed on the 1945 photo-mosaic, and maps were printed and laminated. The names used by Stoddart to describe the cays and centroid coordinates were also included on these maps. During the field work, all coordinates from the 2006 and 1945 centroids were entered into a Garmin 76CSx GPS and each cay or former cay location was visited. In the field, for each cay with vegetation, field notes were added to the previous field data on evidence of erosion and/or accretion. For all cays without vegetation, based on the 1945 photo-mosaic, field notes included: 1) evidence of erosion (e.g., presence of decomposing roots and stumps); 2) presence of dead vegetation (e.g., roots and stumps) and 3) GPS points were taken of any salient features that suggested the location of the cay prior to devegetation and/or erosion.

Polar charts and circular statistics were used to assess directionality. In order to assess the directionality and the magnitude of displacement (centroid movement) from 1945 to 2006, a polyline was created within the ArcGIS connecting the centroid of the 1945 polygon to the centroid of the 2006 polygon of the vegetated area of each cay (n = 31). The azimuth of each

polyline was calculated using ArcGIS spatial statistics tools. The length and azimuth of the digitized polyline was used to calculate the magnitude and angular vectors averaged for all cays. This measure is termed the Rayleigh's concentration coefficient (r). The value ranges from '0', when the headings are uniformly distributed, to '1', when all of the headings are in the same direction (Zar 1996). The resulting mean vector was evaluated to see whether it differed from 0 using a Rayleigh test. One-sidedness occurs when observations are clustered around a single "preferred" direction/angle. The basic idea of the Rayleigh test is to express a sample of independent angular observations through a mean vector. The important properties of this vector are its length ' r ' ($0 \leq r \leq 1$), and its direction ($0-359^\circ$). The significance level of the Rayleigh test is a function of the mean vector's length and the sample size. A relatively long vector indicates significant one-sidedness, while a relatively short vector is evidence against one-sidedness. If significant one-sidedness is detected, the direction of the mean vector indicates the "preferred" direction of movement. The null hypothesis for this test states that the mean vector = 0, and hence the individuals are evenly or randomly dispersed. When the null hypothesis is rejected, the mean vector $\neq 0$, and individuals are oriented in a particular direction (Zar 1996). The calculations for the Rayleigh test were performed using macros created by M. Kölliker (Kölliker and Richner 2004) for use in the SAS system (SAS Institute 9.2 (2008)).

A pair-wise comparison of the x and y coordinates of the vegetation centroid between 1945 and 2006 was conducted. The Wilcoxon's signed rank test for paired comparison is a non-parametric test and was used because the data were non-normally distributed.

The eastern cays appeared to have non-random shapes and to be non-randomly aligned relative to the orientation of the reef crest. To quantify this, the orientation of the polygon from the vegetated area was defined by its longest axis. The longest axis which spanned the polygon of each cay from the 1945 and 2006 photo-mosaic was calculated using a custom code from Jenness Enterprises, (www.jennessent.com), which was ran using the Visual BASIC for Applications (VBA Microsoft) within ArcMap. A section of the coral reef crest directly in front of each cay was examined on the photo-mosaics (1945 and 2006) and a line was digitized to delimit the reef crest, and the orientation of the line marking this portion of the reef crest was calculated with ArGIS (spatial statistics tools). The longest axis from the 1945 and 2006 vegetation polygons and the reef crest polylines were used to test for a relationship of orientation between the cays and the structure of the reef crest. Circular moments, and the V-test, (Batschelet 1981) were used to assess the one-sidedness of the sample. The V-test is a modification of a Rayleigh test that examines whether observed angles are statistically clustered around a hypothesized angle, in this case the mean orientation of the reef crest (Batschelet 1981).

3.2.4 Wind and tide from Carrie Bow Cay and Main Calabash Cay

There was no weather station at the University of Belize Marine Research Station, during field work, nor were there any other long-term weather stations on Turneffe. Hourly records of tide and wind (wind direction and speed) are recorded at the Carrie Bow Cay Marine Field Station (Fig. 3.7), which is 60-km south from the Main Calabash Cay, Turneffe. Wind and tide data from the Carrie Bow Cay weather station was downloaded from Smithsonian

Marine Science Network (Smithsonian Institution 2008; <http://nmnhmp.riocean.com>). Hourly wind measurements were taken at the station, the mean monthly and yearly wind direction averages were calculated from the 2007 and 2008 data. Circular statistics were used to calculate mean wind directions (Batschelet 1981; Zar 1996).

The Carrie Bow Cay weather data are the best available data for making inferential statements on the long-term patterns for the Turneffe area. The weather station at Carrie Bow Cay is the only station in Belize that collects weather and oceanographic parameters of offshore conditions in a consistent manner. Carrie Bow Cay is a small cay and resembles the fringing cays of Turneffe in size (112 m at its longest point to 35 m at its widest point) and formation (reef sediment) and is approximately 130 m from the reef crest (Fig. 3.7). The group of fringing cays on eastern Turneffe is presumably influenced by similar wind conditions to Carrie Bow Cay when the wind is blowing due northeast, east, and south-east due to the presence of the larger islands west of the fringing cays.

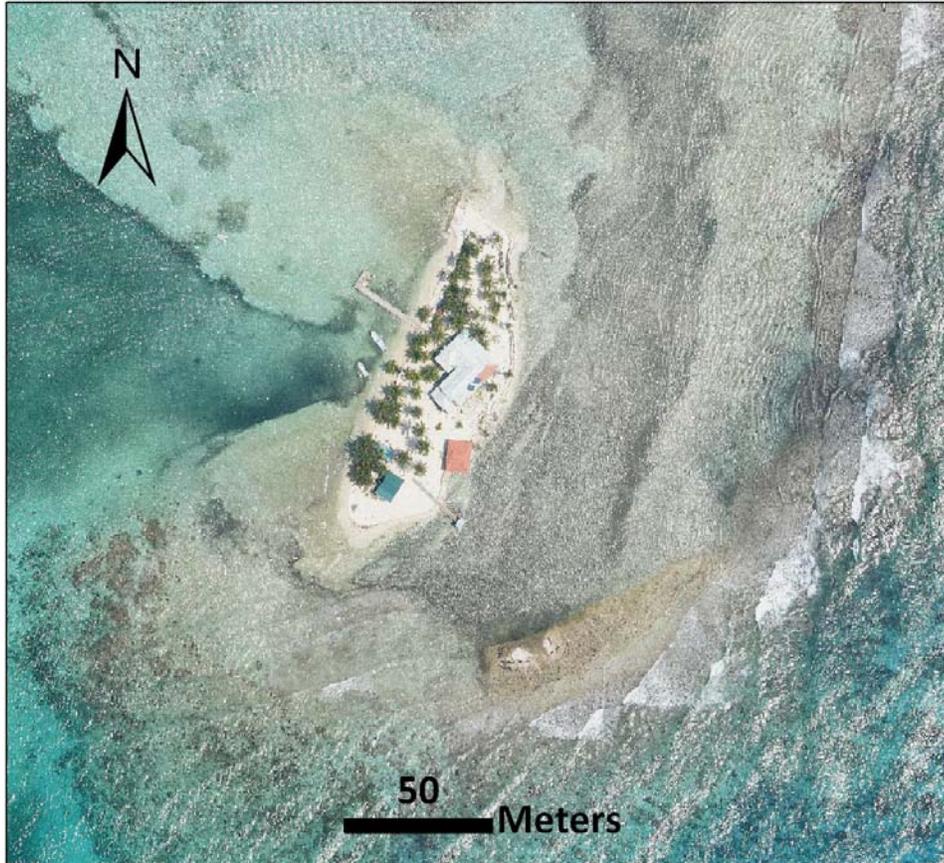


Figure 3.7. Smithsonian's Carrie Bow Cay Marine Field Station houses an Environmental Monitoring Systems which continually monitors real time meteorological and oceanographic conditions (aerial photograph from 2006).

To check for correspondence between tides at Carrie Bow Cay and Turneffe, a tide gauge was set up beside the dock at Main Calabash Cay. For the later part of May and early June 2008, the tide was monitored for 7 days at 1-h intervals from morning to late evening (between 0700 to 2100 hrs). The corresponding tidal data were acquired from the Carrie Bow Cay Marine Field Station. Pearson's correlation coefficient was used for evaluating concordance between the two tidal data sets.

3.2.5 Fringing cay vegetation under the influence of tides

The spring tide high water mark boundary was based on multiple GPS points taken in the field. On the ocean facing side of the fringing cays with beaches, the GPS points were taken along a clear wrack line which primarily consisted of dead seagrass and algae or differences in substrate coloration delimiting the water line. For the leeward side of the cays, with respect to the reef crest, the spring tide high water mark was mostly inside mangrove vegetation. The spring tide high water mark was established by following the boundary area where a high water mark was left on the prop roots and stems of mangrove trees. A cross reference was established in some cays by applying a thin film on roots or on a section of rope with Kolor Kut[®] water finding paste and pinning the rope during low tide along the ground across the intertidal range. The setup was inspected after a 24 hour period. Kolor Kut[®] is a paste that changes color from brown to red upon contact with water.

The coordinates collected on-the-ground were converted to polygons for further processing using ArcGIS and the 2006 photo-mosaic as the base map. The areas of two zones were calculated: 1) vegetation and substrate above spring high tide and 2) vegetation and substrate above and below spring high tide (refer to Glossary for definitions; Fig. 3.8). The edge of vegetation found in a subtidal environment was mapped as the edge of mangrove prop roots or canopies.

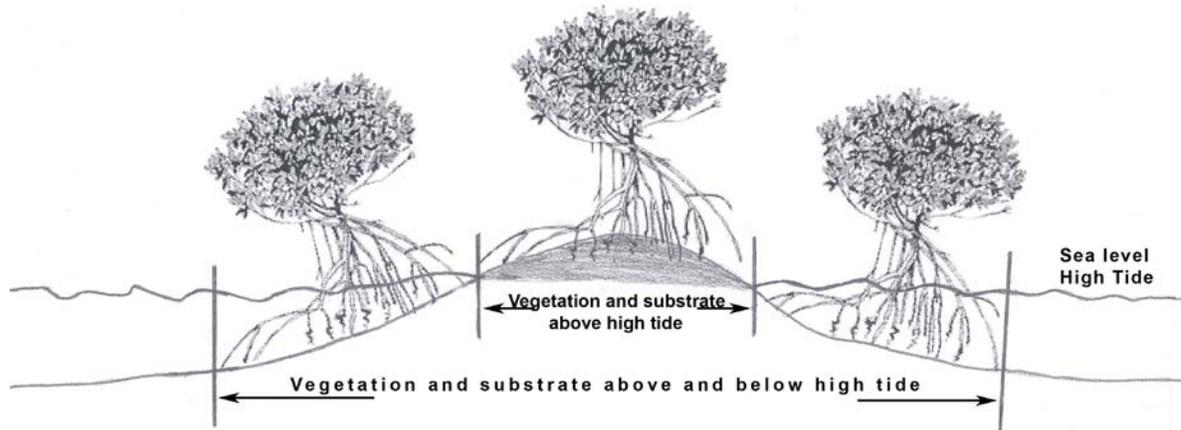


Figure 3.8. A simplified fringing cay showing vegetation and substrate area above spring high tide and vegetation and substrate area above and below spring high tide.

3.2.6 Landfall of hurricanes and tropical storms on Belize's coastline and Turneffe

To investigate land-falling storms on mainland Belize and Turneffe, the HURDAT data were used. For the North Atlantic Basin, the HURDAT (Hurricane Database) online database maintained by the US National Hurricane Center provides track and wind speed data for all known hurricanes since 1851. The HURDAT best track data set is the most complete and reliable source of North Atlantic hurricanes (Jarvinen et al. 1984). Both databases from HURDAT and UNISYS were used to compile the list of storms from 1851 to 2008 for the Belize and Turneffe area. The NOAA online database was consulted to create a Belize coastal area and Turneffe database for all storms that made landfall from 1851 to 2008.

Extraction of relevant storms and storm parameters from the historical database was obtained through the NOAA National Hurricane Centre Archive data, (NOAA 2010a;

<http://www.aoml.noaa.gov/hrd/hurdat/DataByYearandStorm.htm>), namely Hurricane Best Track Files (HURDAT). The Atlantic Tracks File contains the 6-hourly (0000, 0600, 1200,

1800 UTC), center locations (latitude and longitude in tenths of degrees), and intensities (maximum 1-minute surface wind speeds in km/h and minimum central pressures in millibars). Based on the location of the center of the eye of the storm, the points were connected to create polylines. The polylines were used to calculate the storm's angle/direction as it approached or crossed the coastline or atoll. The Belize coastline was digitized from a Landsat 2008 image. The mainland coastline was divided into north and south with the aid of a diagonal running from the northern to the southern Belize border, delimited by the Rio Hondo and Sarstoon River, respectively. A line perpendicular to the diagonal was intersected with the coastal line. The mid-point dividing the northern and southern coastline was 3 km north of the mouth of the Mullins River. The coastline was divided to find out if there is a difference in frequency of storms affecting the northern compared to the southern coastline of Belize. A similar approach was taken to divide Turneffe into a northern and southern section delimited by the reef north of Mauger Cay and the reef south of Bokel Cay, also known as Cay Bokel. The mid-point on the eastern side of Turneffe was at 2 km south of Pelican Cay or 7 km north of Soldier Cay.

According to the National Hurricane Center (NHC), a landfall occurs at the intersection of the surface center of a tropical cyclone with a coastline (NOAA 2010b). For this study, landfall was based on NHC's definition. The last two reported storm track locations upon landfall were used to calculate the storm's angle/direction. Circular statistics were used to calculate mean storm track directions (Batschelet 1981; Zar 1996). The average return periods for hurricanes was derived by dividing the period of record (1851 to 2008) by the total number of landfalls at Turneffe (Keim et al. 2007).

3.2.7 Analysis of the effects of wind and hurricanes on cay shift

The vegetation and substrate of cays and geographic location can be influenced by routine wind and storm surge. Circular statistics were used to analyze average wind directions, average storm track directions and cay vegetation shift (Batschelet 1981; Zar 1996). To test whether the mean angles of two samples differ significantly from each other, the Watson-William test was used (Batschelet 1981; Zar 1996). The directional means of the cay shift angles (north azimuth) between 1945 and 2006 were compared to the track direction of storms (tropical storms and hurricanes) and mean wind direction data from Carrie Bow Cay Marine Field Station. The list of storms used for the analyses includes land-falling storms on Turneffe between 1851 and 2008. The average monthly wind direction for 2007 and 2008 measured at Carrie Bow Cay was used for comparison, with the assumption that historical yearly wind direction had a similar pattern. Wind direction was reported, from Carrie Bow Cay Marine Field Station, as the direction from which it originated while storm track direction was reported in the direction of its movement (NOAA 2010a). The inverse wind directions were used in the analysis (direction of its movement).

3.2.8 Effects of Hurricane Hattie on cay frequency, vegetation area and type

Cays before and after Hurricane Hattie were identified as present or absent based on oblique aerial photographs (1960 and 1962) and vertical photo-mosaic (1961 post-Hurricane Hattie). “New vegetated cays” were identified from the 2006 aerial photographs when it was compared to the historical photo-mosaics and photographs (vertical and oblique). The new

vegetated cays were not visible from the aerial photographs (vertical and oblique) prior to Hurricane Hattie 1961. New cays were areas with vegetation above water and colonizing the intertidal zone. Vegetation from new cays was clearly separated from adjacent vegetated cays, usually by a channel and/or bare areas of more than 4 m. These new vegetated cays comprised of multi-stemmed trees of *R. mangle* with the smallest cay having a cluster of approximately 25 stems (e.g., Little Soldier Cay). New vegetated cays were given names related to the neighboring cays. Stoddart used a combination of names and numbers for the fringing cays, and his name and numbering system was conserved in this study.

Polygons representing the cay vegetation perimeters were digitized for all fringing cays on the 1945, 1961 and 2006 photo-mosaics using ArcGIS and cay vegetation area (ha) was calculated within ArcGIS. The vegetated area on cays from the 1961 photo-mosaic, after Hurricane Hattie, was calculated based on all standing vegetation on the cay, including living and dead trees. The difference between standing dead trees and live trees was impossible to distinguish on these photos since some trees could have been defoliated and re-foliated after the hurricane. Cay vegetated areas (ha), calculated from the polygons, were compared by using Wilcoxon's signed rank test for paired comparison where the pairing criterion were all vegetated cays identified in 1945, 1961 (after Hurricane Hattie), and 2006 photo-mosaic. The Wilcoxon's signed rank paired test is a non-parametric test and was used because the vegetated area data were non-normally distributed.

Oblique aerial photographs also assisted with identification of the presence/absence of *C. nucifera* before and after Hurricane Hattie. *Cocos nucifera* has a distinctive crown and was recognized from the photographs.

3.2.9 Short term effects of hurricanes – direct and indirect

Three cays from the Cockroach group were visited over a 5 year period (2003, 2006 and 2008) after the passage of Hurricane Keith 2000 to observe the rate of mangrove reforestation, and recolonization by both vegetative regrowth and propagules. The area of hurricane damaged forest on Cockroach Cays-20, -22 and -23 was measured by walking the boundary between the dead and live trees, and taking GPS readings at regular intervals along this boundary. A second set of GPS points was taken around the periphery of each cay's vegetation. The GPS point data was imported into ArcGIS and converted to polygon data in order to calculate successive area by year in ha. Previous to Hurricane Keith, the periphery of the Cockroach Cays had been explored in 1999 but no GPS measurements were taken.

Aerial and on-the-ground photographs from Soldier Cay and GPS coordinates and field notes taken in 2003 were used to compare from the storm surge effects of Hurricane Ivan 2004. Soldier Cay was visited two weeks after the indirect storm surge effects from Hurricane Ivan. On-the-ground photographs of the reefward facing side of the cay were taken. Field notes were taken on: 1) type (e.g., *A. palmata* and *A. cervicornis*) and size of coral rubble substrate washed from the reef; 2) distance the substrate was washed on the cay from the reef crest; 3) average depth of new coral rubble substrate washed on the cay, and 4) reefward facing

mangrove vegetation condition (e.g., root burial, scarring of roots and stems and lean of tree stems).

3.3 Results

3.3.1 Contemporary cays and vegetation - 2006 image analysis and ground truthing

3.3.1.1 Cay frequency and size

A high resolution photo-mosaic was produced from the 2006 vertical aerial photographs which covered the eastern fringing cays of Turneffe. The largest cay had an area of 9.7 ha and the smallest had an area of 0.002 ha (Appendix A). The back-reef sediment apron for the northern group of cays was wider than the in southern. For example, the average distance along the Cockroach Cays-20, -22 and -23 (northern group) between the reef crest and the larger islands was approximately 840 m, while along the Dead Man Cays-5, -4 and -2 (southern group), it was approximately 230 m.

3.3.1.2 Cay vegetation cover and type

A total of 35 vegetated cays were identified from the 2006 photo-mosaic. Twenty one cays were from the northern group, eight from the central group and six from the southern group. The average cay vegetated area was 0.8 ha, with a maximum area of 9.7 ha located with the

northern group and a minimum area of 0.002 ha located in the southern group. Only six cays had a vegetated area of more than 1 ha. The combined vegetated area was over 28 ha.

The area of three vegetation classes, coccol, littoral and mangrove, varied widely in 2006 (Fig. 3.9). The cays without *C. nucifera* trees within the Cockroach group were small (mean size = 0.07 ha), when compared to the rest of the Cockroach Cays (mean size = 1.04 ha). The total area covered by coccol forest was approximately 1.5 ha and the total cover of littoral forest was 5.6 ha; while the total cover by mangrove forest was 21.0 ha within the group of 35 cays.

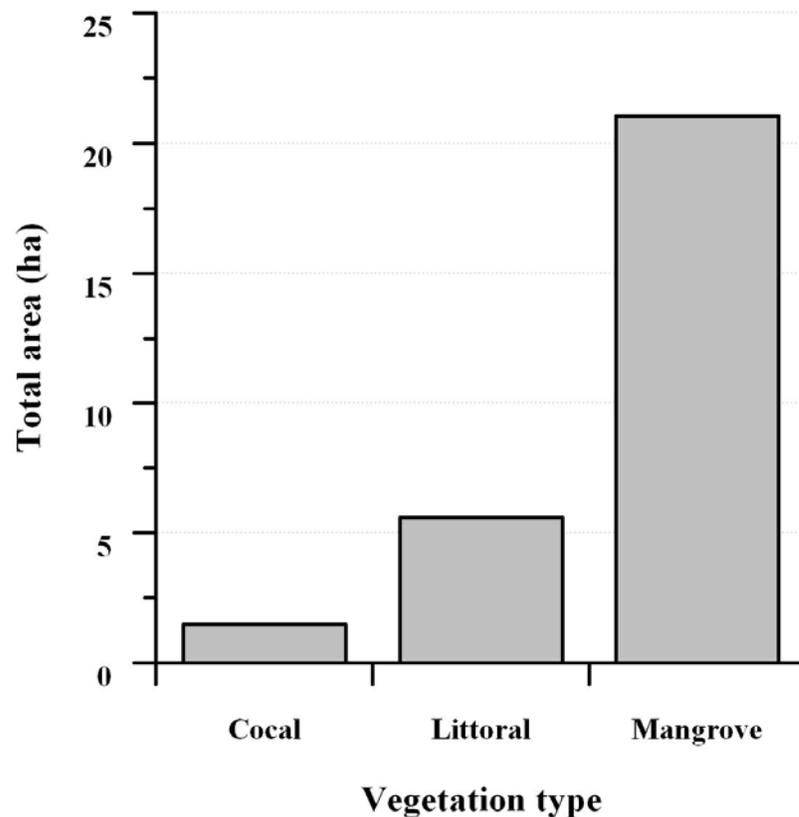


Figure 3.9. Total areas for coccol, littoral and mangrove vegetation types. Areas calculated from a group of 35 fringing cays identified on the 2006 photo-mosaic.

3.3.1.3 Ground-truthing cay vegetation

Ground truthing conducted between 2006 and 2008 confirmed the number of vegetated cays ($n = 35$) which were initially identified from the 2006 photo-mosaic. This was also true for the cay vegetation classes and vegetated areas calculated from the 2006 photo-mosaic.

During the field surveys of 2006 to 2008, littoral forest was found to be widely distributed on the fringing cays and concentrated on the higher elevation zone of the cays. Mangroves were present on all 35 vegetated cays that were surveyed between 2006 and 2008. The dominant mangrove species was *R. mangle*. However, all three mangrove species (*R. mangle*, *L. racemosa*, *A. germinans*), were found to be present on a large number of the fringing cays, including the mangrove associate *Conocarpus erectus*. Mangrove vegetation of the total cay vegetated area accounts for 21.0 ha (75%) within the list of 35 cays (Fig. 3.9). Most of the extensive and continuous mangrove forest was found on the leeward side of cays with respect to the reef crest. There were single mature trees on the ocean facing side of the cays, mostly the *A. germinans* species, in some cases these single trees were the largest from the entire cay vegetation. For example, an *A. germinans* found on the northeast side of Dead Man Cay-5, had a DBH of 33 cm and a height of more than 7 m.

3.3.2 Comparison of historic and contemporary remotely sensed data

3.3.2.1 Cay frequency and size in 1945

On the photo-mosaic from 1945, I identified 42 vegetated fringing cays along the eastern seaboard of Turneffe. In 1945, only eight cays were more than 1 ha in size (Appendix B). Cockroach Cay-28 (northern group), was the largest with an area of 5.9 ha. The smallest cay was Big Calabash East Cay-2 (central group), with an area of 0.02 ha.

3.3.2.2 Location and orientation of cays: 1945 vs. 2006

Thirty one vegetated cays were found on both the 1945 and 2006 photo-mosaic and were in the same general location (Appendix C). For both the 1945 and 2006 photo-mosaics, the northern part of the back-reef sediment apron of Turneffe was wider than the southern part. Between 1945 and 2006, cay centroids of vegetated area shifted west with a northerly component (Fig. 3.10). Based on the Wilcoxon's paired sample test the x and y locations in 1945 and 2006 were significant. The median change from 1945 to 2006 in the x coordinate (11.2 m west) was significantly different from zero ($p < 0.0001$). The median change from 1945 to 2006 in the y coordinate (5.8 m north) was also significantly different from zero ($p = 0.0048$). The shift of the reefward facing edge of the vegetated cays was consistent with the visible eroded substrate surfaces observed from the 2006 photo-mosaic and was also documented during field work between 2006 and 2008.

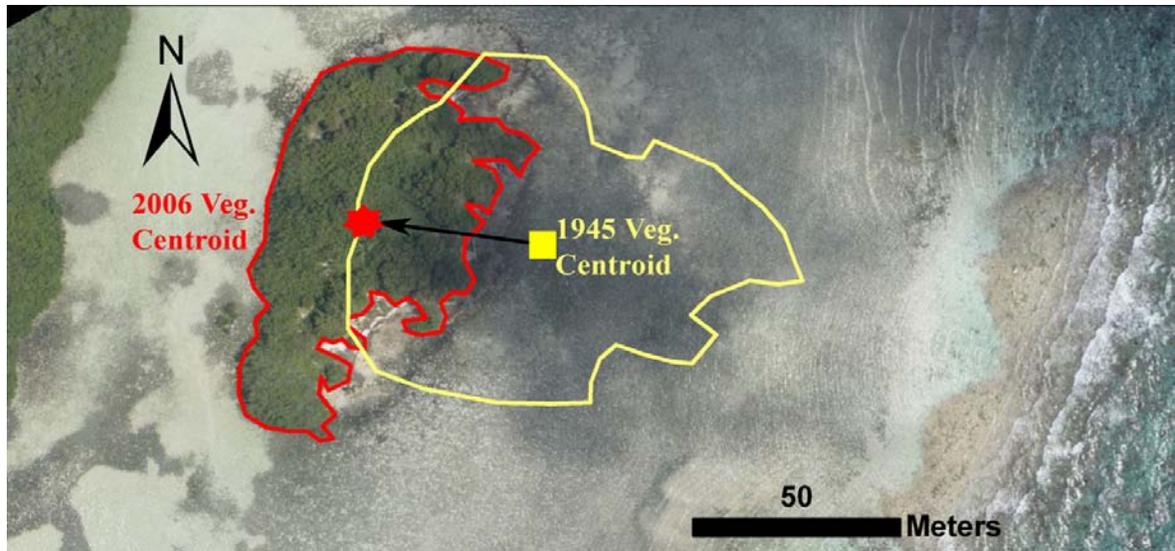


Figure 3.10. Dead Man Cay-5 (southern group cay), 2006 photo-mosaic. Yellow outline shows periphery of 1945 cay vegetation, with yellow square as cay vegetation centroid. The red outline delimits the periphery of the 2006 cay vegetation with red star as the cay vegetation centroid. Black arrow indicates the direction of shift after 61 years (approximately 43 m predominantly west with a northerly component).

For the direction of movement of the cay vegetation polygon centroids (1945 to 2006), the calculated Rayleigh test score ‘r’ of 0.6406, indicates a high level of concentration around the mean (Rayleigh test, $p < 0.0001$), the mean angle of the sample was 302.5° represented by thick arrow in Figure 3.11, the vectors had an angular variance of 0.72, and a mean angular deviation of 48.5° .

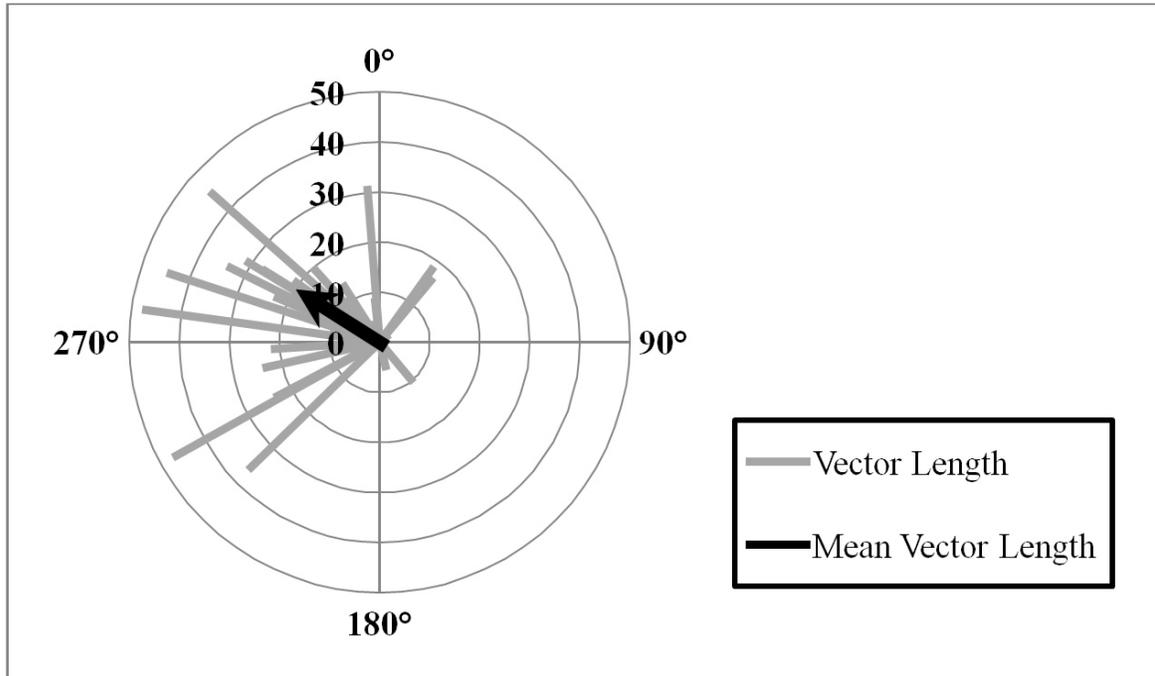


Figure 3.11. Orientation and magnitude (vector) of cay vegetation polygon centroid shift (light colored lines) based from 1945 to 2006 photo-mosaic (n = 31). Distance from center of chart measured in meters. Mean resultant length = 18 m (dark colored arrow), mean angle of the sample = 302.5° (dark colored arrow), 'r' = 0.6406, Rayleigh test, $p < 0.0001$, angular variance = 0.72, mean angular deviation = 48.5°.

Turneffe has a general north northeast to south southwest alignment. The coral reef system surrounding Turneffe is aligned approximately 18° at its longest diagonal, but there are local variations of the reef crest that surrounds the atoll. The directional mean of 46 sections of the coral reef crest directly oceanward of the vegetated fringing cays was 34°, (with a significant level of concentration around the mean (mean vector length 'r' = 0.9596; Rayleigh test, $p < 0.0001$; Fig. 3.12). The vegetated cays were non-circular in shape (Fig. 3.13). The orientation of the longest axis of the vegetated cays from the 1945 photo-mosaic (n = 42), had a mean bearing of 24° with a significant level of concentration, (mean vector length 'r' = 0.6247; Rayleigh test, $p < 0.0001$; Fig. 3.14). While the 2006 photo-mosaic (n = 35), showed a mean

bearing of 20°, with a significant level of concentration, (mean vector length 'r' = 0.6604; Rayleigh test, $p < 0.0001$; Fig. 3.15).

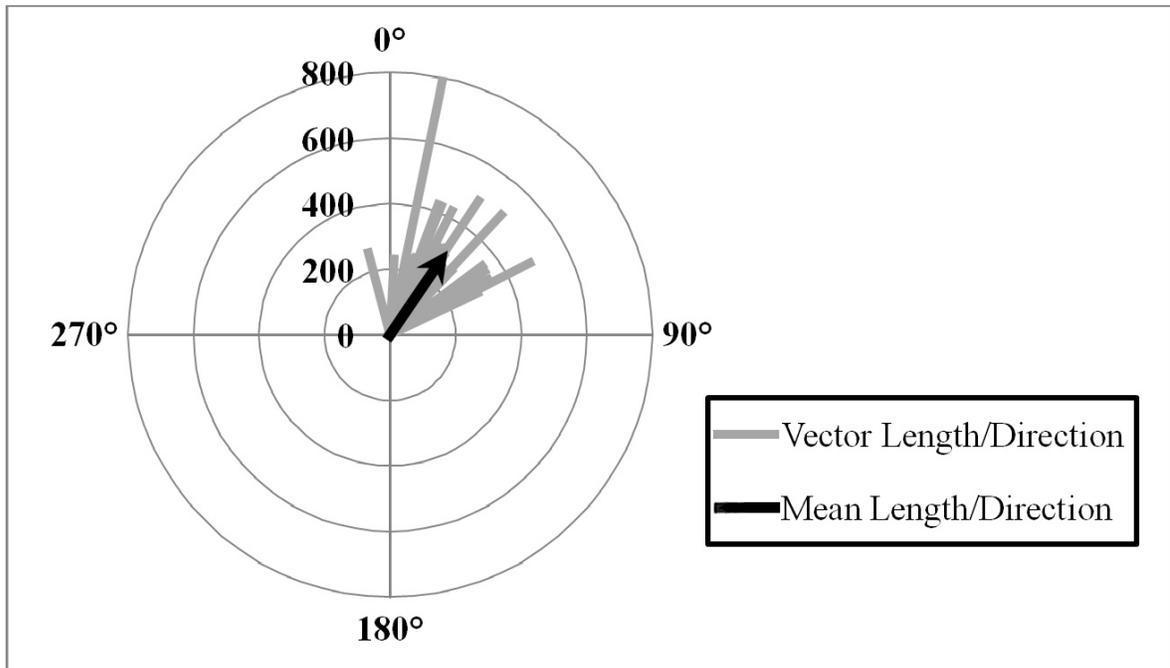


Figure 3.12. Orientation of reef crest directly in front of 46 vegetated fringing cays on Turneffe (light colored lines). Orientation identified from the 1945 and 2006 photo-mosaic. Distance from center of chart measured in meters. Mean length of the section of the protecting reef = 311 m (dark arrow), mean angle of the sample = 34° (dark arrow).

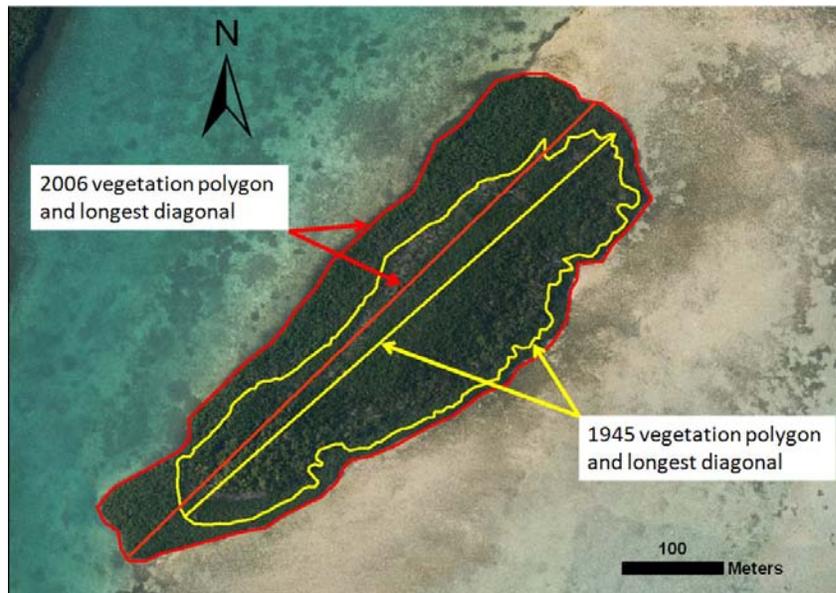


Figure 3.13. Cockroach Cay-28, yellow outline shows periphery of 1945 cay vegetation polygon, with its longest diagonal and the red outline shows the periphery of the 2006 cay vegetation polygon with its longest diagonal.

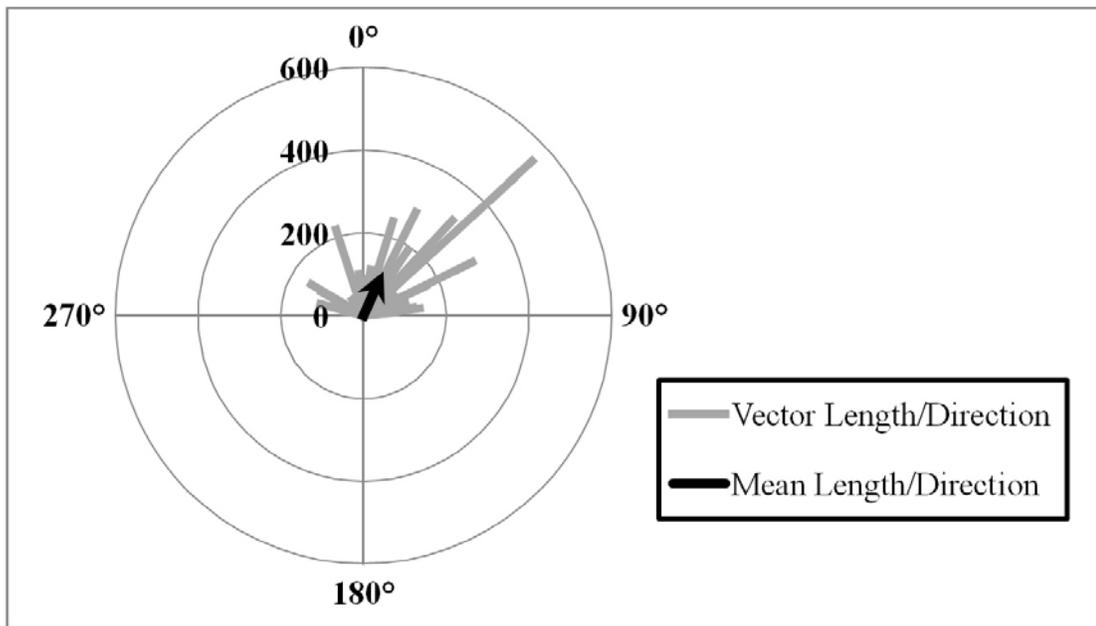


Figure 3.14. Orientation of longest axis of the vegetated fringing cays from Turneffe. Longest axis derived from the vegetation polygon of the 1945 photo-mosaic. $n = 42$ (light colored lines). Distance from center of chart measured in meters. Mean length = 116 m (dark arrow), mean angle of the sample = 24° (dark arrow).

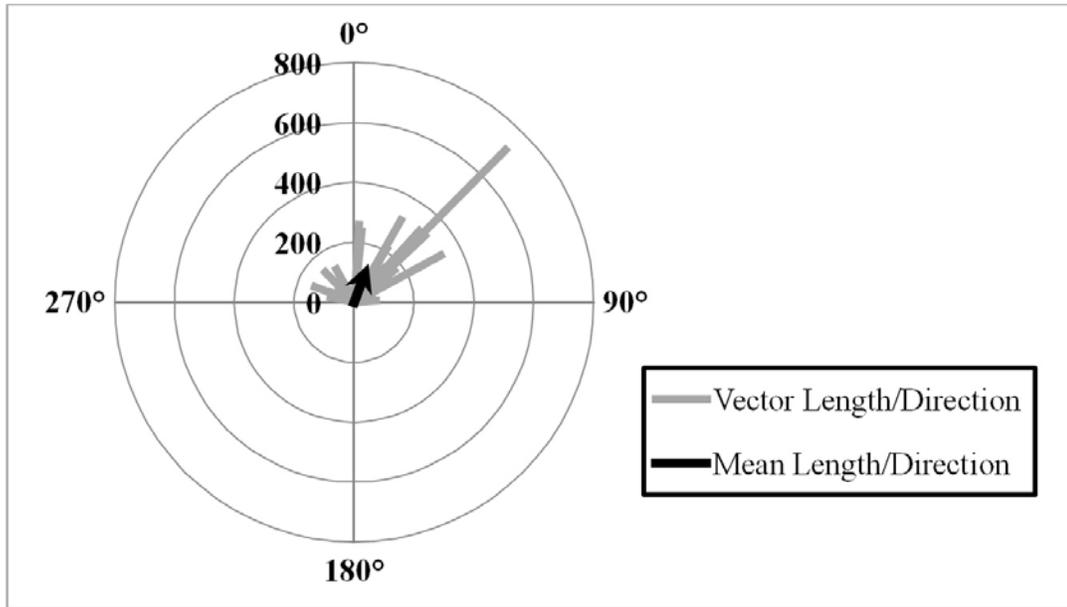


Figure 3.15. Orientation of longest axis of the vegetated fringing cays from Turneffe. Longest axis derived from the vegetation polygon of the 2006 photo-mosaic. $n = 35$ (light colored lines). Distance from center of chart measured in meters. Mean length = 120m (dark arrow), mean angle of the sample = 20° (dark arrow).

The V-test was used to test closeness to expected orientation (the orientation of the reef crest = 34°). The diagonals from the cay vegetation polygons based on the 1945 photo-mosaic were significantly oriented parallel to the reef directly oceanward of the cays (V-test with expected orientation = 34° , $r = 0.6247$, $u = 5.6383$, $n = 42$, $p < 0.0001$). The diagonals from the cay vegetation polygons based on the 2006 photo-mosaic were also significantly oriented parallel to the reef crest (V-test with expected orientation = 34° , $r = 0.6604$, $u = 5.3615$, $n = 35$, $p < 0.0001$).

3.3.2.3 Cay vegetation: 1945 vs. 2006

Between 1945 and 2006 photo-mosaic a total of 11 cays were devegetated and eroded (Table 3.3). This amounts to 26% loss of the fringing cays identified from the 1945 photo-mosaic along the eastern side of the atoll. The majority of devegetated cays and cays for which substrate was eroded were from the northern group of Cockroach Cays (n = 9); the remaining two were from the central group (Soldier Cay and Calabash Cays). All 11 cays lost were less than 0.5 ha (Fig. 3.16).

Table 3.3. Net changes in number of eastern fringing cays on Turneffe since 1945.

Cay Group	n¹	Devegetated by Hurricane Hattie²	Devegetated between 1945 and 2006	New vegetated cays between 1945 and 2006
North	29	1	9	1
Central	7	2	2	3
South	6	0	0	0
Total	42	3	11	4

¹ Number of cays identified in aerial photographs both in 1945 and 1960 before Hurricane Hattie. ² Number of cays devegetated by Hurricane Hattie of October 1961 was based on aerial photographs from 1961 and 1962. Devegetated indicates an absence of dead and living vegetation from cays.

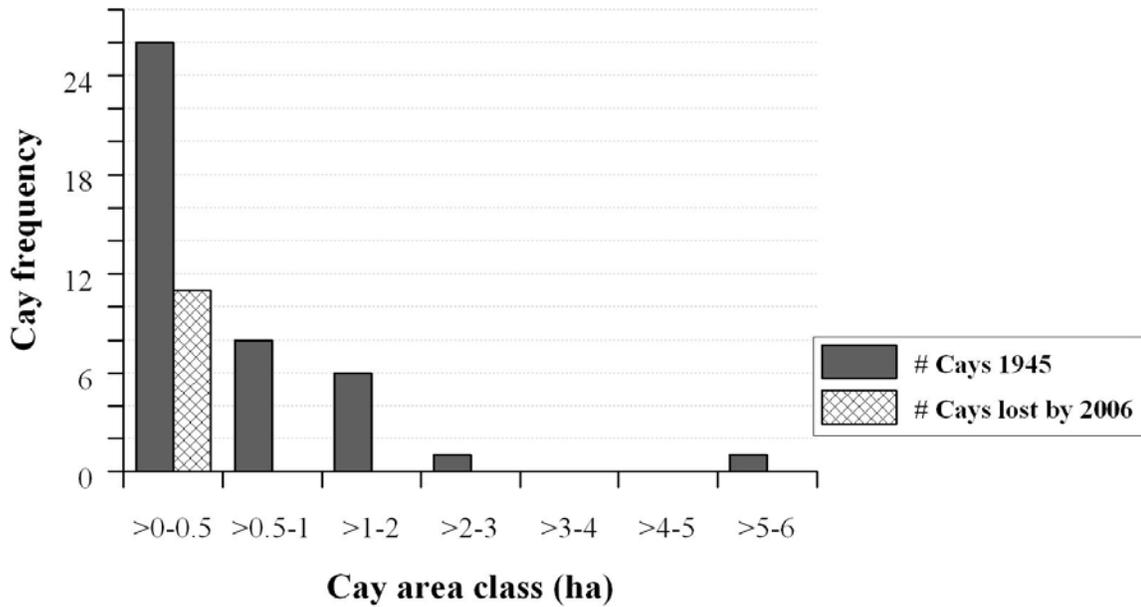


Figure 3.16. Fringing cay vegetated area class by frequency of cays identified from the 1945 photo-mosaic and frequency of cays lost based on the 2006 photo-mosaic.

Base on the photo-mosaics from 1945 and 2006, four new vegetated cays had formed (Table 3.4): 1) Cockroach Cay between 22 and 23 (0.009 ha); 2) Little Pelican Cay (0.031 ha); 3) Little Soldier Cay (0.006 ha); and 4) Big Calabash North Cay (0.033 ha) (Appendix B).

Table 3.4. List of vegetated cays identified from the 1945 and 2006 photo-mosaic. Each cay was given an ID number that can be used to interpret subsequent graphics.

Cay	Cay ID 1945	Cay	Cay ID 2006
Dog Flea Cay	1	Dog Flea Cay*	1
Cockroach Cay 2	2	Cockroach Cay 2	2
Cockroach Cay b/w 2 & 3 ¹	3	Cockroach Cay b/w 2 & 3*	3
Cockroach Cay 3	4	Cockroach Cay 3*	4
Cockroach Cay 4	5	Cockroach Cay 4	5
Cockroach Cay 5	6	Cockroach Cay 5	6
Cockroach Cay 6	7	Cockroach Cay 6	7
Cockroach Cay 7	8	Cockroach Cay 7	8
Cockroach Cay 8	9	Cockroach Cay 8	9
Cockroach Cay 9	10	Cockroach Cay 9	10
Cockroach Cay 10	11	Cockroach Cay 10	11
Cockroach Cay 11	12	Cockroach Cay 11*	12
Cockroach Cay 12	13	Cockroach Cay 12	13
Cockroach Cay 13	14	Cockroach Cay 13	14
Cockroach Cay 14	15	Cockroach Cay 14	15
Cockroach Cay 15	16	Cockroach Cay 15	16
Cockroach Cay 16	17	Cockroach Cay 16	17
Cockroach Cay 17	18	Cockroach Cay 17	18
Cockroach Cay 18	19	Cockroach Cay 18	19
Cockroach Cay 19	20	Cockroach Cay 19*	20
Cockroach Cay 20	21	Cockroach Cay 20	21
Cockroach Cay 21	22	Cockroach Cay 21*	22
Cockroach Cay 22	23	Cockroach Cay 22	23
		Cockroach Cay b/w 22 & 23	23.5
Cockroach Cay 23	24	Cockroach Cay 23	24
Cockroach Cay 24	25	Cockroach Cay 24	25
Cockroach Cay 25	26	Cockroach Cay 25*	26
Cockroach Cay 26	27	Cockroach Cay 26*	27
Cockroach Cay 27	28	Cockroach Cay 27*	28
Cockroach Cay 28	29	Cockroach Cay 28	29

Table 3.4. Continued

Cay	Cay ID 1945	Cay	Cay ID 2006
Pelican Cay	30	Pelican Cay	30
		Little Pelican Cay	30.5
Little Black Bird Cay	31	Little Black Bird Cay*	31
Soldier Cay	32	Soldier Cay	32
		Little Soldier Cay	32.5
Big Calabash Cay	33	Big Calabash Cay	33
		Big Calabash North Cay	33.4
Big Calabash East Cay 1	34	Big Calabash East Cay 1	34
Big Calabash East Cay 2	35	Big Calabash East Cay 2*	35
Little Calabash Cay	36	Little Calabash Cay	36
Little Rope Walk Cay	37	Little Rope Walk Cay	37
Dead Man Cay 5	38	Dead Man Cay 5	38
Dead Man Cay 4	39	Dead Man Cay 4	39
Dead Man Cay 3	40	Dead Man Cay 3	40
Dead Man Cay 2	41	Dead Man Cay 2	41
Dead Man Cay 1	42	Dead Man Cay 1	42

¹ Cockroach Cay between 2 and 3 was visible in the photographs, but was missed during Stoddart's previous surveys. Cays with asterisk (*) were found devegetated in the 2006 photo-mosaic and from field surveys (2006 to 2008). Cay names in bold represent "new vegetated cays" identified in the 2006 photo-mosaic and from subsequent field surveys.

3.3.3 Causes of change to cays

3.3.3.1 Wind and tides

The yearly average wind speed in 2007 at Carrie Bow Cay Marine Field Station (60 km southwest of the Calabash Cays) was 19.6 km/h with a directional mean of 51.5° (Fig. 3.17).

The yearly average wind speed in 2008 was 21.1 km/h with a directional mean of 53.7° (Fig. 3.18), indicating strong consistency in these yearly results. The mean monthly wind data

indicates that from December to September the winds are predominantly from the east northeast, however, during October and November the winds are from the west northwest.

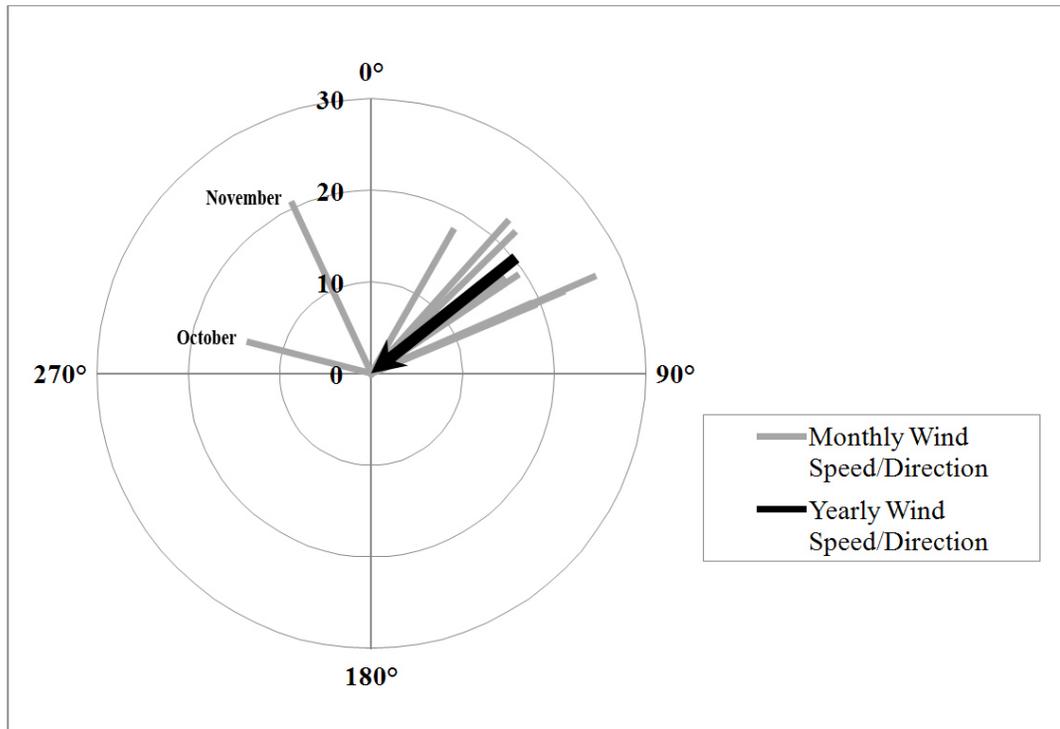


Figure 3.17. Wind speed and direction at the Carrie Bow Cay Marine Field Station in 2007. Distance from center of chart measured in km/h. The monthly mean wind speed and direction represented by the light colored lines. The yearly mean wind speed (19.6 km/h) and direction (51.5°) showed by angle and length of dark arrow.

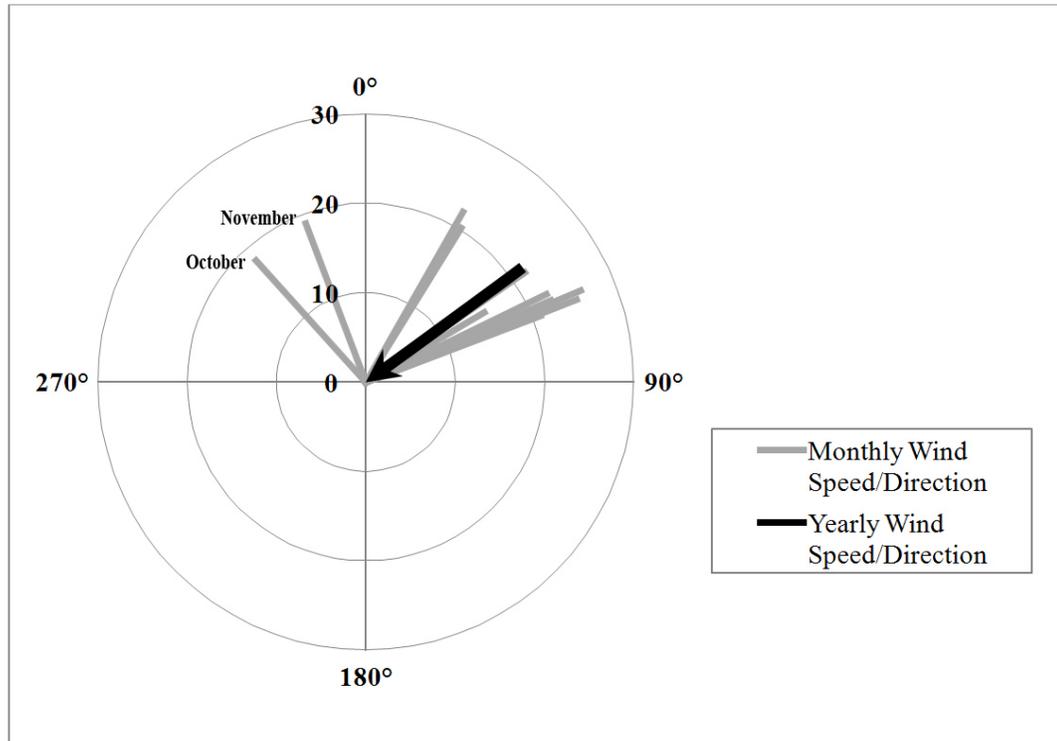


Figure 3.18. Wind speed and direction at the Carrie Bow Cay Marine Field Station in 2008. Distance from center of chart measured in km/h. The monthly mean wind speed and direction represented by the light colored lines. The yearly mean wind speed (21.1 km/h) and direction (53.7°) showed by angle and length of dark arrow.

The tidal fluctuations monitored on Main Calabash Cay confirmed a micro-tidal pattern and a strong correlation with the readings from Carrie Bow Cay Marine Field Station (Fig. 3.19; Pearson correlations $r = 0.89$, $p < 0.0001$). At Main Calabash Cay, an average water depth of 0.62 m with maximum of 0.80 m and a minimum of 0.39 m were recorded from May 29 to June 05, 2008 (total of 7 days with no data available for June 01, 2008). For the corresponding data from Carrie Bow Cay, an average water depth of 0.29 m with maximum of 0.44 m and a minimum of 0.07 m were recorded from May 29 to June 05, 2008.

Table 3.5. Cay area (vegetated and bare substrate) for group of eastern cays on Turneffe from 2008 survey.

Cay Group	n	Total area (ha)¹	Area above high tide (ha)	Area below high tide (ha)
Northern	21	23.9	6.3	17.6
Central	8	2.9	1.4	1.5
Southern	6	3.1	1.6	1.5
Total	35	29.9	9.3	20.6

¹ Total cay area (vegetated and bare substrate) includes cay vegetation (above and below spring high tide) and bare substrate (above spring high tide).

3.3.4 Hurricanes

Since the hurricane record started in 1851, 25 hurricanes and 21 tropical storms have made landfall along the coast of Belize (from 1851 to 2008; Appendix E). Hurricane season in the Atlantic typically lasts from June to November. From the 46 storms that made landfall along the coast of Belize, most storms were skewed toward the latter part of the hurricane season (Fig. 3.20). Specifically in Turneffe, the frequency of storm activity was highest during September and October (Fig. 3.21).

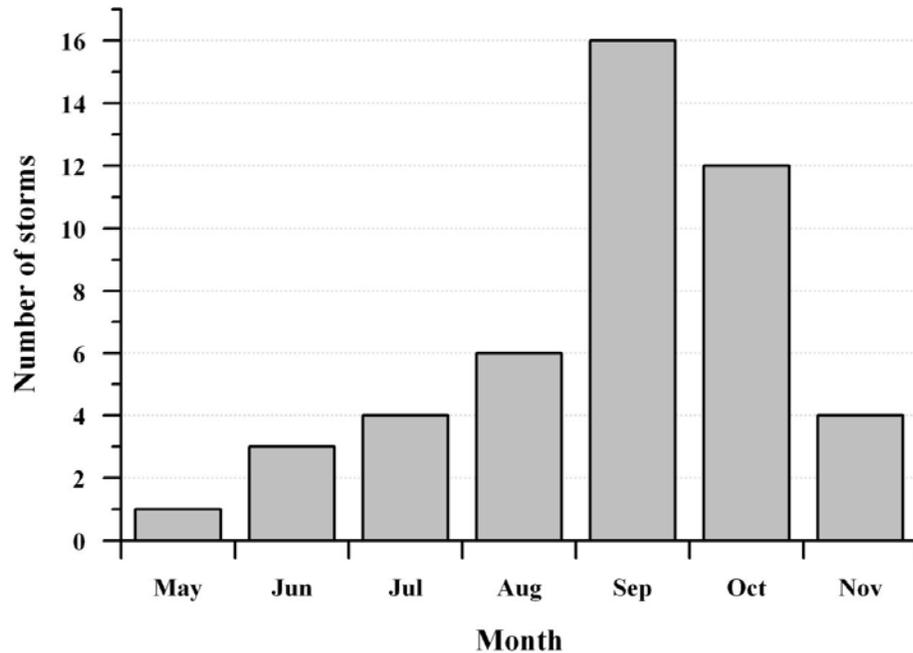


Figure 3.20. Number of hurricanes and tropical storms that have made landfall along the coast of Belize. Storm frequency based on the National Oceanic and Atmospheric Administration (NOAA) database from 1851 to 2008; including Tropical Storm Arthur (May 2008) which occurred outside of the hurricane season which runs from June to November.

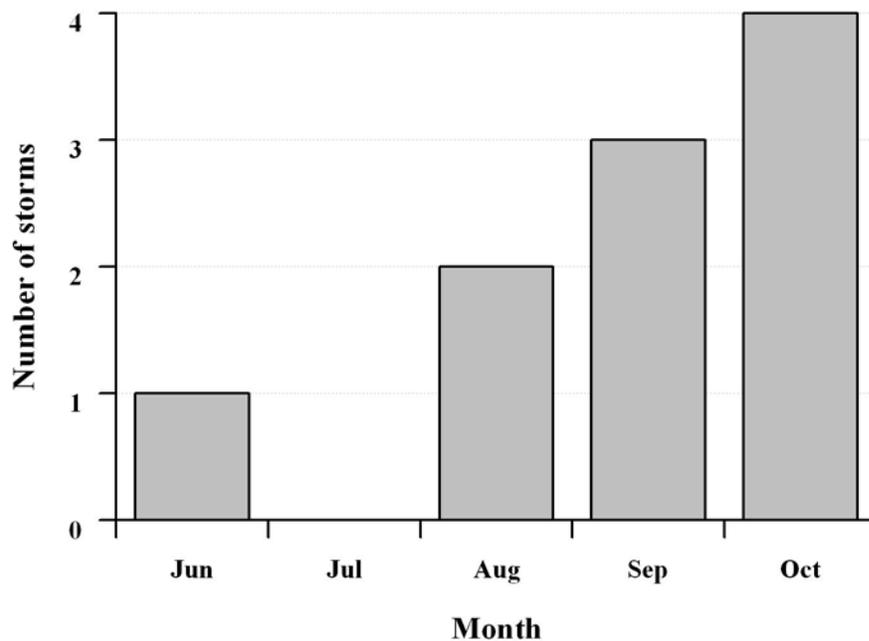


Figure 3.21. Number of hurricanes and tropical storms that have made landfall on Turneffe. Storm frequency based on the National Oceanic and Atmospheric Administration (NOAA) database from 1851 to 2008.

Of 25 hurricanes that affected Belize from 1851 to 2008, 17 made landfall with hurricane force winds ranging from Category 1 to 4, six struck as tropical storms, and two had degraded to tropical depressions. Of the 17 hurricanes that made landfall, four were major hurricanes ranging from Category 3 to 4. From 1851 to 2008, the coast of Belize was affected by two hurricanes in the same year only twice. In July 1961, Hurricane Anna (Category 1) made landfall on the southern part of Belize and was followed by Hurricane Hattie (Category 4) in October. In 1971, Tropical Storm Chloe affected the northern coastline in August and was followed by Tropical Storm Laura along the southern coastline of Belize in November.

The tracks of hurricanes and tropical storms showed that 65% made landfall on the northern part of the mainland coastline of Belize; whilst 35% landed on the southern part of the coastal mainland. Most storms tracked from east to west, with the mean direction of travel or heading of the storm tracks upon landfall was 288° , but convoluted storm tracks can result in some unusual headings. For example, Hurricane #2 in 1934 crossed 7 km south of Turneffe with tropical storm strength and then made a loop on the mainland of both Belize and Guatemala. It then made landfall on the south-west side of Turneffe as a Category 1 hurricane. The storm track heading was approximately 20° as it approached the atoll, and the eye tracked along the western side of the atoll. Also unusual, the eye of Hurricane Keith (2000) passed close north of Turneffe as a Category 3 hurricane, then veered towards the southeast and made landfall on the northern part of the atoll with an approximate storm heading of 153° .

From 1851 to 2008, 10 storms made landfall specifically on Turneffe (Table 3.6) and include seven hurricanes and three tropical storms. Of the 10 storms, six made landfall with hurricane force winds, three as tropical storms and one as a tropical depression. Based on the data from 1851 to 2008 (157 years), for land-falling hurricanes (n = 6), Turneffe had an average hurricane return period of 26 years; however, the average return period for catastrophic hurricanes (categories 3 to 5, n = 2), was 79 years.

Table 3.6. List of hurricanes and tropical storms with landfall on Turneffe based on center of lowest pressure. List based from NOAA database 1851 to 2008.

Storm ID and Category	Year	Category by Turneffe	Landfall, Coastal section^A	Wind Speed (km/h)	Translation Speed (km/h)	Storm Heading (degrees)
3 and 1	1864	1	North	130	25	278
7 and 2	1892	2	South	160	19	294
5 and 3	1931	3	North	205	31	280
2 and 1	1934	1	South-West	120	18	22
4 and Tropical Storm	1942	Tropical Storm	South	70	13	263
6 and Tropical Storm	1945	Tropical Storm	North	70	23	257
Hattie and 5	1961	5	South	240	17	248
Edith and 5	1971	Tropical Storm	South	110	20	312
Frieda and Tropical Storm	1977	Tropical Depression	North	28	13	270
Keith and 4	2000	1	North-West	150	3	153
Mean				128	18	276

^A The mid-point to divide the eastern coastline of Turneffe was at 2 km south of Pelican Cay or 7 km north of Soldier Cay. Storm ID in bold are hurricanes. Wind speed and storm translation speed based on the closest reported readings to Turneffe. Storm heading calculated from the closest pair of coordinate points to the atoll. Storm heading in degrees azimuth, clockwise from north (e.g., a 270° storm heads from east to west).

3.3.5 Fringing cay shift in relation to storm track and mean wind direction

The directional means of the cay vegetation centroid shifts between 1945 and 2006 were compared to the directional means of storm tracks (tropical storms and hurricanes) and mean wind direction data from Carrie Bow Cay Marine Field Station (Table 3.7). Based on the Watson-William test, the direction of cay shift was significantly different from mean wind direction ($p < 0.05$) but not from storm track direction ($p > 0.05$).

Table 3.7. Mean angle and mean angular deviation for the directions of cay shift from a group of fringing cays on eastern Turneffe (1945 to 2006). Cay shift mean compared with hurricane and tropical storms mean directions (1851 to 2008) and 2 yr mean monthly wind direction based on readings from Carrie Bow Cay Marine Field Station (2007 to 2008). Results of Watson-Williams F-test for the two planned pair-wise comparisons.

Parameter	Time span	n	Mean degrees	MAD degrees
Cay shift	1945 to 2006	31	303	49
Storm track direction	1851 to 2008	10	276	46
Mean wind direction	2007 to 2008	24	226	36

Comparison	F	DF	p
Cay shift X Storm direction	1.76	39	> 0.05
Cay shift X Wind direction	33.09	53	< 0.05

Mean degrees = Angular mean in degrees (north azimuth), MAD degrees = Mean angular deviation in degrees (north azimuth).

3.3.6 Effects of hurricanes on vegetation change

3.3.6.1 Case study 1: Direct effects of Hurricane Hattie (1961)

The most severe hurricane to affect Turneffe since 1851 was Hurricane Hattie. It struck Turneffe as a Category 5 hurricane, with winds exceeding 240 km/h and a heading of 248°. The effects of Hurricane Hattie on cay vegetation were severe. A comparison of the vertical and oblique photographs taken before and after Hurricane Hattie illustrates the damage to the cays (Appendix F). Before Hurricane Hattie a total of 42 cays were identified on the 1945 and 1960 historic photographs (Appendix G). Three cays were completely devegetated during Hurricane Hattie and 25 cays experienced severe vegetation loss, since more than 50% of vegetation had been removed or had been defoliated (Table 3.8). The majority of severely damaged cays were from the northern part of the atoll within the group of Cockroach Cays and central group.

Table 3.8. Group of eastern cays on Turneffe severely affected by Hurricane Hattie 1961.

Cay Group	n	Cays severely affected by Hurricane Hattie¹	% in group
Northern	29	19	66
Central	7	5	71
Southern	6	1	17
Total	42	25	60

¹The severity was based from loss of more than 50% of vegetation. Standing defoliated trees were either dead or alive. Effects were visible on aerial photographs, reported on cay maps and described by Stoddart (1963).

Cay vegetated area for 1945, 1961 (after Hurricane Hattie) and 2006 values were paired. Based on the Wilcoxon's paired sample test, the differences in cay vegetated area from 1945 and after Hurricane Hattie (1961) were significant ($n = 42$, $p < 0.0001$), as were differences between 1961 and 2006 ($n = 42$, $p = 0.0016$). In contrast, the difference in cay vegetated area between 1945 and 2006 was not significant ($n = 42$, $p = 0.0682$), indicating the mean vegetated area on the cays had recovered to levels observed before Hurricane Hattie.

The average and maximum cay vegetated areas were greater on the northern group of cays than the middle and southern group in 1945, 1961 and 2006 (Table 3.9). Average vegetation area of the central group was smaller than the northern and southern groups after Hurricane Hattie. The central group was where human settlements and modifications to the natural vegetation were most abundant. During Hurricane Hattie extensive damage was done to cays with *C. nucifera* vegetation. Damage to mangrove vegetation included extensive mortality and defoliation. Mangrove mortality on the fringing cays seemed to be caused by mechanical damage, defoliation, stem breakage, and erosion of substrates based on photograph analysis.

Table 3.9. Estimated cay vegetated area in hectares for group of eastern cays on Turneffe. Cays identified from the 1945, 1961 (after Hurricane Hattie) and 2006 photo-mosaics.

1945				
Cay Group	n	Average	Maximum	Minimum
North	29	0.685	5.934	0.029
Central	7	0.303	0.613	0.017
South	6	0.503	1.033	0.055
1961 ¹				
North	28	0.383	4.786	0.009
Central	5	0.074	0.236	0.001
South	6	0.259	0.527	0.012
2006				
North	21	1.083	9.717	0.009
Central	8	0.318	0.886	0.006
South	6	0.470	1.695	0.002

¹ Vegetation estimates for 1961 includes standing vegetation dead and/or alive.

Since Hurricane Hattie, the vegetation cover has recovered but the type of vegetation changed. *Cocos nucifera* was a dominant species on the fringing cays prior to Hurricane Hattie, but it was significantly reduced by the hurricane and has continued to decline (Table 3.10). Before Hurricane Hattie, 76% of the cays had *C. nucifera* as part of the vegetation but in 1962, immediately following the hurricane, only 52% of the cays appeared to have *C. nucifera* as part of the vegetation (Appendix H). Two of the three devegetated cays had coconut palms as the dominant vegetation and were also inhabited by humans at the time of the storm. Cockroach Cay-6 with the largest cocal forest experienced almost complete loss of *C. nucifera*. The presence of *C. nucifera* on the fringing cays of Turneffe has declined further since Hurricane Hattie. There was an overall decrease of *C. nucifera* presence to 48% of the cays by 2006. Cays without *C. nucifera* trees were found on the northern group of cays in

2006, which also includes the highest number of cays that are periodically overwashed by tides. By 2006, 80% of the fringing cays had mangrove forest as the dominant vegetation type. Other dominant vegetation types were coccol, littoral and mixed forest (Appendix I).

Table 3.10. The proportion of cays with *Cocos nucifera* (Cn) as part of the vegetation before and after Hurricane Hattie (1961) and from the 2006 photo-mosaic and surveys; and the proportion of mangrove forest as a dominant vegetation type on the fringing cays.

Cay Group	Presence of Cn 1960	Presence of Cn 1962	Presence of Cn 2006	Mangrove as Dominant Vegetation 2006
North	19/29	15/29	13/21	18/21
Central	7/7	3/7	4/8	7/8
South	6/6	4/6	5/6	3/6

3.3.6.2 Case study 2: Direct effects of Hurricane Keith (2000)

Hurricane Keith made landfall on the northwestern part of Turneffe on October 2000 as it reversed from its eastern course. Hurricane Keith affected the atoll as a Category 1 hurricane with wind speed of 150 km/h on an approximate heading of 155°. While this event was much less intense than Hurricane Hattie, observed vegetation changes provide insights into the modes of damage and recovery from hurricanes.

Although I could not obtain aerial photographs prior to Hurricane Keith, I had visited the peripheries of Cockroach Cays-20, -22 and -23 prior to the hurricane and observed thriving vegetation and inferred that the interior of these cays were vegetated prior to the storm. At that time there were no signs of windthrow or herbivory that could have caused mass

mangrove mortality. Field inspections and an aerial survey conducted in 2003 documented damage to mangrove vegetation that included extensive mortality and defoliation on the western side of the atoll and a swath of damage of approximately 20 km from Mauger Cay, located on northern Turneffe. There was no evidence of damage on the vegetation of fringing cays south of Cockroach Cay-28. This pattern of vegetation damage was consistent with the documented storm track of Hurricane Keith; therefore, I inferred that the observed damage was due to the hurricane and allowing the following interpretations about the storm effects on cay vegetation and its recovery.

Of the eastern fringing cays, the Cockroach Cays were the most heavily affected by this hurricane. The aerial photographs and ground observations in 2003 of the fringing cays showed that mangrove mortality along the damaged areas seemed to be caused by mechanical damage, defoliation, stem breakage and erosion and deposition of substrates. The damaged mangrove areas were in the process of recolonization from naturally regenerating seedlings and lateral vegetative expansion. As of 2008, the affected mangrove areas were still in the process of recovery.

The rate of forest recovery from Hurricane Keith on Cockroach Cays-20, -22 and -23 were estimated using the oblique aerial photographs and field inspections in 2003, 2006 and 2008. Figure 3.22 shows the photos for Cockroach Cay-20 for 2003 and 2008 (oblique aerial photos were not georectified, hence there is no scale on the photos). Mangrove mortality was pronounced on the leeward side of all three cays with respect to the reef crest. Coconut palms and littoral forest were concentrated on the ocean-facing elevated areas of these cays. There

were no dead *C. nucifera* in any of the three cays in 2003, although their leaves were yellow and they appeared stressed. The damaged area on the cay was covered with dead and decaying mangroves still rooted to the ground suggesting that this was fully occupied by mangrove vegetation before Hurricane Keith. The area of dead vegetation decreased on average by 93% on all three cays over a period of 5 years (Fig. 3.23). As of 2003, among the three cays, more than 30% of the former cay vegetated area was still damaged by the hurricane. Cockroach Cay-20 with the smallest area of dead vegetation had almost complete recovery of the damaged area by 2008.



Figure 3.22. Oblique aerial photos of Cockroach Cay-22 taken in April of 2003 (left) and April of 2008 (right). Center of cay shows zone of vegetation disturbance from Hurricane Keith of 2000. Recolonization had occurred and the disturbed zone had closed considerably in 2008.

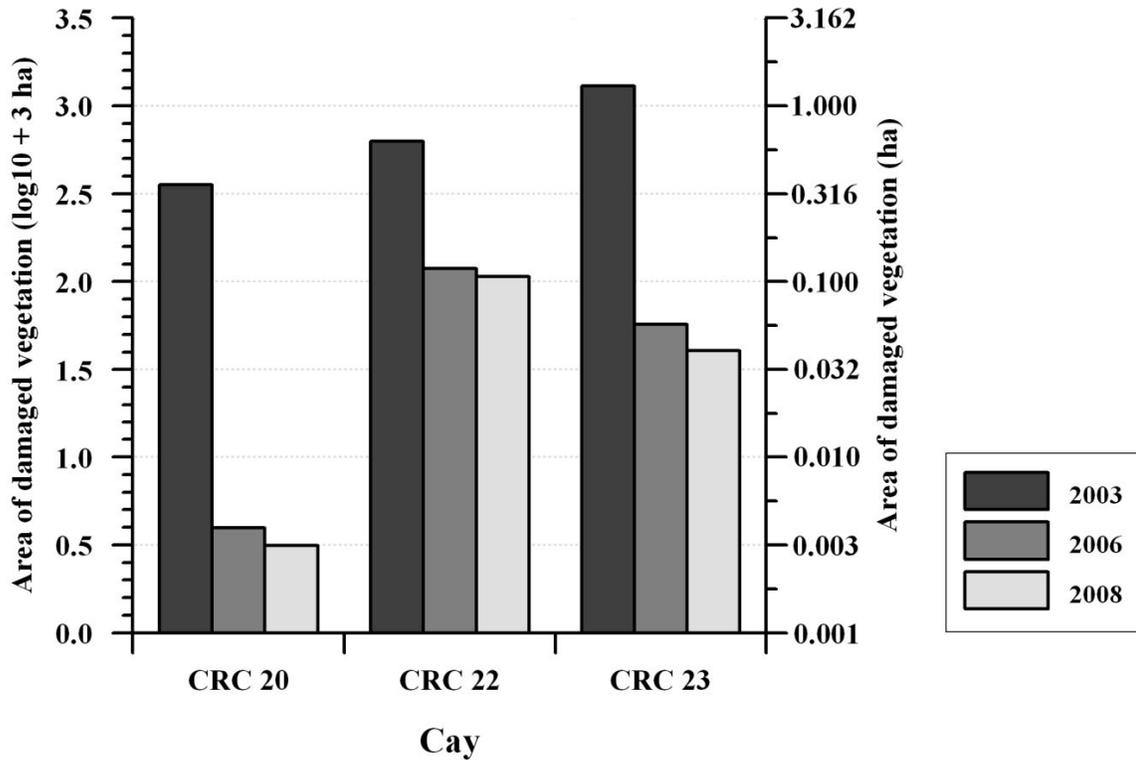


Figure 3.23. Estimated damaged cay vegetation area from Hurricane Keith (2000) based on surveys from 2003, 2006 and 2008. Three cays from eastern Turneffe were surveyed (CRC = Cockroach Cay; Cay numbers 20, 22, and 23).

All three cays experienced colonization inwards and outwards along the fringing vegetation.

The highest rate of recolonization was evident on the leeward side of all three cays with respect to the reef crest. *Rhizophora mangle* was almost exclusively colonizing and

expanding on the leeward side of all three cays with respect to the reef crest. The aerial photographs and cay vegetation estimates (Appendix J), shows a continuous pattern of

recolonization of damaged areas from the edges towards the center of disturbance on all three cays. The colonization of these shallow waters was accomplished by lateral vegetative

expansion of surviving and recently established plants. The fringing mangroves, particularly on the leeward side of these cays with respect to the reef crest, have a tendency to lean

towards the open water. A high number of *R. mangle* branches were found to be expanding laterally by the production of prop roots.

3.3.6.3 Case study 3: Indirect effects of Hurricane Ivan (2004)

On September 12, 2004, the eye of Hurricane Ivan was approximately 700 km from Turneffe with Category 4 strength. The storm surge hit Turneffe on the eastern side causing erosion of the sandy beaches on the large islands (e.g., Main Calabash Cay). New sediment material was washed past the reef crest into the back-reef zone in some areas providing a clear example of the effects that storms can have even at great distances. Sections of the reefward facing mangrove vegetation on Soldier Cay was partially buried with new material from the reef (marine-origin organic matter, sand and coral rubble, Fig. 3.24), and there was evidence that waves had overwashed the cay. Approximately 77% of the cay vegetated area was covered with new material. The blanket of new material varied from a few cm to close to half a meter in certain areas and some of the coral rubble closest to the reef exceeded 40 cm in length. The vegetation, predominantly *R. mangle*, acted as a barrier to the incoming sediment load. Most of the trees received severe abrasions on their stems and prop roots, but the fringing vegetation survived the storm. As a result, in several parts of the cay, the buffered incoming sediment now formed the highest elevations on the cay and was well above the high tide. For the Soldier Cay fringing mangrove, most of the trees that withstood and survived the burial were taller than 1 m. About 40% of the fine deposited material on the beach side was reworked and eroded by routine wave action within 6 months after Hurricane Ivan.



Figure 3.24. Mangrove trees on the ocean side of Soldier Cay, Turneffe, partially buried and scarred by corral rubble from the surge effects of Hurricane Ivan 2004. (Photo taken two weeks after Hurricane Ivan 2004).

3.3.7 Human impacts

Prior to Hurricane Hattie, 20 human-made structures, including houses, huts and piers, on five different fringing cays were visible from the oblique and on-the-ground photos taken by Stoddart in 1960 and 1961. Little Calabash Cay had the highest density of houses ($n = 7$) and two piers, with an estimated area of 0.3 ha that was cleared for the administrative quarters (Fig. 3.25). This cay had an extensive docking facility and one substantive over-the-water housing structure. On the cays inhabited by humans only small and isolated patches of mangroves remained and most vegetation was dominated by *C. nucifera*.



Figure 3.25. Little Calabash Cay (center) and Main Calabash Cay (background), Turneffe. Photo taken during Stoddart's survey of 1960-61 prior to Hurricane Hattie 1961. (Photo credit, Stoddart).

I was unable to obtain a complete set of oblique photographs for all of the fringing cays before and after Hurricane Hattie; however, the subsets of paired photographs and post-hurricane photographs are consistent with documentary records that report high degrees of damage and loss of human lives (Stoddart 1969). Photographs taken in 1962, immediately following Hurricane Hattie, show that all human-made structures on the fringing cays were destroyed (e.g., Fig. 3.26). The coconut trees were also removed from the cays (Appendix F shows aerial photographs of selected cays before and after Hurricane Hattie). The 1962 photographs of Cockroach Cay-6, Pelican Cay and Soldier Cay, which had settlements prior to Hurricane Hattie, showed no signs of human re-settlement. Photographs of the Cockroach Cays taken by Stoddart in 1965 showed no resettlement. In contrast, by 1965, small huts had been constructed on both Big Calabash Cay and Little Calabash Cay. Stoddart (1969) notes that young coconut trees had been re-planted on Big Calabash Cay by 1965.



Figure 3.26. Photo showing Little Calabash Cay (center) and Main Calabash Cay (background) after Hurricane Hattie of 1961. Little Calabash Cay served as the administrative center of the coccolith industry before the hurricane on Turneffe. Photo taken during Stoddart's survey of 1962 after Hurricane Hattie 1961. (Photo credit, Stoddart).

During the 2008 field surveys, human-made structures constructed since Hurricane Hattie were found on eight of the 35 vegetated cays. These structures were in the form of sheds, house foundations, and docks. A total of 10 structures were identified, nine of these structures were found on the Cockroach Cays and Little Rope Walk Cay had a dilapidated 8-m dock. There were no standing houses that were comparable in size to the houses seen on photos from before Hurricane Hattie. The largest human-made structure at the time of the field survey was on Cockroach Cays-5 and -6. A 45 m-long boardwalk above the high tide was constructed in 2007 to connect these cays. Also, Cockroach Cay-23 had a semi-

permanent human presence including an area of 0.3 ha was cleared on the southeast portion of the cay for use during the open fishing season for conch and lobster. Since Hurricane Hattie, other sheds and houses have been constructed on the fringing cays, but have since either been destroyed by storms or abandoned and damaged by looters and weather (personal observation and personal communication with fishers from Turneffe). Although Big Calabash and Little Calabash Cay were re-settled after Hurricane Hattie, there was no sign of human-made structures at the time of the field survey in 2008. Little Calabash Cay had a small wooden shack from 1999 until 2004 but no permanent human presence. The shack was demolished in 2004, but the underbrush was periodically cleared until 2008 (personal observation).

Although the cays are not permanently settled by humans, several impacts on vegetation were observed. Partial clearing of underbrush by humans was observed on Cockroach Cay-6 and -23, Pelican Cay, Little Rope Walk Cay and Little Calabash Cay. Coconuts are frequently harvested from the fringing cays. During harvest small fires are started on the cays to produce smoke to ward off mosquitoes and sand flies while they husk the nuts. In 2008, after the field survey season, a substantial part of the understory of the coral forest of Dead Man Cay-2 burned.

Records from the Lands Department in Belmopan showed that of 35 fringing cays, 13 had been surveyed between 1997 and 2008 and had approved leases for land use. During the 2008 field survey, 17 of the fringing cays had either survey lines or signs of recent surveying

activity, including concrete or wooden pegs marking the edge of properties or used as markers during the survey.

3.4 Discussion

3.4.1 Variability in number of fringing cays, vegetated area and size

Factors controlling forest damage from storms at the landscape level 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). Loss of vegetated cays along the Belizean coast has been attributed largely to the destructive forces of hurricanes since the introduction and conversion to cocal forest by humans around 1800 (Stoddart 1963). Stoddart based his findings on work done by Speers in the 1760's, Jeffreys in the 1800's, and his own work from before and after Hurricane Hattie in 1961. Stoddart (1971) noted that, after the passage of Hurricane Hattie, the damage to islands along the coast of Belize, including on Turneffe, was greater in small, narrower islands than on large, wide ones at any given distance from the center of the hurricane. He also pointed out that damage was more intense on islands that had been stripped of natural vegetation, or where vegetation had been altered by humans. Small low-lying cays are particularly vulnerable to complete overwash during storms and consequent erosion. Since relatively small gains or losses in sediment supply or small changes in

exposure through the destruction of adjacent reefs can create or destroy such islands, they are highly sensitive to hurricanes (Bayliss-Smith 1988).

Stoddart (1963 and 1971) felt that it was clear that those cays with human habitation and with altered vegetation experienced a greater loss in substrate and vegetated area. Although I was not able to calculate the vegetated areas for all cays in 1960 (due to lack of complete aerial photo coverage of the fringing cays), the available data (60% coverage) indicated that vegetated area on the cays had not changed significantly from 1945 and 1960, but was initially lower after Hurricane Hattie. I found that larger fringing cays have higher stability over time while small vegetated cays have suffered significant loss of area. All cays with a vegetated area > 0.5 ha in 1945 were still present during my 2008 survey despite the fact that some of these cays were devegetated in 1961 by Hurricane Hattie. In contrast smaller sized vegetated cays less than 0.5 ha identified from the 1945 photo-mosaic had been devegetated by 2008 (n = 11).

Of the three cays that were completely devegetated by Hurricane Hattie, two were dominated by coral forests. The central group of cays was the most heavily influenced by human habitation and coral plantations. In this group 71% of the cays were severely affected by Hurricane Hattie. Slightly less (66%) of the cays in the northern group were severely affected by Hurricane Hattie, even though most had relatively small vegetated areas before the hurricane. Furthermore, this group was also on the right side of the hurricane's eye as it moved southwestward, so these cays would have experienced higher winds and a larger storm surge than those on the left side of the eye. For the southern group, which was located

on the left side of the hurricane, only 17% of the cays were severely affected by Hurricane Hattie. Between 1945 and 2006 there was no net difference in cay vegetated area. However, the increase in cay vegetated area since Hurricane Hattie was from preexisting cays and not from the new vegetated cays. The new vegetated cays contributed only 0.3% of the total 2006 cay vegetated area.

During this study, four new areas were found with *R. mangle* colonizing new substrate to form patches of vegetation distinct from the adjacent cays and were classified as newly vegetated cays. All four of the new vegetated cays were dominated by *R. mangle* and were under the influence of the tides. However, the majority of the cay vegetated areas were exposed during low tide. In three of the four cases, the new vegetated cays were only a few meters away from the adjacent cays (over 4 m). Storm surges from hurricanes can create channels on islands, thus splitting an island in two. On large islands, this phenomenon was reported when Hurricane Katrina 2005 created a 2 km wide channel on Dauphin Island, Alabama (Froede 2008). There is also the possibility that in the future the new vegetated cays might merge with the adjacent cays. Around the periphery of Big Calabash Cay where the new vegetated cays were found, there was a high rate of colonization by mangrove propagules. Within 2 years (2006 to 2008), a vegetated patch of mangrove on the west of Big Calabash Cay became attached at the southern end.

Distance from the reef crest may influence the level of damage and the subsequent recovery of the vegetation on these cays. For example, Cockroach Cay-28 (northern group), which was the farthest from the reef crest (~700 m), showed a substantial increase in vegetated area

from 5.9 ha to 9.7 ha. Three unvegetated piles of coral rubble above the spring high tide were located close to the reef, northeast of Cockroach Cay-2, Soldier Cay, and Big Calabash Cay. During the 2008 survey, these ramparts did not have any type of vegetation growing on the exposed substrate nor around it, the intertidal zone. In contrast, rapid colonization by the *R. mangle* was occurring in shallow protected areas on the leeward sides of the cays (with respect to the reef crest), dense with seagrass beds, exposed during low tides, with sandy substrate, and with minimal currents and waves. Woodroffe (1992) commented on the variation in mangrove forest types and the dominance of each type in a given environment and how they are related primarily to characteristics of the landforms colonized by the trees. In addition to surface inundation, soil elevation has also been identified as an important factor in mangrove recruitment and survival (McKee 1993). Substrates are colonized by different species and the resulting pattern depends on each individual species' adaptation to growth at different tidal or flood water elevations, and to edaphic differences, such as particle size, redox potential, etc. (Schaeffer-Novelli et al. 1990). For example, under more flooded conditions, survival of *R. mangle* is greater than that of *A. germinans* and *L. racemosa* (McKee 1993).

3.4.2 Vegetation change from coral to mangrove

Humans had altered the vegetation on many of the fringing cays prior to Hurricane Hattie in 1961, mostly by cutting down both mangrove and littoral forest and planting coconut palms. The use of heavy machinery for dredging and filling to increase cay elevation was not practiced on Turneffe before the 1960's, so cays with naturally higher elevation relative to

mean sea-level were the best candidates for human habitation and coconut planting since these palms can tolerate sea spray but not periodic inundation from tides. Cocal forest was tended and maintained by planting and replanting and by the clearing of underbrush to eliminate competition from natural cay vegetation (Stoddart 1963). Since Hurricane Hattie and subsequent abandonment by cocal farmers, the fringing cays have become dominated by mangrove forest, and cocal forest is declining. The field survey of 2008 shows that there is an overall decrease of cocal presence from 76% to 48% between 1960 and 2008.

Hurricane Hattie was the most severe of several hurricanes since coconut planting became widespread in Belize. This hurricane killed many people, and demolished so many plantations and structures that many of the coconut plantations and associated facilities on the Belizean cays were abandoned. Pringle (1982) commented on this and noted recovery of the original littoral vegetation on the cays. Coconuts are particularly vulnerable to hurricane damage. Bayliss-Smith (1988) recorded a great loss in cay area in the Solomon Islands from a hurricane that destroyed coconut plantations. When Hurricane Gilbert made landfall along the coast of Quintana Roo, Mexico, in 1988, damage to coconut palms was the most notable plant damage. Dixon (1991) reported that 70% of the coconut palms had their tops snapped off. Duryea et al. (1996) also accounts how the coconut palm was a poor survivor during Hurricane Andrew in 1992 whereby 68% of the coconut palms in South Florida were uprooted, 29% broken and 3% both. Stoddart (1963) recounts that Big Calabash Cay was temporarily resettled after the passage of Hurricane Hattie and that some coconut seedlings were replanted on this fringing cay. However, at the time of my survey, only three coconut trees with stunted growth were found on that cay. On fringing cays, it was clear that without

the proper cocal forest maintenance from farmers, these plants fail to naturally colonize available areas in high density. However, I have noticed that on the higher elevation cays cocal forests can persist and expand without much human influence.

Hurricanes and lack of cultivation are not the only cause of loss of coconut trees on Turneffe. Lethal yellowing (LY), a coconut palm disease has also affected the cocal forest on the larger islands since 1997 (Platt et al. 1999). However, no sign of this disease was visible on the fringing cays when my study was conducted, nor has it been noticed since 1999 when I started working on the atoll. The highest infestation of LY was observed on Main Calabash Cay, one of the larger islands west of the fringing cays, where littoral forest has replaced the once thriving cocal forest.

The harvesting of coconuts on some of the fringing cays leads to fire, another human-induced disturbance. Dead Man Cay-2 with a healthy population of *C. nucifera* burnt in 2008. Fortunately this event happened after all data had been collected on the cay. The large amount of organic fuel that accumulates from the coconut fronds can easily burn. Coconut harvesters usually light a fire to produce smoke to combat mosquitoes and sand flies while they husk the nuts. In some instances these fires are left unattended and have the potential to damage the cocal forest and this seems to have been the case with Dead Man Cay-2. While there were no permanent residents on the fringing cays at the time of the field surveys, some partial clearing of underbrush by humans was observed on Cockroach Cay-6 and -23, Pelican Cay, Little Rope Walk Cay and Little Calabash Cay.

According to (Stoddart 1963) mangrove trees survived Hurricane Hattie on some of the fringing cays and parts of the larger islands. Little is known about how mangrove forests recover from a state of severe damage. Everham and Brokaw (1996) suggested that recruitment and repression by herbaceous species in severely disturbed mangroves will lead to forests with mixed species, while lower diversity forests may persist where damage is less severe and regeneration is primarily via resprouting and release of advance recruits. In 2008, *R. mangle* was widespread on all 35 cays. *Laguncularia racemosa*, *A. germinans*, and *C. erectus* were also found on most cays. In combination, mangroves species accounted for 75% of the total vegetation cover on these cays. In the New World, *R. mangle* is the dominant pioneer mangrove species, efficiently colonizing emergent substrates (Pool et al. 1977; Jiménez and Soto 1985). When storms are occasional, complete recovery is possible between events (Woodroffe 2002). Successful recovery is dependent on available substrate. While the substrate does not have to be above the spring high tide for mangrove colonization, it is a requirement for other cay vegetation (cocal and littoral forest). Islands can gradually increase in size because of the retention of new sediment, perhaps as a result of storms sweeping in coral rubble from adjacent reefs, or through the more gradual transport sand-sized material by routine waves and currents (Woodroffe 2002).

Mangroves are well-adapted to life in the intertidal zone, including colonization of new habitats via buoyant propagules. A conceptual framework of the biomechanics of *R. mangle* establishment, from settlement of free floating propagules to vegetative expansion of established plants was presented by Boizard and Mitchell (2010). In Belize and elsewhere in the Caribbean, all the mangrove species flower all year round, but with peak propagule

release between August and October (Rabinowitz 1978a), which coincides with the season of greatest hurricane activity (Neumann et al. 1981).

The successful dispersal of propagules to sites of colonization has been linked to closer distances from parent trees (Delgado et al. 2001). At Turneffe, the fringing cays are bordered to the west by large sandy cays with fringing mangrove communities and availability of propagules does not seem to be a limiting factor. Another occurrence on the back-reef where the fringing cays have formed is the exposure of wide zones of substrate during low tides. Low tide and calm wind create extended areas between the reef crest and the leeward edges of the cays to turn dry. These conditions can be pronounced when the wind is blowing from the north northwest for an extended period, sometimes days, and when it coincides with low tides. These conditions could lead to the settlement of mangrove propagules.

Settlement of floating mangrove propagules may also depend on substrate roughness.

Mangrove propagules with developing roots were found nestled in crevices of coral rubble and amongst the seagrass canopy in areas that are usually flooded during high tide.

Propagules were also found tangled with herbaceous vegetation close to the high tide water mark and many times above the spring high tide water mark. The combined energy of wind, waves and tides explains the transport of propagules beyond the high tide water mark on the fringing cays. McKee et al. (2007b) found that patches of herbaceous vegetation may promote mangrove recolonization of disturbed areas by 1) trapping dispersing propagules, 2) promoting establishment and rooting, and/or 3) enhancing survival and growth of seedlings through amelioration of physical and chemical conditions.

The dead trees from storm damaged communities may promote mangrove re-establishment. Stoddart (1963) found that after the storm mangrove trees were still standing in position on various fringing cays even though they were defoliated or dead. Duke (2001) observed that the dead tree trunks in the mangrove canopy gaps remain standing for years. In mangroves forest, woody debris is important as a prolonged nutrient source and sink (Harmon and Hua 1991; Romero et al. 2005). It can promote sedimentation (Krauss et al. 2003), and has been implicated in enhanced seedling growth (Allen et al. 2000).

3.4.3 Effects of waves and tides on vegetation above and below the spring high tide

The primary hydrodynamic influence on the formation and stability of coral cays is wave action caused by winds and regulated by the tides (Gourlay 1988). The coral reefs directly in front of the fringing cays refract incoming waves. When a wave breaks on the reef, water is pumped across the reef crest (Shinn 1963), and some water surges back before the arrival of the next breaker (Kjerfve et al. 1982). This translates into the formation of strong across-the-reef currents capable of moving coarse sediment (e.g., Lugo-Fernández et al. 1994). There is high energy loss across the reef crest. For example, up to 97% loss of energy has been documented on Margarita Reef, Puerto Rico, particularly at low tides (Lugo-Fernández et al. 1994).

Although Turneffe has a microtidal range of approximately 40 cm, the vegetation of the majority of the fringing cays was under the influence of tides. From the 2008 field survey, 69% of the total vegetated area from fringing cays was flooded during spring high tide.

Furthermore, the fringing cays generally have low relief and episodic storm surge can cause cay overwash. In general, where there was no coral rubble rampart above the spring high tide, there was no coral or littoral forest. A combination of windy conditions with spring high tides tends to cause an overflow of ocean water from the reef crest. During windy conditions, higher energy waves make it on the back-reef zone. This phenomenon causes most of these low relief cays to be inundated at least temporarily. Brander et al. (2004) found that wind-driven wave energy dominates the reef flat. However, this was only prevalent for a short time span (2.5 h around spring high tide), and short-period wave energy dominated the remainder of the tidal cycle. He also pointed out that the time of wind wave dominance also appears to diminish landward across the reef platform. Wind conditions can play a significant role on the generation of waves at different tidal stages. At Carrie Bow Cay, northeasterly winds with speeds of 4-5 m/s are frequent (Greer and Kjerfve 1982). During field work in 2007 and 2008, it was difficult to work close to the reef during a windy day due to the amount of wave energy going beyond the reef crest.

3.4.4 Orientation of cay vegetation relative to reef crest

While I found that the fringing cays had shifted away from the reef crest between 1945 and 2006, what remained relatively constant was the orientation of the longest axis of the vegetated cay relative to the reef crest. This general orientation was consistent in both the 1945 and 2006 photo-mosaics. Gourlay (1988) found that reef shape, orientation and exposure were the key factors influencing the formation and stability of cays along the Great Barrier Reef in Australia. Cays are often elongated at right angles to prevailing winds (Bird

1984). In the case of the fringing cays at Turneffe, their longest axes were parallel to the reef crest directly in front of them, and they were not at right angles to the predominant wind direction from the northeast.

The waves generated by hurricanes from four studies were reviewed and compared by Young (2003). Within a translating hurricane, the wave field is characterized by a swell ahead of the storm, radiating out from the intense wind region to the right of the storm centre. This is caused by the significant asymmetry of higher winds and extended translating fetch to the right of the storm centre (Young 2003). It is expected that the storm surge propagating ahead of the storm is responsible for dislodging and moving material from the reef to the back-reef sediment apron. In which case, storm track direction, and position relative to the eye of the storm would have important consequences for transport of substrate.

Substrate for the establishment of cay vegetation includes rubble and sand that comes directly from the coral reef. Depending on the intensity, speed, location and direction of storms, cays can be severely eroded, partially eroded, or built from new storm deposits. Factors that may probably contribute to the alignment of the vegetated cays are: 1) the angle of the spur and groove reef system relative to wave incidence (spur and groove function as effective breakwaters to incoming waves), 2) reef gaps along the fore-reef and reef crest that could facilitate the supply of sand and coral rubble on the back-reef, 3) the relative height of the reef crest and fore-reef with respect to sea level (e.g., a lower reef crest allows more rubble to be transported from the fore-reef area, a higher fore-reef can be exposed to more damage during storm activity, thus providing more material for transport), 4) the

redistribution of sediment material and propagules along the back-reef by longshore currents that run along the edge of the large islands, and 5) vegetation that buffers incoming sediment and helps maintain the initial substrate configuration. Once the vegetation is established, the roots and stems can effectively trap additional sediment load including coarse coral rubble coming from the reef as a result of storm surge. This was evident on Soldier Cay in 2004 from Hurricane Ivan and was reported by Stoddart (1971) for Cockroach Cay-2.

3.4.5 Land-falling hurricanes on Turneffe

Turneffe sits mid-way along the coast of Belize, and its exposure to hurricanes was consistent with hurricane landfall records for mainland Belize. Storm and hurricane data from 1851 to 2008 showed that 65% of storms had affected the northern Belizean coastline, while 35% the southern coastline. Belize's geographic location in Central America and the geometry of the Gulf of Honduras might explain the difference in storm frequency or hurricane track curvature.

Gardner et al. (2005) reported that the average return time of hurricanes in the most hurricane-prone parts of the Caribbean was 9.4 years in Florida, 12 years in the US Virgin Islands and Puerto Rico between 1851 and 2001. The return interval for the coast of mainland Belize was 9 years making it one of the more hurricane-exposed parts of the Caribbean. Turneffe is a smaller target, but based on storm data from 1851 to 2008, the hurricane return interval was 26 years and, for catastrophic hurricanes (categories 3 to 5), was 79 years. This is frequently enough to have significant effects on cay geomorphology

and vegetation dynamics, and for this disturbance regime to be considered in conservation and management plans.

Storm frequency was higher towards the latter part of the hurricane season for Turneffe. More hurricanes had affected the northern than southern part of Turneffe and this appears to affect the deposition of sediments and vegetation community development. The back-reef sediment apron was much wider on the northern part of Turneffe than the southern part. The mangrove forests of the larger islands on the northern part of Turneffe were at a greater distance from the reef crest, probably due to more exposed conditions and recurrent damage. It has been suggested that Lighthouse Reef due east of Turneffe can potentially buffer and protect the eastern side of Turneffe from incoming waves (Burke 1982) but not effectively from the damaging effects of hurricanes. Burke also reported that more than 95% of the waves along the fore-reef come from easterly directions between 0° (north) and 180° (south). The remaining 5% are from westerly directions, particularly the northwest, and have little mechanical effect on the fore-reef communities. Lighthouse Reef is a little over 20 km east of Turneffe. This is also a plausible explanation as to why mangroves have not been able to successfully colonize the extreme northern part of Turneffe.

Storms and hurricanes create varying degrees of disturbance along the exposed eastern side of Turneffe depending on their track and intensity. The energy from the surge can transport sediment from the reef and form and/or elevate existing coral ramparts. At the lower intensity end of the gradient, *R. mangle* serves as sediment stabilizer and barrier to new sediment material coming from the reef. Surviving *R. mangle* is capable of rapid lateral expansion in

shallow waters. Studies of rapid sedimentation in mangrove forests have found that sediment burial is lethal for mangroves if the depth of burial exceeds the height of the specialized root structures, or pneumatophores (Gordon 1988; Ellison 1998).

The fringing cays of Turneffe have experienced the effects of major hurricanes even when the hurricanes don't make a direct landfall on the cays. Hurricane Mitch made landfall in Honduras on October 1998. This hurricane caused substantive erosion in some of the fringing cays, according to the Turneffe Islands Coastal Advisory Committee (2003). The ocean-facing side of fringing cays and large islands experienced changes from Hurricane Ivan in 2004 which tracked 700 km from Turneffe. The mangroves examined on Soldier Cay, although scarred, partially buried, and leaning away from the newly deposited coral rubble were still alive after 4 years. These mangrove trees had an average height of 1 m at the time of Hurricane Ivan. The lethal burial depth for young seedlings is less understood, but they do have a lower tolerance to stressors (Lambers et al. 1998) and would be expected to suffer greater damage from debris impacts than larger plants.

3.4.6 Recovery and location of cay vegetation after storm damage

Fringing cay resilience was observed in their ability to reform and revegetate after being devegetated and eroded by storms. Over the 33 km between the Cockroach Cays and the Dead Man Cays there was a substantial area of back-reef that could potentially give rise to vegetated cays and cay formation. However, the cays largely reformed and revegetated in the same general location they were prior to Hurricane Hattie. Some possible factors that might

explain this include: 1) accommodation space (available space between the coral reef and larger islands); 2) Eroded cays can still be in a position to provide “seed” substrate from which subsequent storms can build on. Stoddart (1963) observed that on certain cays new material was deposited during Hurricane Hattie; 3) Standing dead vegetation reported after Hurricane Hattie can provide the buffer needed to trap and build sediment transported from the adjacent coral reefs; 4) The presence of a type of coral reef composition and morphology reefward of where these fringing cays form (e.g., the primary composition of the ramparts in many fringing cays was coarse coral rubble from *Acropora palmata* Lamarck and *Acropora cervicornis* Lamarck). Both species of coral are known to be fast growing and can reproduce by fragmentation (Lirman 2000; Tunnicliffe 1981); and 5) The production of propagules and seeds from the large islands (the revegetation of cays requires the production of copious amounts of propagules and seeds to ensure survival in these exposed environments).

While most fringing cays at Turneffe reformed in their original locations, they were somewhat mobile. There was a shift away from the reef between 1945 and 2006, and this shift was parallel to mean storm track direction rather than to prevailing wind conditions. The shift was also at right angles to the reef crest directly in front. The net west northwestward vegetation shift of the fringing cays on Turneffe can be attributed to the movement of material and erosional effects on the ocean-facing side of the cays during storms and the colonization of new substrate on the leeward side, which creates a net shift of the vegetated cays. Since the net movement of cays is away from the reef crest, the distance between the system that supplies sediment is increasing.

A well-formed ridge zone is expected to provide better protection on the leeward side with respect to the reef crest. However, cays with a well-formed ridge zone were targeted for *C. nucifera* plantations and for human habitation. The removal of the natural vegetation in the late 1800's until the mid 1900's to coconut plantations could have made this category of cays more vulnerable to erosion during Hurricane Hattie. Between 1945 and 2008, Hurricane Hattie was the only catastrophic hurricane which affected Turneffe. This hurricane approached the atoll from the east, and the majority of storms within that period had similar paths. At one of the fringing cays (Little Calabash Cay) visited by Stoddart (1963) after Hurricane Hattie, he found considerable erosion on the eastern side but this was balanced by deposition on the west. During the field work in 2008, eroded areas on the reefward side were visible from the remnants of roots and stumps and sometimes a mixture of organic sand and were evidence of recent and ongoing erosion. There were also remnants of conglomerate rock on the eastern side of some of the fringing cays (e.g., Cockroach Cay-2). Stoddart and Steers (1977) considered that while erosion predominates on the oceanward side of reef islands, worldwide, accretion continues on the lagoonward side, and thus reef islands appeared to be undergoing a gradual migration into the lagoon. Woodroffe (1982) found that on Barkers Peninsula and West Bay Peninsula on the Cayman Islands, the extension of mangroves has generally been in a landward direction, into previously terrestrial environments, and has rarely been to seaward. As for the fringing cays on Turneffe, the question remains whether these systems are continuously shifting away from the reef crest or if at some point cay location is resettled closer to the reef.

In fringing reef environments, Gourlay (1987) suggested that significant beach change will only occur during tropical cyclonic conditions. When storms are very frequent or very severe, cays can move their location frequently (Woodroffe 2002). In Fiji, the coralline cay of Makuluva was reported to have similarly migrated to the northwest across the reef flat (Bird 1984). Bayliss-Smith (1988) reported the migration of islands on the Ontong Java Atoll, Solomon Islands, as shown by the erosion of their seaward beaches and the formation of shingle spits on their lagoon sides. Sometimes these movements are reversible. A survey of Green Island located along Australia's Great Barrier Reef found that a spit on the western side of the cay shifted from the northwest in the 1940's to the southwest in the 1950's and back again to the northwest in the 1970's, where it has remained (Haslett 2000). This movement is believed to be in response to direction of successive tropical cyclones. Flood (1986) considered cays to be highly mobile, particularly around unstable lee-side tails, which can react rapidly to short-term changing wave regimes.

The fringing cay's shift to the west northwest raises the question of the possibility of these cays merging with the larger islands, particularly in the southern group (Dead Man Cays) where they are closer to the large islands. Bayliss-Smith (1988) reported from a storm on Ontong Java Atoll, Solomon Islands, that small cays can be annexed by the growth of neighboring coral rubble islets. In other areas, small vegetated sand cays adjacent to the main islands survived the hurricane in reduced form, but later became connected to the main islands by beach ridges (Bayliss-Smith 1988). The Dead Man Cays are in close proximity to the larger islands with an average distance of 54 m, and have shown the highest shift of 43 m due west. The rest of the cays were between 200 and 800 m away from the larger islands. It

is possible but very unlikely for the southern group to merge with the larger islands, especially since a strong current of water flows between the cays and the larger islands through fairly deep channels (1 to 2 m). Longshore drift and tidal currents maintain these channels. The depth and current of the channels would prevent new propagules from successfully establishing and poses a challenge even for lateral expansion of *R. mangle*. A substantial amount of sediment load originating from the reef system will be needed to provide enough substrate for mangroves to be able to colonize this area.

3.4.7 Some implications for the sale and development of fringing cays

The regular inundation, aggradation, and erosion of the fringing cays have implications for their management and use. A number of the fringing cays had been surveyed based on the presence of survey markers, survey lines, and information from the Lands Department office in Belmopan, Belize. Unfortunately, some of these fringing cays are currently for sale and are being advertised over the internet (e.g., Regent Realty Limited 2008; <http://www.regentrealtybelize.com> and Vladi Private Islands 2008; <http://www.vladi-private-islands.de/islandsforsale.html>). Property markers found on the fringing cays show that surveyors include low lying permanently flooded vegetated areas as part of the area for those cays that are for sale. In addition, the advertised cay total area exceeded the area of cay vegetation and bare substrate above the spring high tide. This was a common practice on all the websites that had some of the fringing cays for sale. For example, Pelican Cay (central group cay), had an area of 0.64 ha (which included vegetated area above and below spring high tide and bare substrate above spring high tide) with 57% of that area being flooded

during spring high tide. This cay was being advertised with an area of 2.02 ha. The elevation of Pelican Cay at its highest point relative to spring high tide is approximately 40 cm. Soldier Cay (central group cay), had an area of 1.12 ha (which included vegetated area above and below spring high tide and bare substrate above spring high tide) with 26% of that area being flooded during spring high tide. This cay was being advertised with an area of 2.02 ha. The elevation of Soldier Cay at its highest point relative to spring high tide is <1 m. With the current situation on the sale of fringing cays and other islands it is very important to understand the laws of Belize that govern the ownership, sale and development of islands. There is an urgent need for a consistent definition of land, particularly one that is clear on submerged and emerging cays (e.g, mangrove cays). For example, the Belize National Lands Act 2000 (CAP. 191) includes land underwater in the definition of “land” but the Belize National Environmental Guidelines on Overwater Structures (2010) recognizes that land underwater cannot be owned.

For any of these cays to be developed and made habitable for humans, edges must be armored with coral rubble or concrete and additional sediment material needs to be dredged continually from nearby seagrass beds and coral reef patches to raise and maintain their elevation and create a “false beach”. Examples of these destructive practices can be observed in many of the cays along the Belize Barrier Reef and along the larger islands on Turneffe. In spite of these efforts to mitigate the effects of routine wave energy, these cays are mobile and remain highly vulnerable to damage during hurricanes.

3.5 Conclusion

Fringing cays are vulnerable to human and recurrent storm disturbance, but have the capacity for recovery. The hurricane return interval for Turneffe is 26 years based on storm data from 1851 to 2008. In cases where severe erosion occurred during Hurricane Hattie, these cays reformed and revegetated in the absence of human settlements. Accretion of sediment from the adjacent coral reef coupled with colonization of mangrove and littoral vegetation drive cay formation and recovery. However, a number of the fringing cays present in 1945 are now devegetated and eroded, particularly the smaller sized cays.

The coccol forest that once dominated the fringing cays has been replaced by littoral and mangrove forest. This can be attributed to the vulnerability of coconut palms to storm damage and lack of human reintroduction and cultivation of coconuts after Hurricane Hattie. By 2008, mangroves dominated the fringing cay vegetation, but the majority of the vegetated area is under the influence of tides. The vegetation of the fringing cays at their longest axis is parallel to the reef crest. This orientation is likely due to refraction of waves by the reef. Most of the devegetated cays after Hurricane Hattie revegetated and did so in the same general location. However, the fringing cays have shifted away from the reef crest between 1945 and 2006, and this shift seems to be related to the path of storms as well as wave refraction by reefs rather than prevailing wind conditions.

The fringing cays contribute to local ecosystem diversity and productivity. They provide an excellent site to study the interaction between mangrove, seagrass, and coral reef ecosystems

and the effects of disturbances on these systems. Fringing cays subject to recurrent disturbance are not suitable for development, particularly in hurricane prone landscapes. Coastal areas can be successfully mapped using aerial photographs or high resolution satellite imagery. Historic photos can play an important role in reconstructing the historic landscape of these cays. Historic photos should be scanned and saved digitally to preserve the information. In addition, the group of fringing cays should be revisited and a comprehensive vegetation list should be generated in order to understand the details of mangrove and littoral forest distribution and competition in this high energy environment. Naturally occurring vegetation species that are found in these cays can be the prime candidates for reforestation projects of cays with similar geomorphology.

Chapter 4: Stand-level growth in fringing mangrove

4.1 Introduction

Key processes in mangrove ecosystems include biomass production, nutrient cycling, litter dynamics, sedimentation, disturbance and succession, and exchange of materials and energy among biotic and abiotic components and across the terrestrial-aquatic ecotone (Twilley 1995). Examining litter, standing biomass and changes in biomass with time provides insights into site productivity and growth rates in mangrove forests. Estimates of biomass are important to resource managers and disturbance ecologists. Mangroves are important in the carbon cycle of tropical coastal systems as such landscape-level estimates of mangrove biomass are needed (Simard et al. 2006). The net balance of carbon in mangrove and coastal ecosystems can be altered by natural and anthropogenic perturbations. These include tropical storms, forest reclamation, and eutrophication (Twilley et al. 1992).

4.1.1 Forest biomass

Above-ground biomass is the amount of standing organic matter or standing biomass per unit area at a given time. The amount of standing biomass stored in a forest is a function of the systems' productivity, age and organic matter allocation and exportation strategies (Kasawani et al. 2007). The allocation of photosynthetic products to leaves, stems, roots and reproductive parts determines the growth characteristics of a plant. This allocation pattern is strongly influence by environmental conditions, with root to shoot ratios increasing with

aridity, infertility, light intensity, grazing and fire (Mooney 1972; Iwasa and Roughgarden 1984). Plant competition may also influence allocation of mass (Kozlowski et al. 1991). Twilley et al. (1992) contend that there is a time scale for a mangrove forest to reach maturity based on steady-state levels of biomass and this is dependent on the regional and local attributes of the environmental setting. For example, in the Caribbean and the Gulf of Mexico, 25-30 years may be enough time for forests to reach maturity given the maximum biomass that can be supported in these areas (Twilley et al. 1992).

Biomass estimation methods fall into three broad, but overlapping, categories: clear-felling, representative tree sampling, and the establishment of allometric relationships (Saenger 2002). Clear-felling to obtain biomass is destructive and time-consuming. Consequently, surrogate measures based on allometric relations are often used. Allometric relations are developed by quantifying a mathematical relationship between some easily measured individual plant parameter (e.g., diameter at breast height or 1.3 m, DBH) and some variable that is much harder to measure (e.g., biomass; Lieth and Whittaker 1975). Once the allometric relationship has been established, the technique can be applied in a non-destructive way in other sites. In mangrove forests, the DBH of the trunk is commonly used for species without aerial roots such as *A. germinans*, and *L. racemosa*. For *R. mangle*, stem diameter is usually taken above the last buttressing prop root. This method of non-destructive assessment allows estimation of biomass through time, from which growth rates can be deduced (e.g., Smith and Whelan 2006). Equations to predict above-ground biomass using stem diameters for mangroves have been developed for a variety of locations (e.g., Woodroffe 1985; Putz and Chan 1986; Clough and Scott 1989; Fromard et al. 1998). For

North and South America and the Caribbean, studies developed by Golley et al. (1969), Lugo and Snedaker (1974), Cintrón and Schaeffer-Novelli (1985) and Sherman et al. (2003) provide allometric relationships.

Biomass estimates can be summed for all individuals and for each species within a known area, and can be subsequently expressed on an area basis. In tropical forests, the live, above-ground biomass plays an important role in the global carbon cycle, accounting for a significant fraction of the total carbon and nutrient stocks (Brown and Lugo 1984; Phillips et al. 1998). Above-ground biomass estimates are still an important source of uncertainty in the carbon balance from the tropical regions, in part because of shortage of reliable estimates of live above-ground biomass and differences across landscapes and forest types (Houghton 2007; Saatchi et al. 2007). Therefore, improved local and regional above-ground biomass estimates provide essential data that enable the extrapolation of biomass stocks to ecosystems-wide carbon cycle modeling (Alves et al. 2010).

4.1.2 Forest litter

In addition to measuring or estimating periodic change in standing biomass, litter production has also been used to approximate productivity (Teas 1979), as has accumulation of organic matter, which includes accumulation of biomass standing stock and litter (Putz and Chan 1986; Day et al. 1987). Ovington (1961) made calculations of energy flow in plantations of *Pinus* and confirmed that often one-third to one-half or more of the energy and carbon that is annually fixed in forests is contributed to the forest floor as leaves and other litter. Because

of this large proportion and because litter is related to the quantity of the photosynthetic capability of the system, it is an interesting index of ecosystem productivity (Olson 1963). Litter also provides temporal information about phenological development of the stand (Pitman et al. 2010). Litter plays an important role in nutrient cycling within forest ecosystems. It is a major pathway for transfer of carbon and nutrients from vegetation to the soil and affects below-ground processes (Sayer et al. 2007). Rates of litter fall and subsequent decomposition affect nutrient availability to vegetation. In ecosystems where nutrients such as nitrogen and phosphorus limit primary productivity, the turnover rate of litter is a key determinant of nutrient uptake by plants (Jorgensen et al. 1975; Cole and Rapp 1981).

Methods of directly measuring primary productivity in mangrove ecosystems are technically difficult, so litter production has been widely used as a proxy for primary productivity (Woodroffe et al. 1988; Chale 1996; Morrissey et al. 2007). Litter production and fall vary with geographic location (Twilley 1985; Woodroffe et al. 1988) and seasons (Bosire et al. 2005). In some locations, litter production and fall occur throughout the year with peak fall in the summer rainy season as documented by Tam et al. (1998) in China. At Twin Cays in Belize, litter production was highest in October for the interior plot and November for the shoreline plot (Koltjes et al. 1998). Mangrove leaf litter degradation depends mainly on seasonal variability and on the degree and frequency of tidal inundation (Twilley 1985; Wafar et al. 1997; Dick and Osunkoya 2000; Bosire et al. 2005).

A substantive amount of research on mangrove biomass and litter production has been conducted on the mainland and/or systems that are highly influenced by river discharge. This reflects the fact that mangrove forests are the major vegetation form that dominates tropical river deltas, lagoons and estuaries that have significant input of terrigenous sediments (Thom 1982). There are biomass studies for mangroves on the Atlantic coast of North and South America and the Caribbean (e.g., studies done on the mainland by Golley et al. 1969, Cintrón and Schaeffer-Novelli 1985, Day et al. 1987, Fromard et al. 1998, Ross et al. 2001; studies done on islands Golley et al. 1962, Sherman et al. 2003) and litter measurements done in Puerto Rico (Pool et al. 1975), Mexico (Lopez-Portillo and Ezcurra 1985; Day et al. 1987; Flores-Verdugo et al. 1987), USA (Pool et al. 1975; Teas 1979). There are two studies on mangrove forest biomass and litter from the Belize offshore cays (Koltes et al. 1998 and Garcia and Holtermann 1998); however, the sites are different from the fringing cays of Turneffe, which are more exposed and closer to the reef.

4.1.3 Nutrients in coastal areas

Mangrove forests are generally considered oligotrophic ecosystems and the species that grow there are considered adapted to low-nutrient conditions (Hutchings and Saenger 1987). Coastal ecosystems typically experience inputs of nutrients from marine sources, including guano from seabirds. Throughout the Gulf of California, marine inputs to terrestrial systems have been well studied (Polis and Hurd 1996; Anderson and Polis 1998; Rose and Polis 1998; Stapp et al. 1999). Inputs from a relative large island to smaller islands in the form of bird guano from terrestrial birds have not been reported. 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 their description of the Dry Tortugas, Florida, attributed the dieback of mangroves to beach erosion and excessive input of bird guano. According to Doyle et al. (2002), bird guano can lead to chlorotic mangrove stands. However, within the same island, bird guano provided fertile growing conditions for mangroves and was correlated with an increased internode elongation patterns within the mangrove nesting site of frigate birds (Doyle et al. 2002). Feller and Mathis (1997) found that bird guano on a Belizean cay (Man-of-War Cay, Southern Belize), resulted 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.

4.1.4 Rationale

The three fringing cays examined in this study (Soldier Cay, Big Calabash Cay and Dead Man Cay-5) are relatively small in size, with an average vegetation and substrate area of 0.71 ha. These cays were selected for study because they were accessible from the University of Belize research station at Calabash Cay, had fringing mangroves, had been mapped by Stoddart in the early 1960's and had minimal human disturbance since Hurricane Hattie in 1961.

Permanent sample plots were established at these three sites in 2002 as a component of my Master's Degree (Chi 2003) in order to estimate mangrove forest above-ground biomass and above-ground litter. The amount of bird guano input on the Turneffe sites, and the production of an algal bloom at Soldier Cay, prompted resurveys of litter fall collection after the 5-month 2002 survey in order to complete a 12-month period. These plots were remeasured in 2008 during the course of my Doctoral thesis project. The specific objectives of this study were: 1) to assess the fringing forest structure and composition of three cays; 2) to examine changes in plot level characteristics over a period of 6 years; 3) to quantify above-ground litter fall over a period of 12 months (6 additional months added to previous study to get a 12 month representation); and, 4) to quantify guano deposition and effects.

I tested the following hypotheses: 1) there is a significant increase in mangrove forest above-ground biomass on Soldier Cay, compared to Big Calabash Cay and Dead Man Cay-5 over a period of 6 years; 2) leaf litter is the primary component of litter fall on these fringing cays and is the major component in ground litter exported to adjacent systems; and, 3) bird guano deposition on these cays is restricted to specific months during the year, and affects mangrove growth and productivity.

4.2 Methods and data available

4.2.1 Approach

The Caribbean Coastal Marine Productivity program, CARICOMP, is a regional scientific program and a network of marine laboratories, parks and reserves to study land-sea

interaction processes in the wider Caribbean region (Kjerfve 1998). The program's focus has been on understanding and comparing the structure and function of mangrove, seagrass, and coral reef ecosystems. The CARICOMP program was established in 1985 and the network started in 1990. In 2001, an updated manual of research procedures was published. The "CARICOMP methods manual levels 1 and 2: manual of methods for mapping and monitoring of physical and biological parameters in the coastal zone of the Caribbean", is available online. A chapter dedicated to "Mangrove Communities" covers the general methods for measurement of mangrove ecosystem structure and function as described by Lugo and Snedaker (1975), and Pool et al. (1977).

For this study, the CARICOMP Methods Manual Level I and II (2001) was used in conjunction with the methods described by Cintrón and Shaeffer-Novelli (1984), to measure forest structure, above-ground biomass, above-ground litter and forest floor litter mass (ground litter).

4.2.2 Plot set up

To characterize the mangrove forest, permanent monitoring plots were set up in 2002 in the fringing forest of three cays on the eastern side of Turneffe to study above-ground biomass and litter (Chi 2003). From north to south, these cays are Soldier Cay, Big Calabash Cay, and Dead Man Cay-5 (SC, BCC and DMC-5 in Fig. 4.1). Three permanent plots measuring 10 x 10 m each were established on each cay in predominantly fringing *R. mangle* forest. On each cay, the plots were labeled as A, B, and C and were oriented parallel to the shoreline with

gaps of 3 to 4 m between adjacent plots (Fig. 4.2). The plots were established by marking the corner at the left side closest to the fringing vegetation edge as the zero point and using a compass and measuring tape to complete the 10 x 10 m square. The corners were marked with 2.5 cm PVC pegs standing approximately 50 cm above the ground. GPS coordinates were taken for all four corners of each plot. The borders of the plot were temporarily defined with a fluorescent string to facilitate the identification of stems that were within the plot.

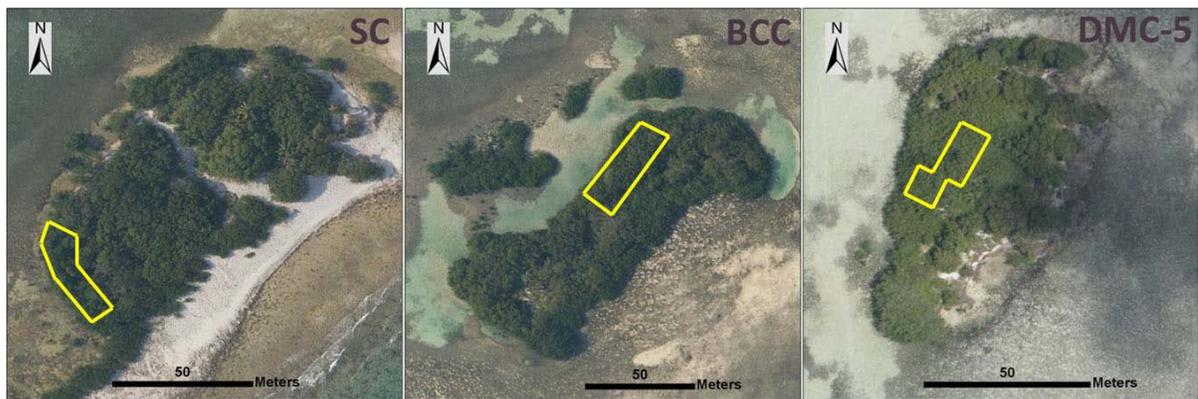


Figure 4.1. Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5). The location of each cluster of 3 permanent plots is highlighted in yellow.

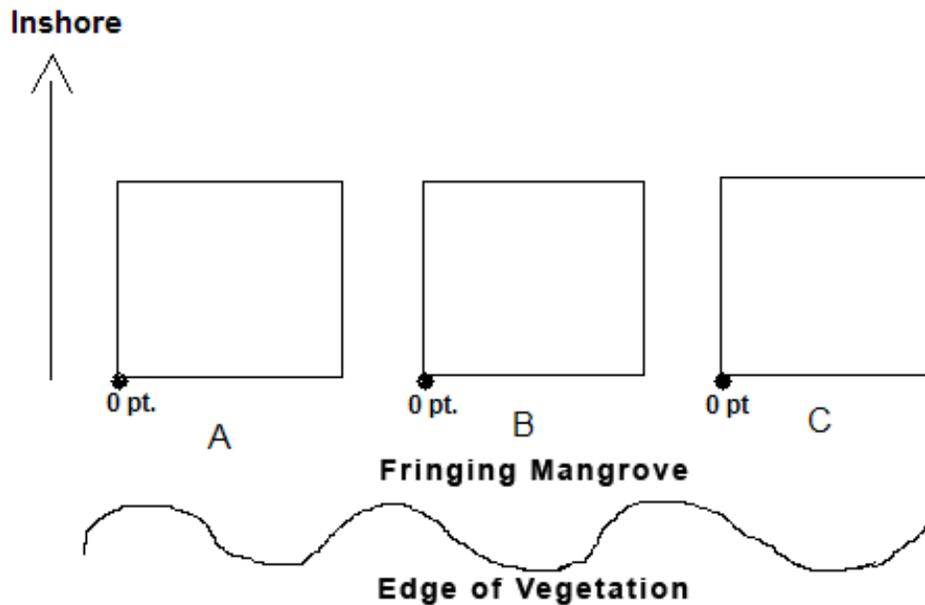


Figure 4.2. Orientation and layout of plots relative to the edge of vegetation.

Litter traps were constructed from PVC pipes (1.5 cm diameter) with side dimensions of 0.5 m, at right angles, thus, completing a square of 0.25 m². Plastic screening (1 mm mesh size) was used to make the litter trap resemble a basket. The litter traps were secured beneath the mangrove canopy to the branches and/or stems of the mangroves with monofilament at each corner. The traps were suspended approximately 1 to 1.5 m above the ground to prevent water from incoming tides from contaminating or disturbing the litter collected on the traps (Fig. 4.3). 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 edge of vegetation within the plot with five more perpendicular to the edge of vegetation. In all, 30 litter traps were deployed per cay, giving a total of 90 traps.



Figure 4.3. Above-ground litter traps under the fringing mangrove canopy at Big Calabash Cay (BCC).

4.2.3 Field measurements

Stem diameter was measured at 1.3 m trunk height (referred to as diameter breast height - DBH) for all species except *R. mangle*. For *R. mangle*, the stem diameter was taken above the highest buttressing root. All mangrove trees with trunk DBH at or greater than 2.5 cm were numbered and labeled with an aluminum tag. All trees within a plot were identified to species, and measured as follows: DBH was measured in cm perpendicular to the trunk axis with a graduated tape (Luftkin[®] Executive Thinline Diameter Tape) around the tree trunk that

converts the girth of the tree to equivalent diameter in cm. All measured trunks were marked with an all weather crayon at the point where DBH was taken. In the case of trees with multiple trunks, each trunk was measured and considered separately. It can be problematical to distinguish stems from branches in *R. mangle* forests. For this reason, a list of criteria recommended by Cintrón and Shaeffer-Novelli (1984) were used to determine where the measurements were taken: 1) when a stem forks below breast height, or there are multiple sprouts from a single base close to the ground, then each stem/sprout was considered as a separate trunk; 2) when the stem forked at breast height or slightly above, measurements were taken of the single stem just below the swelling caused by the fork; 3) in the case of *R. mangle*, stem diameter was measured just above the highest buttressing root, which is considered as the uppermost supporting root, (adopted from the CARICOMP Methods Manual 2001); 4) in cases where at the point of measurement the tree trunk had abnormalities, measurements were taken slightly above or below the swelling. In addition, only stems whose diameter measurement points were within the plot boundaries were counted as 'in' and measured. Leaning trees with DBHs above the last buttressing root and outside the plot boundaries were excluded from the plot measurements. This situation of leaning trees was problematic especially at the time of re-survey in 2008. Some leaning trees which had diameter measurement points inside the plot in 2002 were regarded as outside of the plot during the 2008 survey because new buttressing roots had formed above the previous measurement point since 2002. In these instances, the new location for diameter measurements were now outside of the plot and these trees were not remeasured.

Total tree height was taken as the linear vertical distance between the sediment surface and the tip of the tree crown. Height was measured for all tagged tree trunks with a graduated telescoping measuring rod to the nearest 0.1 m. Leaning stems in fringing mangroves can be problematic to measure, especially where the substrate is not level. Leaning stems were measured by identifying the highest part of the stem and then measuring down from it to the sediment surface, which in many cases meant measuring from a surface position outside of the plot.

4.2.4 Above-ground litter and ground litter

Litter resulting from the shedding of plant parts to the ground was from two categories: above-ground litter which was captured in traps, and ground litter collected from the surface of the ground. Due to time constraints for field work during my Masters thesis program, above-ground litter data was collected only from October 2002 to February 2003. For the present study, litter traps were re-deployed on the same cays and plots, and a second collection was conducted from March to September 2004 in order to have a 12-month period. The accumulated litter was collected from each trap at the end of each month. Litter was collected in ziploc bags for transportation and labeled according to the trap identification numbers.

Loose ground surface litter (L horizon) was collected during low tide from a 0.25 m² quadrat placed directly below the above-ground litter traps. Ground litter was collected by skimming the loose litter from the substrate surface (e.g., peat, sand). This collection was carried out

one time in 2002 at the time the traps were deployed in the field. Ground litter was collected in ziploc bags and transported to the field station for preparation and analysis.

4.2.5 Plots remeasurements

In 2008, the permanent plots were remeasured using the same procedures as in 2002. All tree trunks 2.5 cm and above were measured, old tags were replaced. Some tags were missing and trunks without tags were assigned a new one. Table 4.1 shows the type of data and collection times that were conducted between 2002 and 2008 within the permanent plots. In 2008, the percent substrate surface composition within the 10 x 10 m plots was estimated by dividing the plot into four equal quadrats. The following categories were identified: peat, sand, coral rubble and mixture (mixture is a combination of two or more substrate types). The percent plot area under the influence of tidal inundation was also estimated during spring high tide.

Table 4.1. Summary of data collected within permanent plots between 2002 and 2008.

Date	Measurements/Collection	Comments
Oct. 2002	Height and DBH	All tree trunks within plots meeting criteria
Oct. 2002	Ground litter	Once below litter traps
Oct. 2002 to Feb. 2003	Above-ground litter	Monthly collection
Mar. 2004 to Sep. 2004	Above-ground litter	Monthly collection
Measurements/Remeasurements		
May 2008	Height and DBH	All tree trunks within plots meeting criteria
	Percent substrate	With tidal influence
	Percent substrate type	Peat, sand, and rubble

4.2.6 Sample and data processing and analysis

4.2.6.1 Stand-level measurements

Stand density was calculated as the number of stems or tree trunks in a given area and was expressed as stems per ha.

$$\text{Stand density (stems/ha)} = \text{stems in plot} / \text{plot area (ha)}$$

Basal area was determined by calculating the area of the tree trunks at the place of DBH or adjusted location for *R. mangle* and expressed as m²/ha. The following calculation was used to convert DBH into basal area (BA).

$$BA = (\pi/4) * (DBH^2)$$

To express BA in m² as a function of DBH measured in centimeters:

$$BA = \pi * (DBH_{\text{cm}}/200)^2$$

The following measurement requires marking out a plot of known area, which for this study was 100 m². Basal area (m²) was converted to basal area per hectare (BAPH; m²/ha):

$$BAPH = BA * (10000/\text{plot area})$$

At the site level, height (m) and DBH (cm) were grouped into classes. Four classes were created for height (>0-3, >3-6, >6-9 and >9-12); and four classes for DBH (2.5-8, >8-13, >13-18 and >18).

4.2.6.2 Above-ground biomass

Above-ground biomass is defined as the amount of standing organic matter per unit area at a given time. Two above-ground biomass estimates were calculated: 1) using the equation in Cintrón and Shaeffer-Novelli (1984) to calculate above-ground biomass for all mangrove species and 2) using the equation in Cintrón and Shaeffer-Novelli (1984) for *R. mangle* and the equation in Fromard et al. (1998) for *A. germinans*, *L. racemosa* and *C. erectus*. The equation given by Cintrón and Shaeffer-Novelli (1984) for above-ground biomass in grams is: Above-ground biomass = $b [(DBH)^2 (\text{height})]^m$

DBH measured in centimeters and height in meters and where b and m are constants designated by the values 125.9571 and 0.8557, respectively. Calculations from the above equation can be converted and expressed in dry weight (kg/m^2) by taking into account plot area and converting grams to kilograms.

For the mangrove species *A. germinans* and *L. racemosa*, the following equations from Fromard et al. (1998) were used:

(a) *A. germinans*, DBH > 4cm; $a = 0.14DBH^{2.4}$ (a = biomass expressed in kg)

(b) *L. racemosa*, DBH > 1cm; $b = 102.3DBH^{2.5}$ (b = biomass expressed in g)

Conocarpus erectus, a mangrove associate, was found on one site (BCC). For this species, the above-ground biomass was calculated using equation (b) since the structure of *C. erectus* resembles *L. racemosa* more than the *A. germinans*.

4.2.6.3 Above-ground litter and ground litter

Above-ground litter was transferred to paper bags and oven dried at 70 °C for 72 h or until constant dry mass was obtained. Due to the high humidity of the environment, the sorting and weighing of litter fractions had to be done as soon as the bags were retrieved from the drying oven. Each litter trap was processed separately, and the oven-dried contents were separated into the following fractions: leaves, bracts, flowers, fruits, twigs, guano and miscellaneous. The traps and collection regime were not designed to measure guano, however a substantial quantity of guano was found in the traps and was therefore tallied separately. Each fraction was weighed to the nearest 0.01 g and values were converted to $\text{g/m}^2/\text{day}$ for each plot. Values for the three plots per site were then averaged to obtain a mean rate of litterfall ($\text{g/m}^2/\text{day}$). The litter components identified as ‘miscellaneous’ were the combined fractions of non-mangrove leaves, insects and seeds from littoral vegetation.

The loose ground litter (L horizon) was carefully washed with fresh water the same day it was collected to remove salt water, peat fragments and sand. Samples were air dried then oven dried at 70 °C from 92 to 108 h or until a constant mass was obtained. Samples were grouped into: leaves, flower and fruit, twigs and bark, seagrass, and miscellaneous fractions.

The above fractions were converted to g/m^2 based on the amount of dry matter per 0.25 m^2 quadrat. The means were calculated for each site.

To evaluate the turnover rate of mangrove litter, I used the mathematical model proposed by Nye (1961) and Olson (1963) $k = L/X_{ss}$, where k is the turnover rate, L is the litter fall rate (steady input, $\text{g/m}^2/\text{yr}$), and X_{ss} is the litter mass on-the-ground (amount accumulated, g/m^2). Residence time is $1/k$. This model assumes that litter fall input is equal to litter losses. This model has proven useful for mangroves by Twilley et al. (1986 and 1997) in conjunction with litter degradation rates.

4.2.7 Weather data

Weather data from the Carrie Bow Cay Marine Field Station for the months during which above-ground litter was collected were downloaded online from the Smithsonian Marine Science Network: Real Time Environmental Monitoring Program website. Carrie Bow Cay is approximately 60 km southwest of the Calabash Cays, Turneffe. The data for the following parameters were downloaded: air temperature, wind speed, and rainfall. The hourly data were converted to monthly averages.

4.2.8 Statistical analysis

SAS 9.2 (2008) was used for data analyses. Untransformed above-ground biomass data met assumptions of normality and homogeneity of variances of the residuals. Because the same

plots were remeasured, a split plot model was used to determine the main effects of Site and Time, and the Site * Time interaction for changes in above-ground biomass (Kuehl 1994). Differences between mean values for sites and year were assessed using pair-wise planned comparisons. The Bonferroni adjustment was used to adjust the alpha (0.05) value. Pearson's Correlation tests were used to examine relationships between above-ground litter and weather parameters, and with above-ground litter and height, DBH, biomass and guano.

4.3 Results

Substrate characteristics varied between plots and sites. Peat was the dominant substrate in most of the plots (Fig. 4.4). At Soldier Cay, the surface of plot A was lacking any peat. For Big Calabash Cay, a high percentage of the plot surfaces were peat. At both Soldier Cay and Dead Man Cay-5, there was evidence of stem and root burial by accumulations of coarse sand and coral rubble. During the 2008 remeasurements, some of the *R. mangle* tags were found buried in sediment. Tidal inundation varied between the permanent plots (Fig. 4.4), from 10% of the plot area under the influence of tides, to 100%. The percent cover of peat increased as the percent of plot area below the spring high tide increased.

Changes in percent species composition (by stems/ha) from 2002 to 2008 were minimal and *R. mangle* continued to dominate the plots (Table 4.2). Dead mangrove trees were found at all three sites. Soldier Cay had the least number of dead trees (3 trees, average DBH = 5.0 cm), Big Calabash Cay (10 trees, average DBH = 5.5 cm) and Dead Man Cay-5 (7 trees,

average DBH = 3.0 cm). The breakdown in mortality by species was *R. mangle* (60% of dead trees), *L. racemosa* (25%), *C. erectus* (15%). No *A. germinans* had died.

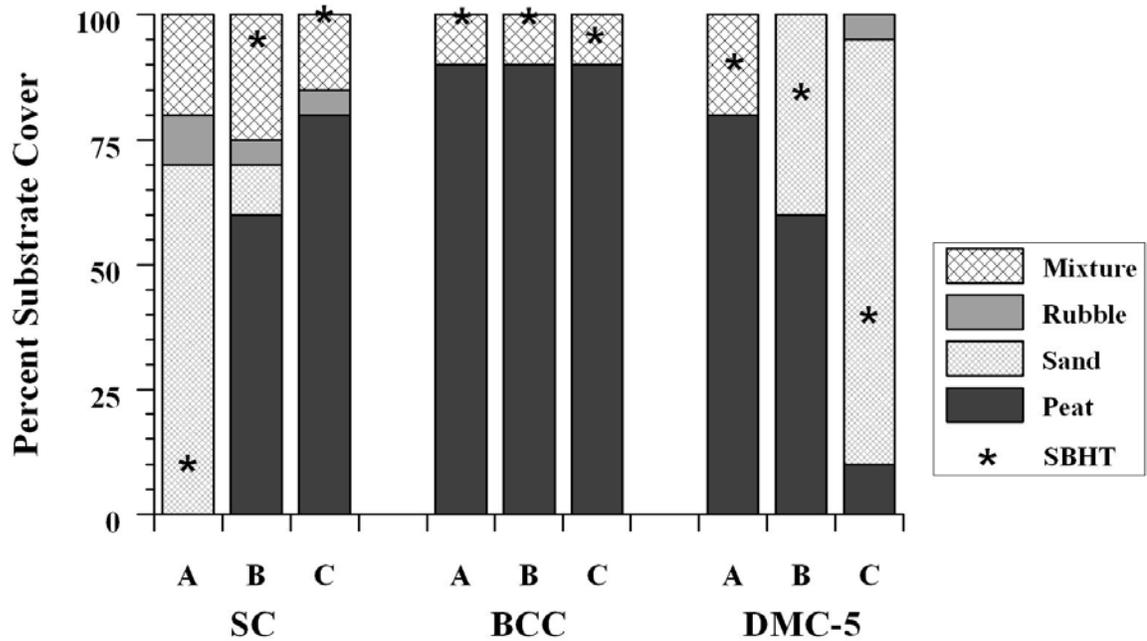


Figure 4.4. Percent plot surface substrate composition for Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5) an asterisk represents the percent of plot substrate below the spring high tide (SBHT). Mixture = combination of two or more substrate types (estimates from 2008).

Table 4.2. Mean percent species composition (by stems/ha) in permanent CARICOMP plots for 2002 and 2008 surveys on Soldier Cay, Big Calabash Cay and Dead Man Cay-5; 9 plots, standard deviation in brackets.

Mangrove species	2002 %	2008 %
<i>R. mangle</i>	92 (2.37)	93 (2.75)
<i>L. racemosa</i>	6 (1.19)	5 (2.57)
<i>A. germinans</i>	1 (0.32)	1 (0.27)
<i>C. erectus</i>	1 (1.27)	1 (0.95)

Dead man Cay-5 had the highest stand density in 2002, and the stand density increased by 2008. Density changes were minimal at Big Calabash Cay and Soldier Cay (Table 4.3; Appendices K and L). Trees previously measured that were no longer inside the plots were evident on Soldier Cay and Big Calabash Cay, and were all *R. mangle* species. The stems of these trees had lean angles as high as 75° from vertical when measured from the highest above-ground buttressing root. Soldier Cay had the greatest increase in height and DBH while height and DBH were unchanged at Big Calabash Cay. However, above-ground biomass calculated using the allometric formulas from Cintrón and Shaeffer-Novelli (1984) and Fromard et al. (1998) were not significantly different ($p > 0.05$). There was a general increase in above-ground biomass from 2002 to 2008 in all plots. The average increase in biomass for the three sites over the six year period at the plot level was 3.20 kg/m² (0.53 kg/m²/yr).

Table 4.3. Plot characteristics of three Turneffe sites (Soldier Cay (SC)), Big Calabash Cay (BCC)), and Dead Man Cay-5 (DMC-5)) in 2002 and 2008. Means are from three plots.

Site	Characteristics	2002		2008	
		Mean	SE	Mean	SE
SC	Height (m)	4.46	0.22	6.06	0.22
	DBH (cm)	6.48	0.40	7.27	0.53
	Density (stems ha ⁻¹)	6100	1300	6067	849
	Basal area (m ² ha ⁻¹)	23.0	5.0	29.3	2.2
	Total Biomass ^a (kg m ⁻²)	8.65	1.03	13.00	0.78
	Total Biomass ^b (kg m ⁻²)	8.64	1.03	13.00	0.76
BCC	Height (m)	4.66	0.03	4.67	0.02
	DBH (cm)	5.50	0.07	5.52	0.08
	Density (stems ha ⁻¹)	8500	520	8567	688
	Basal area (m ² ha ⁻¹)	26.1	2.1	27.2	2.3
	Total Biomass ^a (kg m ⁻²)	10.49	0.50	11.28	0.46
	Total Biomass ^b (kg m ⁻²)	10.33	0.51	10.77	0.50
DMC-5	Height (m)	3.51	0.20	4.87	0.28
	DBH (cm)	3.81	0.03	4.33	0.05
	Density (stems ha ⁻¹)	13900	811	15167	718
	Basal area (m ² ha ⁻¹)	16.7	1.7	29.3	1.7
	Total Biomass ^a (kg m ⁻²)	5.41	0.38	10.14	0.64
	Total Biomass ^b (kg m ⁻²)	5.44	0.36	10.23	0.59

Note: SE = standard error of the mean. Above-ground biomass (Total Biomass^a) was estimated using allometric equation from Cintrón and Shaeffer-Novelli (1984) for *R. mangle* species; for *A. germinans*, *L. racemosa* and *C. erectus*, allometric equations from Fromard et al. (1998) were used. Above-ground biomass (Total Biomass^b) was estimated using allometric equation from Cintrón and Shaeffer-Novelli (1984) for all species.

The analysis of variance for above-ground biomass between 2002 and 2008 reveals a significant Site*Time interaction (Table 4.4). Thus, these two factors cannot be interpreted independently. Three of the nine pair-wise comparisons were significant (Table 4.5).

Table 4.4. The results of the analysis of variance for above-ground biomass (kg/m^2) of 2002 and 2008, which were calculated using allometric equation from Cintrón and Shaeffer-Novelli (1984). Permanent plots from three sites were compared: Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5).

Source	DF	SS	MS	F	Pr > F
Site	2	32.6586	16.329315	2.52	0.1603
Plot(Site)	6	38.8313	6.471877	4.57	0.0435
Time	1	46.0157	46.015725	32.46	0.0013
Site*Time	2	17.2777	8.6388698	6.09	0.0359
Error	6	8.50428	1.4173797		
Corrected Total	17	143.26			

Note: DF = degree of freedom, SS = sum of squares, MS = mean sum of squares, F = F-value approximation, Pr > F = probability of greater F-values occurring by chance.

Table 4.5. Results of pair-wise comparisons of above-ground biomass (kg/m^2). Interactions of Time (2002 and 2008) and Sites (Soldier Cay (SC)), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5)).

Time	2002	2008
SC	8.64	13.00
BCC	10.33	10.77
DMC-5	5.44	10.23
Site	2002	
SC	8.64	
BCC	10.33	
DMC-5	5.55	
Site	2008	
SC	13.00	
BCC	10.77	
DMC-5	10.23	

Note: bold face denotes significance. The Bonferroni adjustment was used for $\alpha = 0.05$.

At the site level, the height class distributions in 2002 for both Soldier Cay and Big Calabash Cay follow the same trend (Fig. 4.5). The 2008 distributions are similar for Big Calabash Cay

and Dead Man Cay-5. Both Soldier Cay and Dead Man Cay-5 had trees recruiting to larger height classes between the two years while Big Calabash Cay showed minimal recruitment. For both Soldier Cay and Big Calabash Cay, more than 45% of stems were within the 3- to 6-m height class for both years; however, for Dead Man Cay-5, more than 70% of stems were within that same height class for both years. Only Soldier Cay and Big Calabash Cay had heights above the 9- to 12-m class. For DBH, all sites had a high percentage (above 70%) of stems within the 2.5- to 8-cm DBH class for both 2002 and 2008 surveys (Fig. 4.6). Recruitment to larger DBH classes was lower at Big Calabash Cay and Dead Man Cay-5 than Soldier Cay. By 2008, only 1.5% of stems had grown into the 8- to 13-cm DBH class at Dead Man Cay-5.

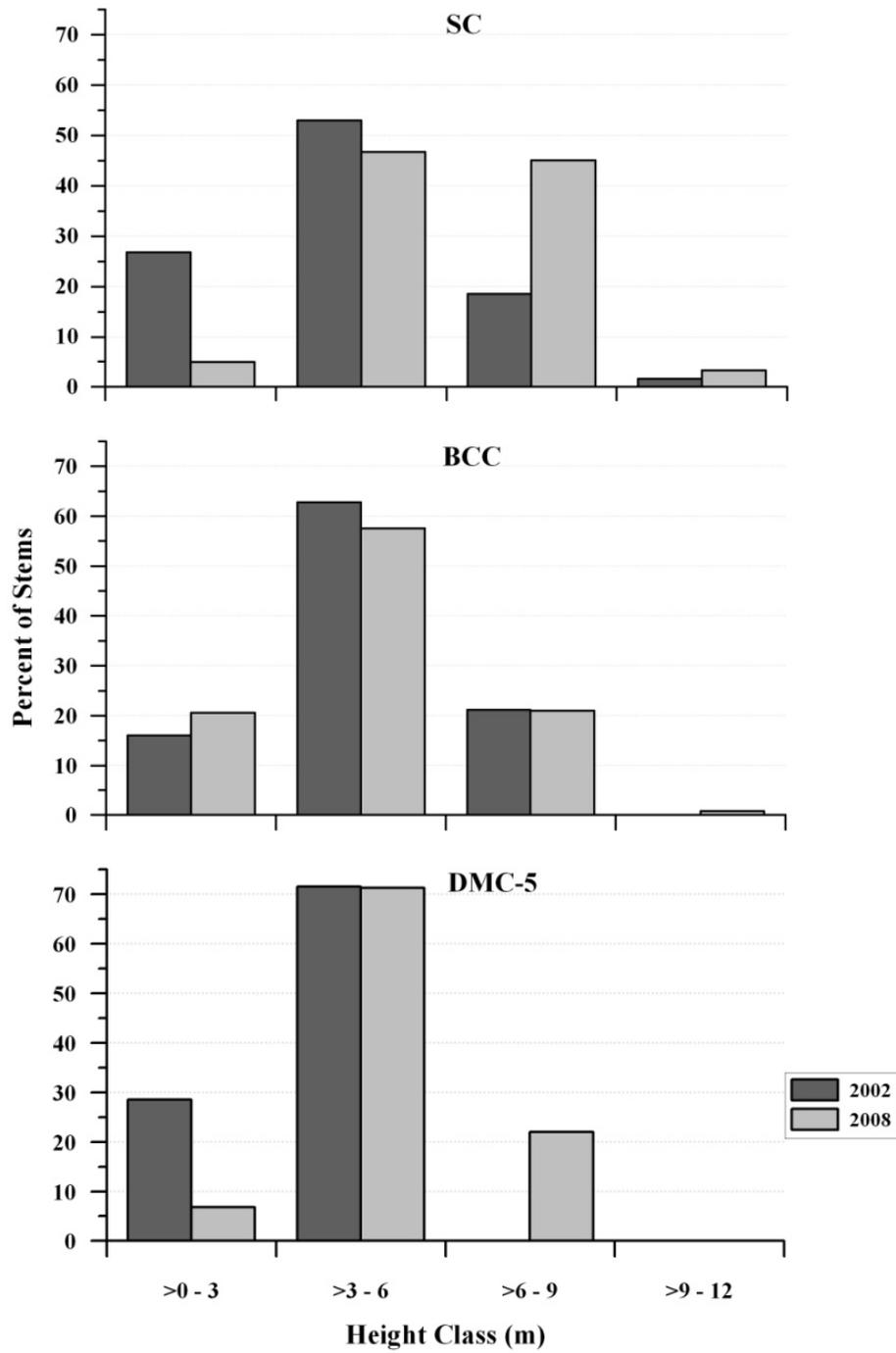


Figure 4.5. Percent of stems within four height classes in meters for Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5) for 2002 and 2008.

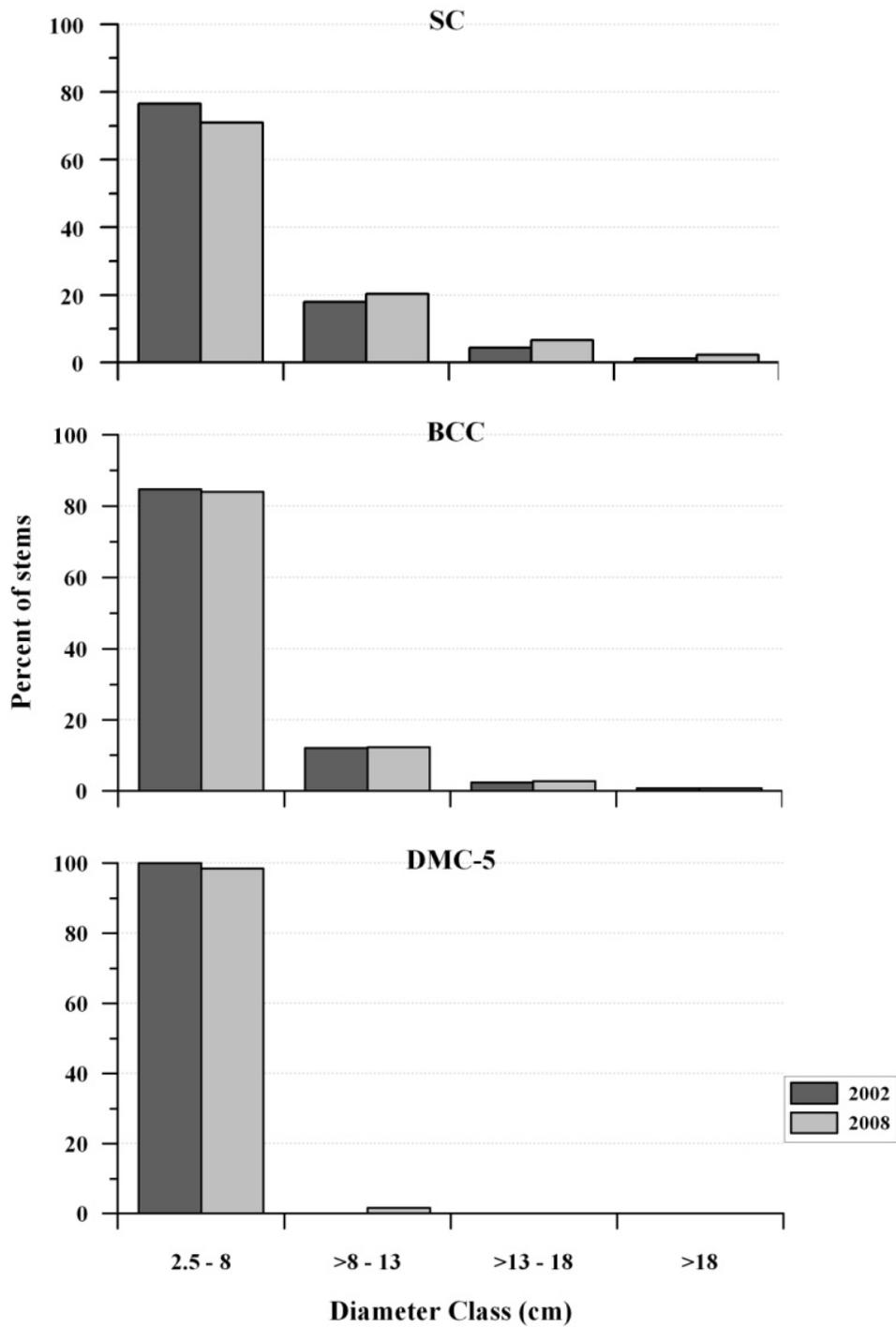


Figure 4.6. Percent of stems within four diameter classes (DBH in cm) for Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5) for 2002 and 2008.

Pearson correlations between mean litter (without guano and miscellaneous) and biomass at the site ($n = 3$) and plot level ($n = 3$) were non-significant ($r = 0.67$, $p > 0.05$); correlations between mean litter (without guano and miscellaneous) and mean DBH were also non-significant ($r = 0.52$, $p > 0.05$). However, there was a significant correlation between mean litter (without guano and miscellaneous) and mean height ($r = 0.70$, $p = 0.03$). The litter component termed miscellaneous were the combined fractions of non-mangrove leaves, insects and seeds from littoral vegetation.

Leaves were the dominant fraction of plant-derived litter at all sites. There is a seasonal trend in above-ground litter for all three sites (Fig. 4.7). This trend is also reflected for all four litter fractions. Both leaf litter and bract-flower-fruit fraction peaked between August and October for all three sites. Guano input from birds was evident on Soldier Cay and Big Calabash Cay, and was highest on Soldier Cay during August, September and October, when it greatly exceeded the mass of plant-derived litter. Pearson correlations between litter (without miscellaneous) and guano for the three sites at the plot level ($n = 3$) and month ($n = 12$) were significant for Soldier Cay ($r = 0.76$, $p < 0.0001$), and for Big Calabash Cay ($r = 0.52$, $p < 0.0011$); however, it was non-significant for Dead Man Cay-5 ($r = -0.06$, $p > 0.05$).

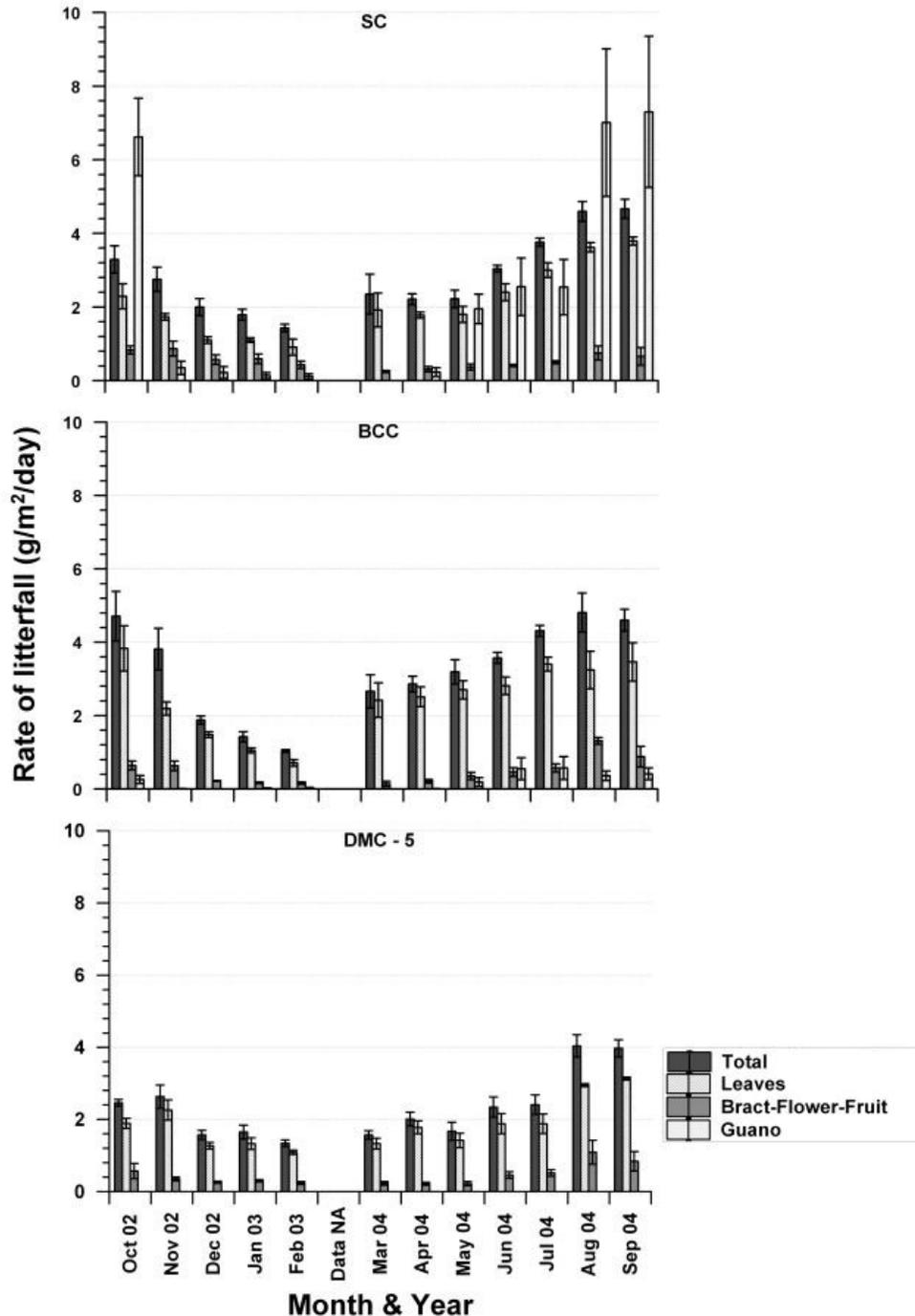


Figure 4.7. Above-ground litter from three Turneffe fringing cayes stacked from north to south: Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5). Above-ground litter covers a 12 month period; litter was not collected between March 2003 and February 2004 (Data NA = Data Not Available). Total litter was calculated by summing all the litter fractions with the exception of guano and miscellaneous fractions. Leaves fraction was for all mangrove species combined. The bract, flower and fruit fractions were also combined. Error bars indicate standard error of the mean.

Guano was present in each of the months on Soldier Cay except in March 2004, while at Big Calabash Cay, it was absent during December 2002 and March 2004 (Fig. 4.8). At Dead Man Cay-5, guano was absent throughout the entire period.

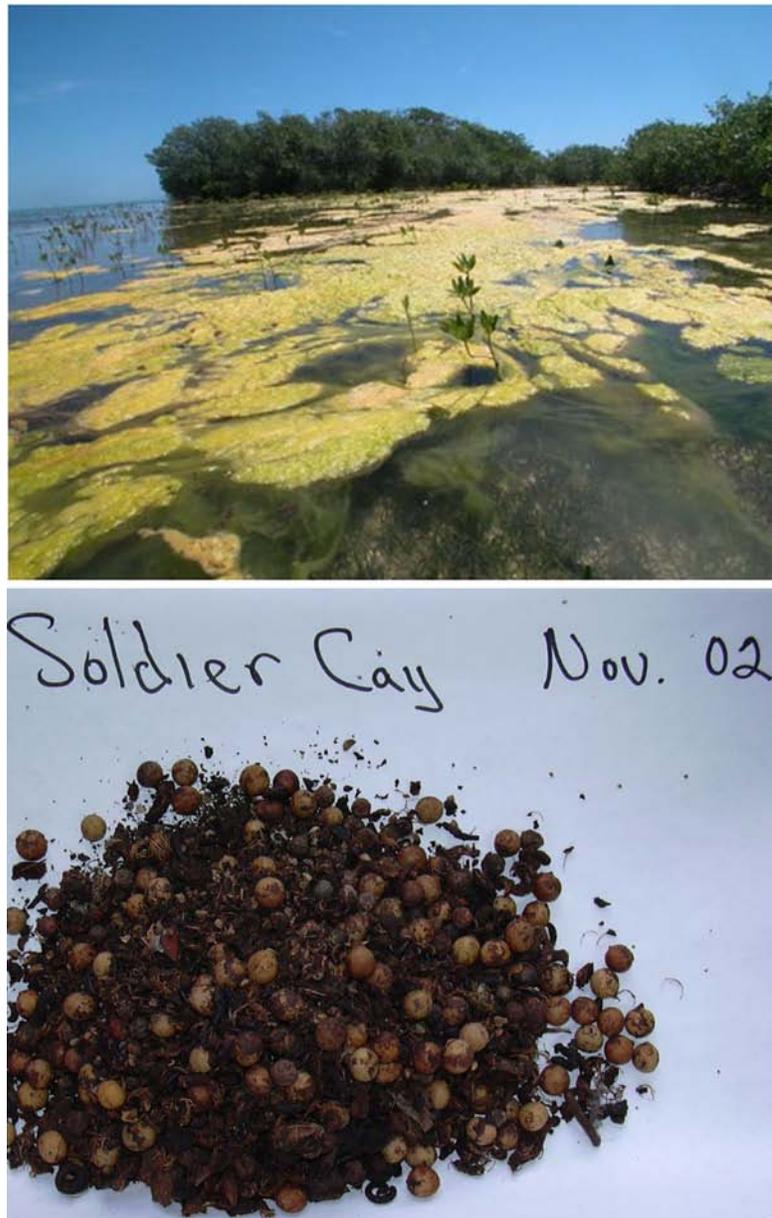


Figure 4.8. Top photo - algal bloom southwest of Soldier Cay (August 2002). Bottom photo - bird guano mixed with littoral forest seeds collected in November 2002.

Air temperature at the Carrie Bow Cay Marine Field Station ranged from 24 to 29 °C during the period of above-ground litter collection (Fig. 4.9). There was a significant correlation between the mean monthly total litter production (without guano and miscellaneous) at all three sites with the monthly mean air temperature ($r = 0.85$, $p = 0.0005$) and with leaf litter only ($r = 0.88$, $p = 0.0001$). There were no significant correlations between monthly mean wind speed (km/hr) and leaf litter ($r = -0.25$, $p > 0.05$), or monthly mean rainfall (mm) and leaf litter ($r = 0.08$, $p > 0.05$).

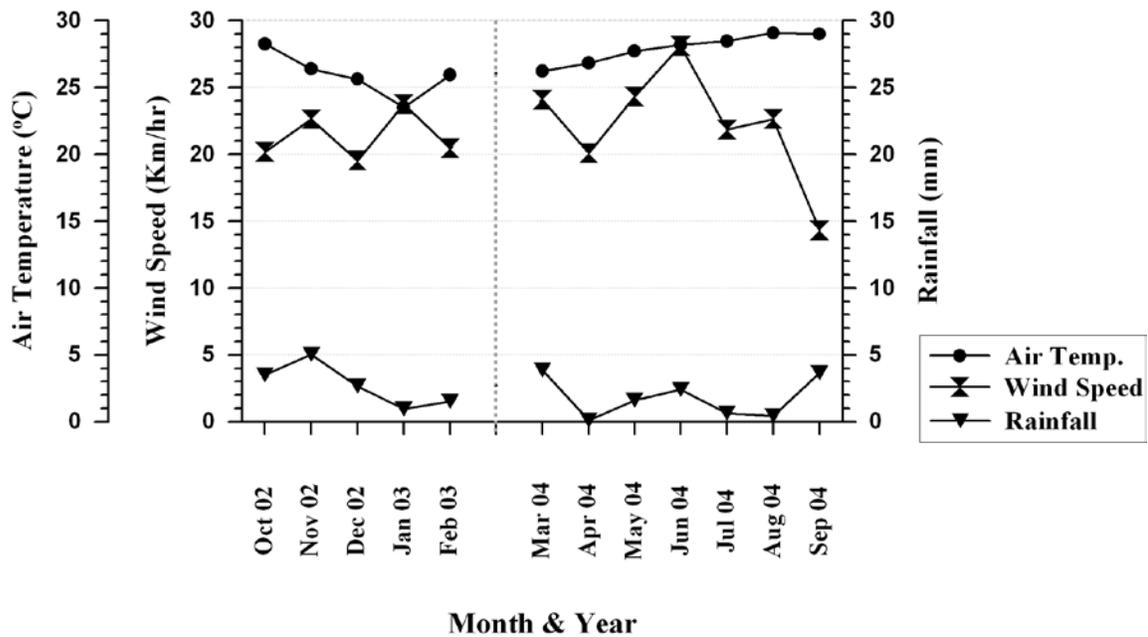


Figure 4.9. A twelve month period of mean monthly weather data (air temperature, wind speed and rainfall) from Carrie Bow Cay Marine Field Station. Weather data between March 2003 and April 2004 were omitted (broken line) in order to coincide with above-ground litter data from the Turneffe sites.

Ground surface litter was a mixture of organic matter at various stages of decomposition. The thickness of this layer varied among sites particularly for those plots with tidal inundation.

Mangrove leaf litter was the dominant fraction from the ground surface litter (Fig. 4.10) and contributed 52% of the total dry mass with an average of 100.8 g/m² for the three sites. Fragments of broken and/or uprooted seagrass was found on all three sites and was an important component of the ground litter in portions of the plots that were within the intertidal zone. The seagrass (*Thalassia testudinum*, Banks ex König) contributed 6% of the total ground litter. Based on the Nye-Olson model (Nye 1961; Olson 1963), leaf litter residence time was 1.6 to 4 months and was higher on Dead Man Cay-5 than Soldier Cay and Big Calabash Cay (Table 4.6).

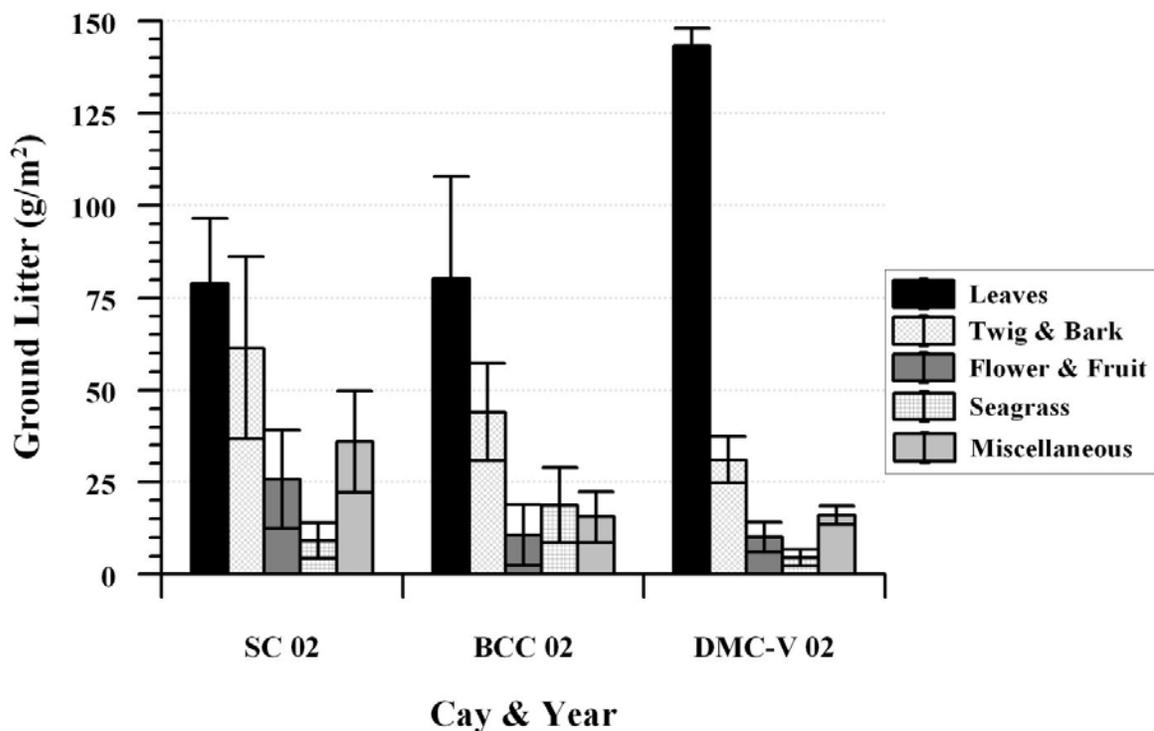


Figure 4.10. Ground litter from Soldier Cay (SC), Big Calabash Cay (BCC) and Dead Man Cay-5 (DMC-5). Ground litter collected in 2002 from underneath above-ground litter traps from a 0.5 x 0.5 m quadrat. Error bars indicate standard error of the mean.

Table 4.6. Estimates of leaf litter turnover coefficients (k, per yr) and residence time (yr), based on estimates of leaf litter fall rates (g/m²/yr) and leaf litter standing crop (g/m²) for three sites: Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5).

Site	Turnover Coefficient (yr ⁻¹)	Residence Time (yr)
SC	7.06	0.14
BCC	7.79	0.13
DMC-5	3.05	0.33

4.4 Discussion

4.4.1 Mangrove above-ground biomass

Various studies have concentrated on species composition changes over time and space as it relates to the relationships between natural disturbance and forest dynamics, but biomass changes and related patterns of mortality are also important (Peet 1981; Sprugel 1985; Harcombe et al. 1990). The average above-ground biomass measured in 2008 was larger than in 2002; however, there was no significant change in biomass at one of the three sites (Big Calabash Cay). The 2008 average above-ground biomass was similar for all three sites (11.3 kg/m²) and was at the low end of the range for mangrove communities (9-29 kg/m²) reported by Twilley et al. (1992), who included data from Asia, the Caribbean, and Florida. It was in the middle of the range for fringing mangroves in Florida (8.6 - 15.3 kg/m²) reported by Lugo and Snedaker (1974).

Unlike Big Calabash and Soldier Cay, where the plots were well stocked with mangrove trees in 2002, plots on Dead Man Cay-5 had some open space in 2002. This site had the highest number of trees recruited into the 2.5 cm DBH class and showed a substantial increase in basal area and above-ground biomass between 2002 and 2008. The height:diameter ratios were highest at Dead Man Cay-5 and this was not surprising given the high density of these stands. Trees were becoming more slender over time at Dead Man Cay-5 and Soldier Cay, likely due to competition (e.g., Mason 2008). In spite of this, the lack of mortality at the plot level indicated that the mangroves on Dead Man Cay-5 were not at the self-thinning stage.

The surveyed plots on Turneffe were still dominated by *R. mangle* in 2008 although changes in substrate composition as a result of storm-deposited material could trigger future changes in species composition. Non-mangrove species were present at the edge and adjacent to the plots. The percentage of substrate above the spring high tide was increasing in some plots. Continued monitoring substrate elevation will provide additional data on sediment accretion and trends in encroachment from non-mangrove species. Modeling by Sternberg et al. (2007), on the interaction between hardwood hammock and mangroves in coastal areas, produced spatiotemporal distributions of these two vegetation types that resembled field observations in south Florida. Hardwood hammock is a dense stand of broad-leafed trees that grow on a natural rise of only a few cm in elevation. The study from Sternberg et al. (2007) highlighted the effects of microtopography on mangrove and hammock distribution in relation to salinity and elevation.

Big Calabash Cay had the largest biomass in 2002 but had little change in tree size or plot biomass between measurements. Relatively small differences in gross photosynthesis, respiration or allocation of carbon into woody material *versus* expendable organs can lead to large differences in rate of accumulation of mangrove biomass. These processes are particularly responsive to localized environmental conditions such as climate, tidal amplitude and flushing, freshwater-seawater interaction, nutrient inputs and surficial geology (Clough and Attiwill 1982). Unlike the other two cays, almost all of the plot area at Big Calabash Cay was below spring high tide suggesting a continued stress from salt water. Salinity is a key environmental factor in mangrove ecosystems. Lugo (1990) suggested that there is a characteristic, declining, tree-height gradient with increasing salinity and decreasing nutrient availability.

There were very few dead trees in the plots. It was noted in 2008 at Big Calabash Cay that in two plots various dead trees (average DBH = 5.5 cm) were infested with arboreal termites, particularly *L. racemosa*. It is very likely that the termites were feeding on dead wood and are considered as decomposers (Lugo 1997). The mortality on Soldier Cay was due to windthrow. These plots had the highest number of mangroves in the 9 to 12 m height class by 2008. It is possible that these trees reach their maximum heights in these environments since the higher the tree canopy, the higher the probability of being affected by windthrow (Bardsley 1985). This is worth monitoring in future remeasurements.

One of the challenges in measuring stem diameter and height for *R. mangle* was the production of multiple stems and various prop roots along the main stem and lateral

branches. For height, the problem was of leaning stems, especially for those trees within 2 to 4 m from the edge of the mangrove forest, some which assumed horizontal growth. For stems that had formed additional buttressing prop roots, this moved the location for stem diameter measurements outward, and in some cases, beyond the boundary of the plot, thereby affecting the number of trees that qualified to be removed. Of course, there is the possibility that stems outside the plot could grow into the plot in the same manner. But, the general growth habit of mangroves in dense stands is to grow towards the stand edge, where space and sunlight are available and where these plots are located. Clough et al. (1997) investigated multi-stemmed trees of the mangroves *R. stylosa* and *A. marina*. The investigation showed that it is possible to obtain robust allometric relationships between stem (or main branch) diameter and the above-ground biomass under a range of environmental conditions. This was achieved by treating each stem as a discrete tree and allocating the dry weights of the common butt and above-ground roots to each stem according to its relative cross-sectional area. The problem of multi stems in mangrove forest has also been addressed by Dahdouh-Guebas and Koedam (2006). They concluded that measuring the central stem of aggregating mangrove trees was better suited than the closest stem when using the Point-Centered Quarter Method (PCQM is a plot-less method which yields quantitative data by studying trees nearest to sampling points as an estimate of numbers and distribution).

The *R. mangle* root/stem system has a high degree of plasticity that renders it capable of adapting to changing environments (Gill and Tomlinson 1977). Lateral expansion in these environments by the production of prop roots gives *R. mangle* the opportunity to rapidly colonize new local substrate without the risks and challenges associated with propagule

dispersal and establishment. Leaning *R. mangle* trees tend to produce prop roots along the stem. Prop roots most often originate from lateral branches as the tree crown grows towards sunlight and/or available space. The form of edge trees also differs from the form of trees within the fringe. Duke (2001) commented that edge trees in *Rhizophora* stands are characterized by gnarled and lateral structures with greater numbers of stems and lateral branches, as well as higher and more numerous root structures. This suggests that biomass equations developed for interior mangrove stands may be different for mangrove stand edges.

The growth habit of trees along edges can provide advantages over other mangrove species by enabling *R. mangle* to: 1) colonize new substrate without the need of propagules; 2) grow outward and minimize competition within the stand; and 3) expand outward and remain low in stature to minimize blowdown. Bardsley (1985) determined that dwarf mangroves sustained little impact in contrast to tall emergent mangroves from the Australian cyclone Kathy. Stem orientation relative to stand edge on the fringing cays should be further investigated.

Setting up plots on fringing cays to measure mangrove forest is always challenging because of the narrow bands of mangrove forests and steep gradients of environmental conditions. The lateral expansion of *R. mangle* on these plots toward the open water adds to the challenge. I noted that trees measured at the interior of the stand were less likely to exhibit extreme leaning stems or branching with prop roots than trees near the edge of the stand, but it was necessary to characterize the full range of conditions including edges. The issues of *R. mangle* multiple stems, leaning trees and deciding where to measure stem diameter and

height will be a continuing issue for field scientists and biometricians. To facilitate future surveys and monitoring of above-ground estimates from these sites, it would be wise to improve the method for tagging and remeasuring trees. Measuring height and DBH will always be a challenge in fringing mangrove forests, but creating a system to permanently mark the location of the last DBH measurement and a means of securely tagging trees would be very advantageous for tracking individual tree growth and morphological changes in future surveys.

4.4.2 Mangrove litter

Above-ground 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 pattern of total above-ground litter at Turneffe indicated a seasonal trend with peaks during the months of August and September. Garcia and Holtermann (1998) also found that maximum litter fall in Belize occurs from August to October. Above-ground litter fall from mangrove forests has been correlated with mean monthly air temperature (Day et al. 1996), and this was also found at Turneffe. Studies of litter fall production in mangrove forests around the globe have shown that trees drop their leaves throughout the year, although higher litter fall rates have been observed at the end of the dry season and at the beginning of the wet season (Pool et al. 1975; Williams et al. 1981; Twilley et al. 1986; Flores-Verdugo et al. 1987). Although the Turneffe cays might not receive as much rainfall as mainland Belize, overcast conditions during the rainy season do influence daily temperatures.

The litter fall rates at Turneffe (1.86 g/m²/day, excluding guano) were at the lower end of the range of litter fall reported from the five CARICOMP sites that have data for a complete year (1.38 to 5.75 g/m²/day; CARICOMP Program 1997). They are closer to the mid-point of the range reported by Lugo et al. (1988) for fringing mangrove forests (0.68 - 2.66 g/m²/day). There was a significant correlation between mangrove height and litter for the Turneffe plots. Saenger et al. (1983) found a significant relationship between litter with height based on published and unpublished reports worldwide. Saenger et al. comment that vegetation height is a general index of structural development, and the correlation reflects growing conditions that result in increased carbon turnover via litter fall. The mean vegetation height for Soldier Cay was higher than the other two sites. Mangroves growing on this cay had less stress from tidal inundation and greater access to nutrients from bird guano.

Leaf litter was a major component throughout the sampling period at Turneffe, contributing 60% of the total litter and 52% of the total ground litter, but this falls at the low end of the range for mangroves (60 to 90%) reported by Pool et al. (1975) and Bunt (1982). Higher litter fall rates in mangroves with greater tidal activity and water turnover has been reported in mangroves zones with stagnant water (Pool et al. 1975). However, as tidal activity increases, surface litter is more susceptible to export (Twilley 1985). Twigs and roots degrade more slowly than leaves. Roots are thought to contribute most to peat formation due to high root biomass production and turnover within the substrate (Middleton and McKee 2001). According to Twilley et al. (1986), the residence time of surface litter in fringing mangrove forests is lower than in basin forest due to tidal action. The fringing and overwashed mangroves in Rookery Bay, Florida had residence times of 2 and 1.5 months,

respectively (Steyer 1988). Pool et al. (1975) reported similar values for fringe and riverine sites in the Caribbean. The residence time at Soldier Cay and Big Calabash Cay was consistent with these values. However, the residency time at Dead Man Cay-5 was 4-months, probably because the plots are bit more in the interior. A review of the literature, Adame and Lovelock (2011) concluded that mangrove forests are in general sources of C and nutrients in the form of litter and particulate organic carbon.

In mangrove forests of the Caribbean, the accumulation of plant litter has a high variability depending upon litter fall rates, consumption by macrodetritivores, microbial decomposition rates, and tidal flushing (Middleton and McKee, 2001). Buildup of soil organic matter occurs where plant matter input is high and/or decomposition rates are slow (McKee 2011). The plots at Dead Man Cay-5 were further into the cay and from the mangrove edge compared to the other sites, which could influence the effects of the tides. Furthermore, in 2002, when the plots were installed, some zones within the plot seemed to have recently received a load of reef sediment (sand and fine coral rubble), which elevated parts of the plot above the spring high tide. Prop roots from *R. mangle* were partially buried and underneath some of the sand there was mangrove peat, indicating burial from storms.

Studies done on mangrove peat accretion and subsidence in Florida and Belize showed that elevation losses occurred in dwarf and scrub forest types, whereas elevation gains occurred in fringing stands (McKee et al. 2007a). Mangrove root accumulation was found to be a major contributor to soil development, accounting for up to 55% of vertical change (McKee 2011). Less litter accumulates in fringe forests in Belize, due to frequent removal by ebb tides and

detritivore feeding (Middleton and McKee 2001). Because of the intertidal location of most of the Turneffe plots, it is expected that most of the leaf litter is exported to nearby systems and that mangrove roots are the primary contributor to peat accumulation on these fringing cays. Plots with a greater influence of tidal inundation (e.g., Big Calabash Cay) had the highest percent cover of peat. In certain plots, the peat was buried with new sediment material (e.g., Dead Man Cay-5).

The sudden increase in nutrient to the soil as a result of hurricane litter fall on forests in Puerto Rico has shown to significantly alter nutrient cycling patterns (Lodge et al. 1991). Litter fall is typically lower in the year following a major hurricane disturbance than in the year prior to the disturbance, which has been viewed as an indication of the forest undergoing a recovery process (Bellingham et al. 1996). During this study on Turneffe, there were no major wind storms that could have affected the collection process with the exception of one occasion when a southwesterly wind partially emptied a couple of the litter traps. During windy conditions and heavy rains, it is best to collect litter over shorter intervals than at the end of the month. Excessive rain and moisture can initiate decomposition on the contents of the litter trap if left for too long in the field. Although the plots were located on the leeward of the cays to minimize litter loss, some of the litter might be lost from falling into the traps on windy days.

Tidal dispersal of mangrove litter could contribute to nutrient influx to adjacent seagrass beds and coral reefs. The leaching of nutrients from bird guano at Soldier Cay, which coincided with an algal bloom, provided an example of the local spread of nutrients. Litter can be

transported to greater distances by tides and currents. Mangrove leaves were seen amongst adjacent patch reefs floating atop or settled to the bottom covered with epibionts and/or decomposers.

Mangrove forests are generally considered oligotrophic ecosystems and the species that grow there are considered adapted to low-nutrient conditions (Hutchings and Saenger 1987). The carbonate base of the cays on the eastern side of Turneffe also influences the availability of nutrients. In a high carbonate environment, CaCO_3 causes phosphates to precipitate out of the water, reducing the availability of phosphorus (Littler and Littler 1990; Binkley and Vitousek 1989). Thus, mangrove plants take advantage of any additional nutrients coming from other sources. Field experiments involving nutrient enrichment have also found that mangrove species may enhance their growth and change patterns of biomass allocation as a response to increased availability of limiting resources (Feller 1995; Feller et al. 1999, 2002 and 2003; Lovelock et al. 2004). However, these responses were strongly controlled by stress factors such as salinity and tidal inundation regimes. Although most of the substrate surfaces on the plots were under the influence of tidal inundations, some plots had significant amounts of sand and/or coral. Parts of those substrates were above the spring high tide, allowing litter to stay longer under the mangrove canopy with potential nutrient recycling benefits.

Onuf et al. (1977) documented the enrichment of an *R. mangle* stand by bird guano in Florida. They found that bird guano stimulated plant growth and resulted in higher nitrogen concentrations of some parts in comparison to a nearby stand with no enrichment. The deposition of bird guano on both Soldier and Big Calabash Cay is likely providing nutrients

to the fringing mangrove forest of these cays. There was a significant correlation between the production of litter and guano for both Soldier Cay and Big Calabash Cay. However, the amount of bird guano collected on Soldier Cay was higher than at Big Calabash Cay. At Soldier Cay there was a pulse of guano during August, September and October. It seems that bird guano was a good source of nutrients as the August-October pulse corresponded with the formation of the algal bloom at Soldier Cay. I have noticed that the fruiting of gumbo-limbo (*Bursera simaruba*) and seagrape (*Coccoloba uvifera*) in the littoral forest on the larger islands coincides with the pulse of guano input by birds at Soldier Cay. These trees offer substantive amount of food for the great-tailed grackle (*Quiscalus mexicanus*), which was the dominant bird roosting on Soldier Cay, although guano from seabirds was also collected. It is likely that this small cay is selected for roosting because it has fewer potential predators than the larger cays. The litter traps used for this study employed plastic screening with 1 mm² mesh and were designed primarily to capture mangrove litter. To more accurately measure the amount of bird guano contribution to the fringing mangrove and adjacent systems, it would be best to collect guano on non-porous containers on a daily basis.

4.5 Conclusion

There was a significant increase of biomass at two of the three cays during the 6-year period from 2002 to 2008. Although the biomass was low compared to other sites in the Caribbean, mangrove trees at Soldier Cay were becoming increasingly slender and may be reaching a mechanical stability threshold in these high density stands. Some trees in and outside the plots had been blown down. In these fringing stands, *R. mangle* was exploiting a strategy of

lateral expansion. Though *R. mangle* vegetation dominates the plots, subsequent remeasurements should provide information on the dynamics of species composition over time and how this relates to substrate accretion (lateral and vertical). Different factors may be driving above-ground biomass accumulation patterns on the three cays. Tidal inundation increases salinity stresses and removes litterfall, while bird guano deposition presumably adds nutrients. It appears that the fringing forests of these cays were exporting carbon and nutrients to adjacent systems via leaf litter and guano, while receiving inputs of sediment and nutrients from adjacent coral reefs and seagrass beds. The potential export-import from one system to the other underscores the interdependency of these adjacent ecosystems.

The nine permanent plots established on Turneffe are useful monitoring sites. These offshore sites are in hurricane-prone zones, and permanent plots provide an opportunity to study the effects of storms. Follow-up studies at regular intervals will improve our understanding of above-ground biomass and litter fall seasonal trends and the influence of bird guano on these systems. Although data collection has been conducted for 12 months on these sites, I recommend a multiple-year litter study with monthly sampling to better understand year to year variation. It appears that nutrients are being imported into the fringing cays in the guano of roosting birds. Further research on bird roosting patterns, and food sources would provide insights into nutrient fluxes between large islands and fringing cays.

Chapter 5: Spatial patterns in cay substrate and vegetation

5.1 Introduction

The term 'fringing cays' is used in this study to describe a group of cays which forms on the sediment apron of the back-reef, and the substrate and vegetation of these cays can be above and/or below the spring high tide. On Turneffe, this type of cay is predominantly found on the eastern side of the atoll and in close proximity to the coral reefs. These fringing cays are dominated by mangrove forest but also include areas of littoral and coccol forest. These cays are an important component of the atoll environment, are interconnected with adjacent reef and seagrass ecosystems and provide nesting sites for birds and crocodiles (Meerman 2006; personal observations). Fringing cays are small and low-lying, and in consequence are vulnerable to disturbance from tropical storms, followed by periods of recovery. Two storms with hurricane force winds have made landfall on Turneffe since 1945. Hurricane Hattie affected the fringing cays in 1961, and Hurricane Keith affected the northern group of fringing cays in 2000. Both hurricanes damaged cay vegetation; however, Hurricane Keith affected the cays from the leeward side with respect to the reef and was less intense and destructive than Hurricane Hattie.

Coral reefs are effective barriers that dissipate wave energy and create low energy environments in their lee (Lowe et al. 2005). Large amounts of skeletal materials are constantly produced in the reef-front. The coral structures are fractured by wave energy or collisions with moving material, then ground into smaller fragments by abrasion. Feeding or

excavation by fishes, urchins, and boring sponges are also important in the breakdown of these calcareous materials (Bertram 1936). Some of the resulting coral rubble, sand, and silt are transported by waves and currents into the lower energy depositional environment behind the reef crest.

Fringing cays are composed primarily of sediments swept in from the adjacent coral reef. Cay development can be a process of accumulation around a central (depositional) node, controlled by wave convergence across reef platforms (Kench et al. 2005; Woodroffe et al. 1999). Transported sediments are further molded by waves and currents, leading to the formation of shallow water, coral terraces and shingle ridges within the back-reef area. It is these shallow areas and terraces that make up the fringing cays. This is a highly dynamic environment and the substrate area above the spring high tide and associated vegetated area are expanded or reduced by the action of storms, which are common in these exposed environments (Chapter 3). Understanding the processes that drive post-storm substrate and vegetation developmental patterns will provide insights into geomorphic and successional dynamics, and the role that mangroves play in these dynamics.

The leading edge of fringing cays is often a ridge of coral rubble that forms a rampart. Scoffin et al. (1978) found that there is a strong correlation between shingle rampart distribution and the occurrence of mangroves on cays along the Great Barrier Reef. He also noticed that on the local level, mangroves were “preferentially” colonizing the less exposed parts of shingle ramparts. Stoddart et al. (1978) also observed this phenomenon, and remarked that the formation of windward shingle ridges was a critical event, which makes

possible the establishment of mangroves on suitable substrates in areas otherwise highly exposed to wave action. Stoddart et al. also noted that on Low Isles Reef along the Great Barrier Reef the superimposition of coral rubble ridges occurred where movement of rubble away from the reef crest was directly obstructed by presence of dense mangrove vegetation. This suggests that there is a feedback loop and potentially an acceleration of cay formation once mangroves establish. Once established *R. mangle* can expand laterally, and prop roots that reach the substrate act to stabilize the tree as well as the substrate (Perry 1988). In this manner, mangroves stabilize substrates both above and below the spring high tide, and enable accretion of coral and organic sediments.

Differentiation of species into zones is a common feature of coastal plant communities, and there are various theories as to why zonation occurs. There is continuing debate on the degree to which pore water characteristics such as salinity and accumulation of toxic substances are a cause or a result of plant zonation (Boto and Wellington 1984; Nickerson and Thibodeau 1985; Sherman et al. 1998; Matthijs et al. 1999, Vilarrúbia 2000, Marchand et al. 2004). Lopez-Portillo and Ezcurra (1989), found predictable relationships between substrate particle size and height and stem diameter of three mangrove species (*A. germinans*, *R. mangle* and *L. racemosa*), in Mexico. Zonation patterns may also depend on the density of mangrove propagules and tidal sorting (Rabinowitz 1978a and b; Clarke and Kerrigan 2002).

Studies conducted on floodplain forests generally find that tree species composition, basal area, diversity, and other community attributes are critically affected by elevation (Bell and del Moral 1977; Franz and Bazzaz 1977) or its correlates: flooding frequency (Bell 1980),

duration of inundation (Pierce 1981), soil moisture (Adams and Anderson 1980), or soil texture (Robertson et al. 1978). Ellison (1994) has suggested that measuring mangrove substrate elevation with respect to absolute datum will indicate the “preferred” elevations of different mangrove species. However, in marsh studies, local mean tide level is a more ecologically meaningful reference datum than geodetic datums or mean sea level (Van de Plassche 1986). There are other potential explanations for zonation, including predation and competitive interactions. In their review of the properties of mangrove ecosystems, Feller et al. (2010) review zonation theories and the evidence for them. They found that no one theory explains all of the observations.

In fringing cays, gradients in wave energy and disturbance could also explain vegetation patterns. Waves may affect shoreline plants directly (e.g., by uprooting seedlings) or indirectly (e.g., by eroding fine sediments) (Keddy 1982). Studies of marsh vegetation have demonstrated clear relationships between species composition and environmental factors (Harris and Marshall 1963; Walker and Wehrhahn 1971; Auclair et al. 1976). Keddy (1982) showed that the zone widths of selected lakeshore vegetation and the proportion of silt and clay in the substrate were correlated with calculated measures of exposure to wave. In another study, Keddy (1984) concluded that zonation patterns were affected significantly by exposure from waves and that the proportion of silt and clay in the substrate appeared to be a more appropriate axis for direct gradient analysis. Observations made along the Tobacco Reef apron in Belize by Macintyre et al. (1987) showed that very little coarse debris was transported more than 150 m from the reef crest.

The theories of Grime (1977, 1979 and 2001) concerning plant life history strategies provide a useful framework for exploring the factors driving plant community patterns in fringing cays. Grime (1977) classified plants according to their response to stress and disturbance. He defined stress as something that slows growth, while a disturbance causes destruction of biomass. Grime identified three major plant strategies: competitive plants (low stress environments with low disturbance), stress-tolerant plants (high stress environments with low disturbance), and ruderal or disturbance plants (low stress with high disturbance). This latter group of plants are those species that are first to colonize disturbed areas. In the fringing cay environment, salinity would represent a stress, while exposure to wave energy would represent potential for disturbance. Saenger (1985 and 2002) used triangular ordination to explore the distribution of Australian mangrove species according to stress, disturbance and competition. To explore the adaptive strategies of fringing cay vegetation communities at Turneffe, the effects of the following environmental variables on establishment, growth and distribution were explored: soil salinity, substrate elevation relative to spring high tide, distance from the edge of the reef crest (which is a proxy for exposure to wave energy), and distance from the edge of the large islands (which is a proxy for proximity to propagule source).

The following questions are addressed in this study: 1) how does distance from the reef affect substrate elevation and composition; 2) how does the distribution of *R. mangle* and other tree species vary with distance from the reef, soil salinity, and substrate elevation; 3) which environmental variables best describe the presence and size of *R. mangle*; 4) where does *R. mangle* fit into Grime's plant strategy concept and Saenger's triangular ordination; 5) is there

any difference in plant size between the leeward zones of the cays (with respect to the reef crest), affected by Hurricane Keith and those that were not?

5.2 Methods

5.2.1 Selection of study sites

A total of 33 vegetated cays on the eastern (windward) side of Turneffe were explored as candidate study sites (Chapter 3). From these, a sample of eight cays was selected. Selection criteria included the absence of permanent human settlements in recent years, representation of a range of cay size, cay vegetation communities (mangrove, coccolith, and littoral forest), and distribution from north to south. Of the eight fringing cays selected for this study, two of the cays had permanent settlements before Hurricane Hattie in 1961 (Soldier Cay and Big Calabash Cay), all eight cays were affected by Hurricane Hattie, and three cays were affected by Hurricane Keith in 2000 (Cockroach Cays-20, -22 and -23). Three of the selected cays were from the north (Cockroach Cays-20, -22 and -23), two in the central (Soldier Cay and Big Calabash Cay) and three in the south (Dead Man Cays-2, -4 and -5) (Fig. 5.1; Appendix M). The inter-tidal or sub-tidal mangrove patches that were immediately adjacent to these cays were included during field sampling, along with adjacent areas of non-vegetated substrate.

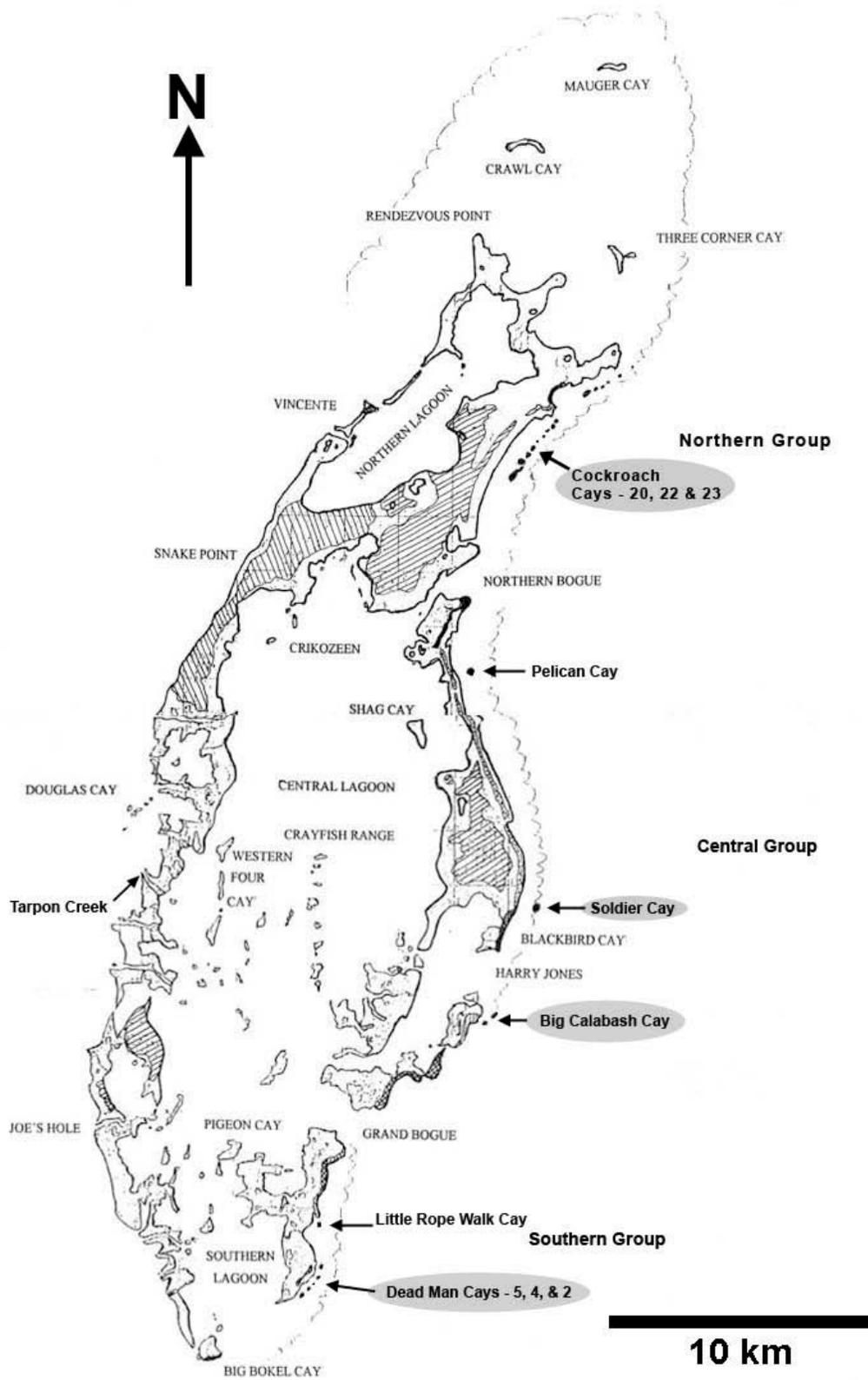


Figure 5.1. Map of Turneffe highlighting group of eight cays surveyed for this study. (Redrawn from McGill 1996).

5.2.2 Image and map preparation

High resolution aerial photos from 2006 were georectified and mosaicked using 2005 QuickBird imagery as described in Chapter 3. High resolution images of the fringing cays were printed and used during the sample cay selection phase.

5.2.3 Identification of strata, transect layout and field plots

Preliminary vegetation and substrate strata on and in the vicinity of the eight sample cays were identified from the 2006 photo-mosaic based on visual assessment of differences in image texture and color, and knowledge of the relationship between image characteristics and field characteristics obtained during reconnaissance. The strata were digitized and given preliminary names, based on biophysical properties, prior to establishing field transects. The strata were: fringing mangrove, mixed mangrove, dead mangrove, littoral forest, coccol forest, seagrass bed, beach, exposed and non-vegetated coral rubble and/or sand. These strata types were identifiable from the 2006 photo-mosaic. The edge of the reef crest facing the fringing cays and edge of the vegetation of the larger islands facing the fringing cays were digitized and verified on the ground.

The vegetation and substrate strata mapping and transect layout were initially completed using the 2006 photo-mosaic within a GIS. Strata boundaries were adjusted based on ground-truthing during field work. At each cay, a baseline transect was laid parallel to the reef crest. For cays that were in close proximity to each other, a single continuous baseline was used.

For consistency, the point of commencement (POC) of the baseline was always at the southern end of each surveyed cay. Line transects were oriented perpendicular to the baseline. The POC of the line transects were strategically placed along the baselines in order to ensure sampling of the mapped vegetation and substrate strata. The line transects ran in both directions from the baseline where necessary to cover the cay and adjacent mangrove and reef flat areas. Along the line transects, each stratum boundary was flagged at the strata edge and the stratum width was recorded. Within each stratum width, a randomly selected distance along the line transect was chosen for the location of circular field plots, the one condition being that the entire plot had to fall within the stratum. For narrow strata such as beaches, circular plots of radius 2.82 m were used, while for wider strata, plots with a 5.64 m radius were used. The center of each plot was marked and labeled. Each plot had a unique name including the name of the cay, distance along the baseline, distance from baseline to center of plot and a plot identification. In addition to the field survey measurements, the global positioning system (GPS) coordinate was recorded at the center of each plot.

5.2.4 Field and plot level measurements

All trees and seedling species within a plot were identified. Non-mangrove trees with the exception of coconut trees were grouped as 'littoral vegetation' to facilitate analysis. For *R. mangle*, the diameter of each stem was measured above the last buttressing root, for all other species stem diameter was measured at 1.3 m from the ground (diameter at breast height, stem diameter). Tree heights were measured with a graduated telescoping pole in m. For *R. mangle*, seedlings were considered those plants without prop-roots and/or plants with a

recognizable hypocotyl still forming the base of the plant. For all other species, seedlings were considered to be those plants less than 1.3 m tall. Seedlings of each species were assigned to height classes of 5, 10, 20 cm, and above in 10 cm increments. Canopy closure was estimated with a spherical densiometer. Mirror densiometer readings were taken in the four cardinal directions from the plot center, averaged and expressed as a percentage canopy closure.

A photo was taken of the representative plot surface substrate within a 40 cm quadrat. A 30 cm sediment core of the representative substrate was taken within the plot with an aluminum cylinder coring device (7.5 cm diameter). Two vertical photos of the core lying on its side were taken with a scale beside the sediment core, one with the intact core and the other with a lengthwise split of the core. The substrate layer length of the core was read from the scale, and the composition of the core was expressed as a percentage of peat, sand, coral rubble or mixed substrate (mixed substrate was a combination of two or more substrate types). Where plots were primarily on coarse coral rubble and a core could not be obtained with the coring device, an estimate was made of the composition of the upper 30 cm of substrate by either moving the coral rubble or by excavating a pit.

Ground salinity was measured close to the plot center. For plots above the spring high tide, a pit was dug to obtain a sample of pore water, the depth varied depending on the substrate's elevation relative to high tide. The water was then siphoned with a syringe attached to a clear tube and the clear tube attached to a porous fiberglass tube. After siphoning the water, the hole was allowed to refill and a sample was extracted for salinity measurement. For those

plots at or below spring high tide, the fiberglass tube was inserted into the ground at approximately 15 to 20 cm from where ground water was extracted. The first sample obtained from the syringe was discarded and the second was used for measurement. Salinity was measured with a handheld salt refractometer (300011 SPER Scientific Ltd.).

The spring tide high-water mark on the cays was used as the datum as described in Chapter 3. As illustrated in Figure 5.2, the term ‘cay’ refers to an area of vegetation that has colonized above and below the spring high tide along with contiguous areas without vegetation (bare substrate), which are also above the spring high tide (see Glossary). In order to capture a relatively detailed elevation of the substrate around and on the fringing cays a system of gridded transects were used (Fig. 5.3). The substrate elevation was measured relative to the spring tide high-water mark for the eight cays using an adaptation of the water level method (Appendix N). Elevation transects were installed to closely match where possible the strata transects. Elevations were recorded at 10 m intervals along the line transects. Adjustments to the 10 m distance were made in order to capture major strata boundaries and abrupt changes in terrain. Figure 5.3 shows the general order in which transects were laid out across the surveyed cays. Elevations were measured along the baseline (A), line transects (B, C, D, E, and F); two more elevation transects were installed parallel to the baseline, one at the end of the line transects (G) and one that bisected the cay vegetation (H). The latter was located so as to intersect the higher elevation portion of the cay. Elevation data was imported into ArcGIS and the Geostatistical Analyst tool was used to perform an ordinary kriging on the data to create a surface elevation map. The resulting grid of elevation points was interpolated to produce an elevation map (Fig. 5.3). An average of 191 points was collected per cay to

produce the elevation maps. Distances from the center of each plot to the edge of the reef crest and to the edge of the larger islands were estimated using rectified aerial photos and the buffer wizard tool in ArcMap, for 1 m buffer resolution.

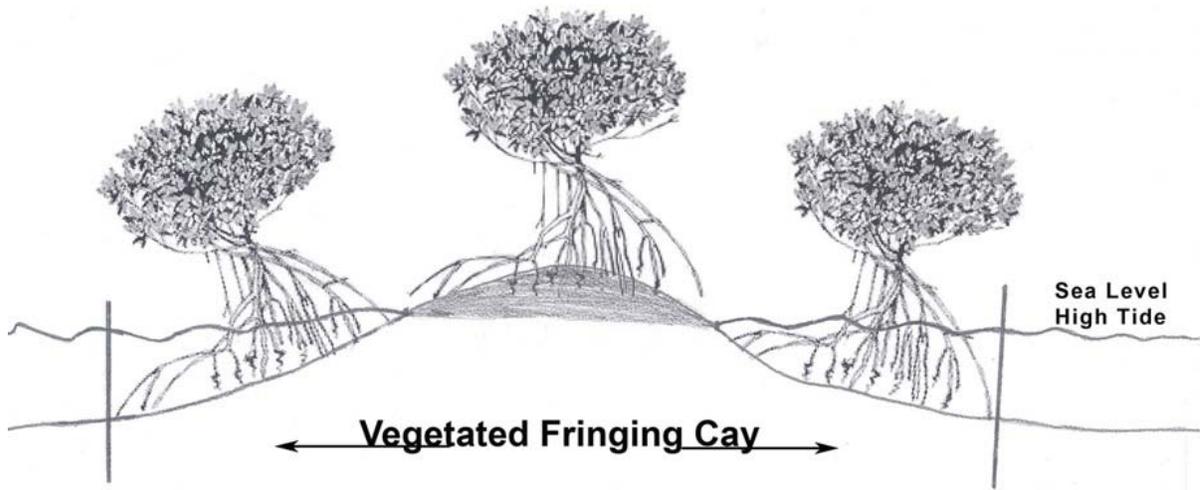


Figure 5.2. A simplified fringing cay showing vegetation and substrate above and below spring high tide.

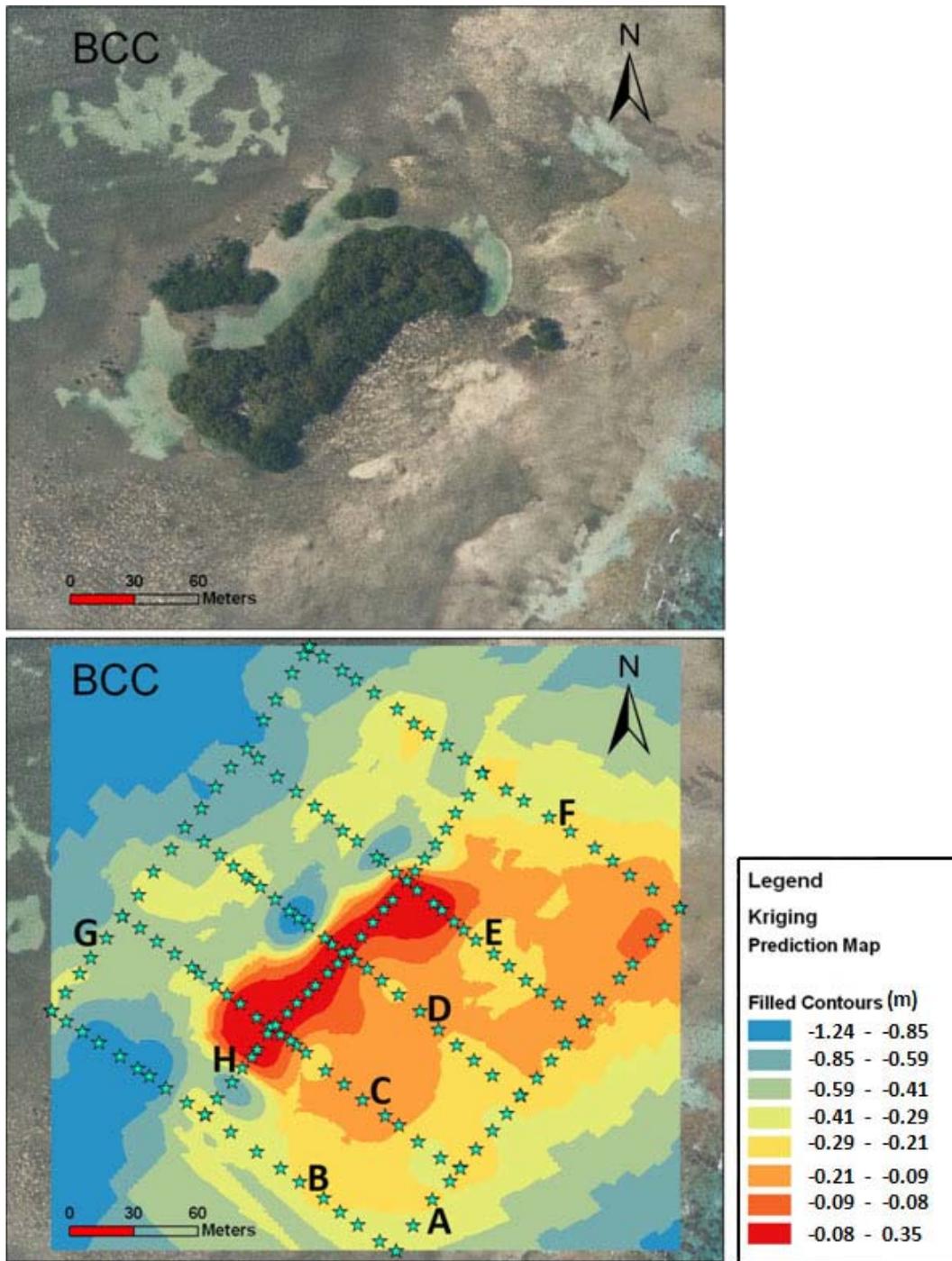


Figure 5.3. Big Calabash Cay (BCC) and point locations used to produce an elevation surface from which plot elevations were obtained.

5.2.5 Data analysis

At the plot level, the stems per ha, number seedlings per ha, and basal area per ha were summarized by species. Plot elevation was extracted from the elevation surface. Plot data were summarized at the cay-level to enable overall comparisons. There appeared to be a gradient in cay conditions from the north to the south and from reefward to leeward. The field plots from each cay were assigned to these distinct zones for analysis. For consistency, and to make it easier to explore locational trends, the cay-level results were laid out by listing the cays from a north to south direction (Cockroach Cay-20, -22 and -23, Soldier Cay, Big Calabash Cay, Dead Man Cay-5, -4 and -2).

The SAS statistical package (SAS Inst., Inc. 2002-2008) was used to examine trends and perform statistical analyses. I used an alpha level of 0.05 for all statistical tests. Independent-samples t-tests were used for comparison of group means between: 1) plots above and below the spring high tide; and 2) leeward zone of northern group of cays with respect to the reef crest affected by Hurricane Keith with the leeward zone of combined central and southern cays. Pearson's correlation coefficients were used to assess the relationship between variables. Scatter plots were created to explore relationships between various plot level parameters, and the effect of distance from the edge of large islands and from the edge of the reef crest. Multiple linear regressions were fitted to explore relationships between plot basal area and maximum tree height and potential predictors. Maximum tree height was considered to be an important variable since it is directly related to the overall scale of many ecological and environmental quantities and is an important indicator for understanding several

properties of plant communities including resource use (Kempes et al. 2011). The dependent and independent variables were used in their original metric units with the exception of basal area which was square root transformed to meet the assumptions of normality tests. A backward elimination procedure with a SLS (significance level for staying in the model) of 0.05 was used to determine significant subsets of independent variables in multiple linear regressions. A correlation index squared (I^2) was calculated for transformed dependent variables (Ezekiel and Fox 1959; Kozak and Smith 1993). Logistic regression models were fit to explore relationships between mangrove and *R. mangle* seedling presence (1 or more seedlings within the plot) or absence (0 seedlings) and the independent variables, using a backward elimination procedure. Independent variables were continuous and dichotomous. The dichotomous variables were wave energy (0 signifies low wave energy, while 1 is for high wave energy), tidal inundation (0 signifies low frequency from tidal inundation while 1 is for high frequency from tidal inundation). Plots were assigned to those categories based on the three zones (leeward, ridge and reefward). The Wald statistic was used to test the null hypothesis that the coefficient B in the logistic regression model is zero, and the Hosmer and Lemeshow Goodness of Fit statistic was used to test for a lack of fit.

Saenger's triangular ordination method (Saenger 1985) was used to evaluate mangrove strategies based on Grime's model (1974 and 1977). The equilateral triangle was used to fix the position of each species by using two sets of coordinates. Species were plotted with respect to potential maximum rate of dry matter production and a morphology index. Morphological index (dominance index) refers to the structure (e.g., tree size, canopy density, root spread, etc.) of a plant that provides it with a competitive advantage in terms of

light interception or nutrient acquisition over less morphologically dominant plants (Saenger personal communication). This analysis incorporated the data on above-ground mangrove litterfall, height and tree density collected in 2002-2003 using the CARICOMP methodology (see Chapter 4). For the plant strategy analysis, monthly above-ground leaf litter from October 2002 –to February 2003 (total 5 months) was used because leaf litter from this data window was sorted at the species level. Based on Saenger's methods (1985), the maximum monthly above-ground litterfall measured over a period of five months at three sites was used as a measure of potential maximum dry matter production. To express the morphological dominance of each species, a dominance index was computed by multiplying maximum tree height and mean density of each species in the area. The dominance index was calculated from the permanent plot data described in Chapter 4 and this along with potential maximum dry matter production (max monthly above-ground litter) from those plots was used in the triangular ordination. The dominance index was also computed for the four mangrove species from the temporary circular plot data in order to compare with permanent plots; however, leaf litter was not available from these temporary plots.

5.3 Results

The vegetated area of the eight fringing cays ranged from 0.2 to 3.0 ha. Based on the location of all the plots, elevation ranged from -81 cm below spring high tide to 91 cm above spring high tide. Average height for all tree species was 3.6 m and average stem diameter was 4.7 cm. A maximum height of 11.5 m and maximum stem diameter of 62.4 cm was also

recorded. The northern group of cays had a greater vegetated area compared to the central and southern cays (Table 5.1).

Table 5.1. Plot summary of eight fringing cays (all tree species) on eastern Turneffe. Cays arranged from a north to south direction.

Cay	Veg Area	n	Min Elev	Max Elev	Avg Sal	Avg Ht	Avg Dia	Avg Den	Avg BA
Cockroach Cay-20 ⁿ	1.6	24	-41	63	36.2	3.4	5.9	5370	18.3
Cockroach Cay-22 ⁿ	1.8	20	-38	90	36.5	2.7	6.2	12558	21.4
Cockroach Cay-23 ⁿ	3.0	23	-49	76	37.2	3.7	5.0	14991	23.2
Soldier Cay ^c	0.9	27	-30	70	34.3	4.3	6.9	3789	20.0
Big Calabash Cay ^c	0.9	19	-81	27	35.3	3.9	4.6	6252	15.4
Dead Man Cay-5 ^s	0.4	19	-34	23	35.0	3.7	4.4	7532	16.0
Dead Man Cay-4 ^s	0.5	16	-47	64	32.3	4.5	8.5	4030	27.3
Dead Man Cay-2 ^s	0.2	12	-61	91	34.7	3.2	5.4	2943	13.0

Note: Veg Area = cay vegetation area (ha), n = number of plots per cay, Min Elev = minimum plot centre elevation relative to spring high tide (cm), Max Elev = maximum plot centre elevation relative to spring high tide (cm), Avg Sal = average salinity at plot center (ppt.), Avg Ht = average height (m), Avg Dia = average stem diameter (cm), Avg Den = average tree density (number of stems per ha), Avg BA = average basal (m²/ha). (ⁿ = northern group, ^c = central group, ^s = southern group).

The eastern fringing cays on Turneffe occurred within a zone of shallow water in the back-reef area (refer to Chapter 3, Fig. 3.3 for cay-layout). The substrate elevation profiles from the reef to leeward showed the narrowness of the ridge zone and the generally low substrate elevation of the eight surveyed cays (Fig. 5.4).

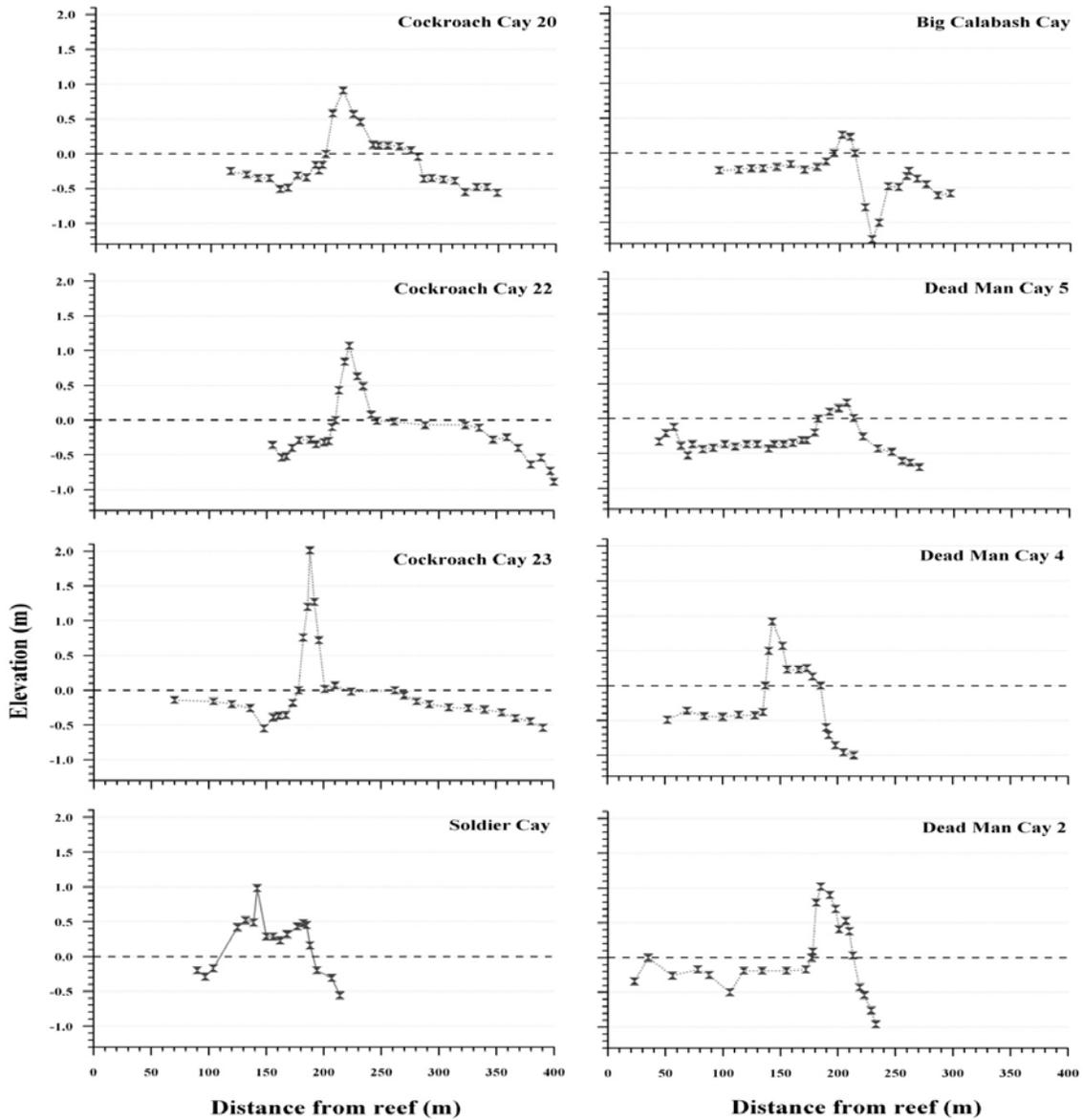


Figure 5.4. Group of eight cays located on the eastern side of Turneffe. Cay and substrate elevation relative to spring high tide (vertical axis) vs. distance from the edge of the reef crest. Profile based on mid-transect bisecting the cay from reef to leeward showing highest points of cay substrate.

Distance of the ridge zone from the reef varied from 50 and 250 m, with the greatest amount of ridge zone area occurring between 100 - 150 m (Fig. 5.5). At the northern cays

(Cockroach Cay-20, -22 and -23), there was a gradual increase in water depth in the lee of

the cay. At the central (Soldier Cay and Big calabash Cay) and southern group of cays (Dead Man Cays-2, -4 and -5) there was a more abrupt increase in water depth on the leeward side of the ridge zone. Six of the eight cays had a well-developed ridge zone (Cockroach Cay-20, -22 and -23, Soldier Cay, Dead Man Cay-2 and -4).

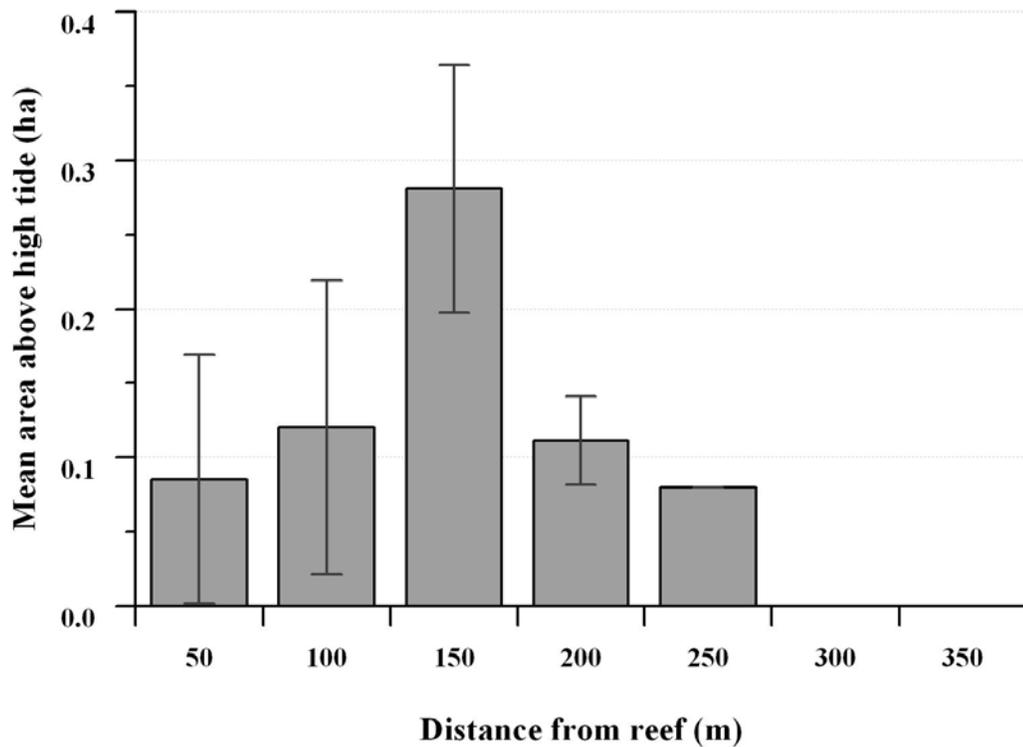


Figure 5.5. Mean substrate area above the spring high tide for eight cays (Cockroach Cay-20, -22 and -23, Soldier Cay, Big Calabash Cay, Dead Man Cay-2, -4 and -5) located on the eastern side of Turneffe vs. distance from the edge of the reef crest with SE bars.

Rhizophora mangle dominated the vegetation on these cays (Fig. 5.6); however, the mangroves *L. racemosa*, *A. germinans*, and *C. erectus* were also present. Littoral forest and coconut (*C. nucifera*) were also present on all cays. The relative density of *R. mangle* was

higher on the northern cays than the southern cays, while the opposite trend occurred with *C. nucifera*.

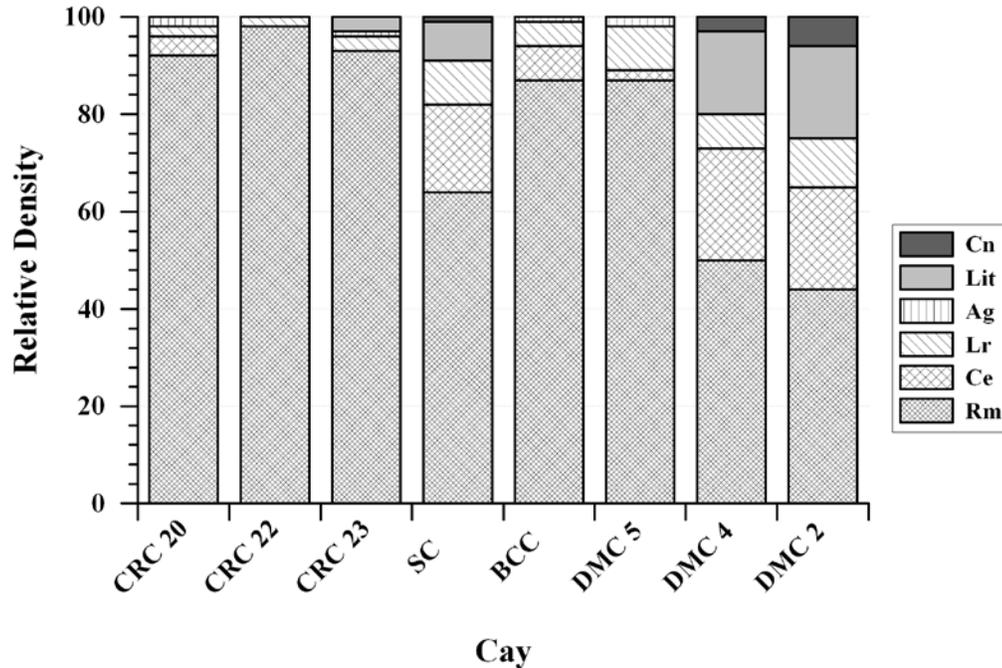


Figure 5.6. Relative density (stems/ha) of *C. nucifera* (Cn), Littoral (Lit), *A. germinans*, (Ag), *L. racemosa* (Lr), *C. erectus* (Ce), and *R. mangle* (Rm) for eight cays (Cockroach Cays (CRC-20, -22, and -23), Soldier Cay (SC), Big Calabash Cay (BCC), Dead Man Cays (DMC-5, -4 and -2) on eastern Turneffe, cays ordered from north to south.

An independent-samples t-test was conducted to compare plot average tree height and stem diameter (all tree species pooled) above and below spring high tide. The test indicated that average tree height was significantly higher for vegetation above ($mean = 4.75, SD = 1.71$) than below the spring high tide ($mean = 2.95, SD = 1.88$), $t(169) = 5.74, p < 0.0001$. For plot average stem diameter, the test indicated that square root transformed stem diameter was significantly higher for vegetation above ($mean = 2.83, SD = 0.81$) than below the spring high tide ($mean = 1.91, SD = 0.78$), $t(169) = 6.83, p < 0.0001$.

Of the three geomorphic zones (leeward, ridge and reefward), the ridge zone had the highest elevations above the spring high tide. The ridge zone formed the sedimentary backbone of the fringing cays. Stem density (all species) was higher on the leeward zone than ridge and reefward zones (Fig. 5.7). However, the basal area of trees (all species) was significantly higher in the ridge zone compared to the leeward and reefward zones reflecting the larger size of trees in this zone (Fig. 5.8).

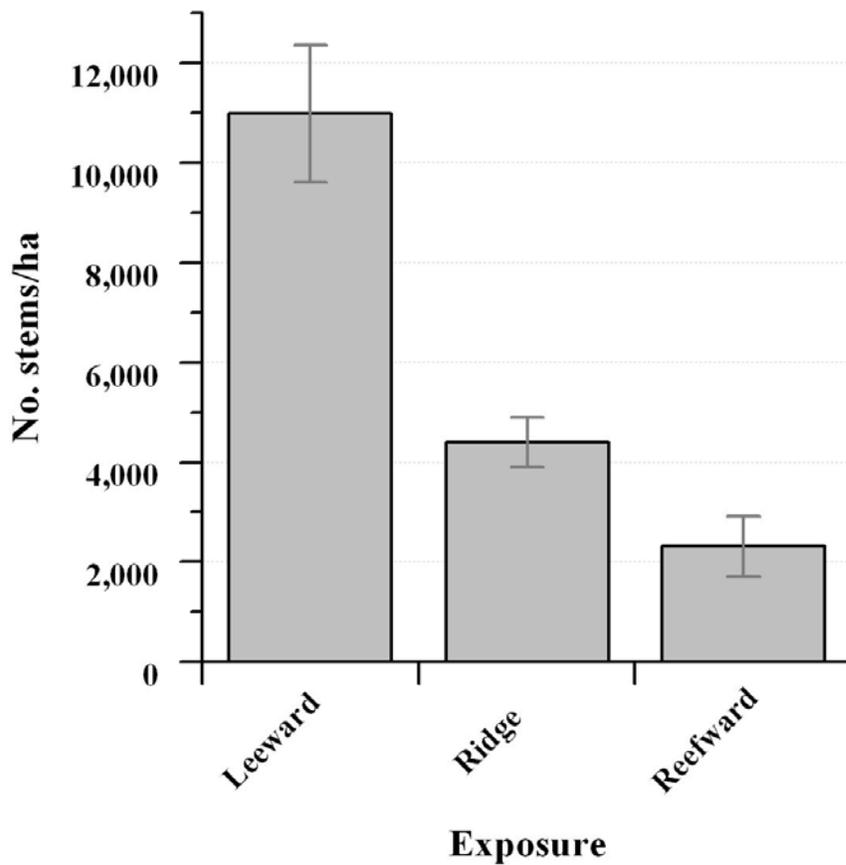


Figure 5.7. Average number of tree stems/ha (all species) vs. exposure from reef, relative to spring high tide with SE bars. Ridge represents the group of plots that were located on substrate above the spring high tide.

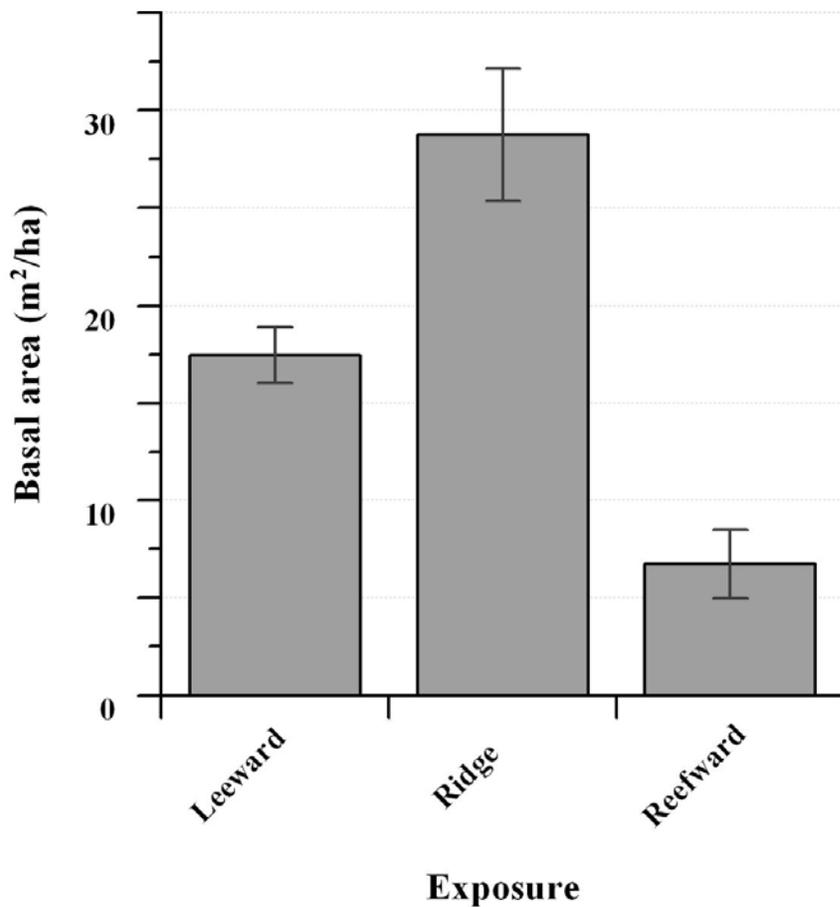


Figure 5.8. Average tree basal area (all species) vs. exposure from reef, relative to spring high tide with SE bars. Ridge represents the group of plots that were located on substrate above the spring high tide.

The ridge zone supported the greatest number of tree species where the four species of mangroves were found in addition to *C. nucifera* and the group of non-mangrove species under the littoral forest vegetation type. Average basal area of *R. mangle* was higher on the leeward zone with respect to the reef crest than the other mangrove and non-mangrove species (Fig. 5.9) while *C. erectus* and *C. nucifera* had the highest average basal area on the ridge zone.

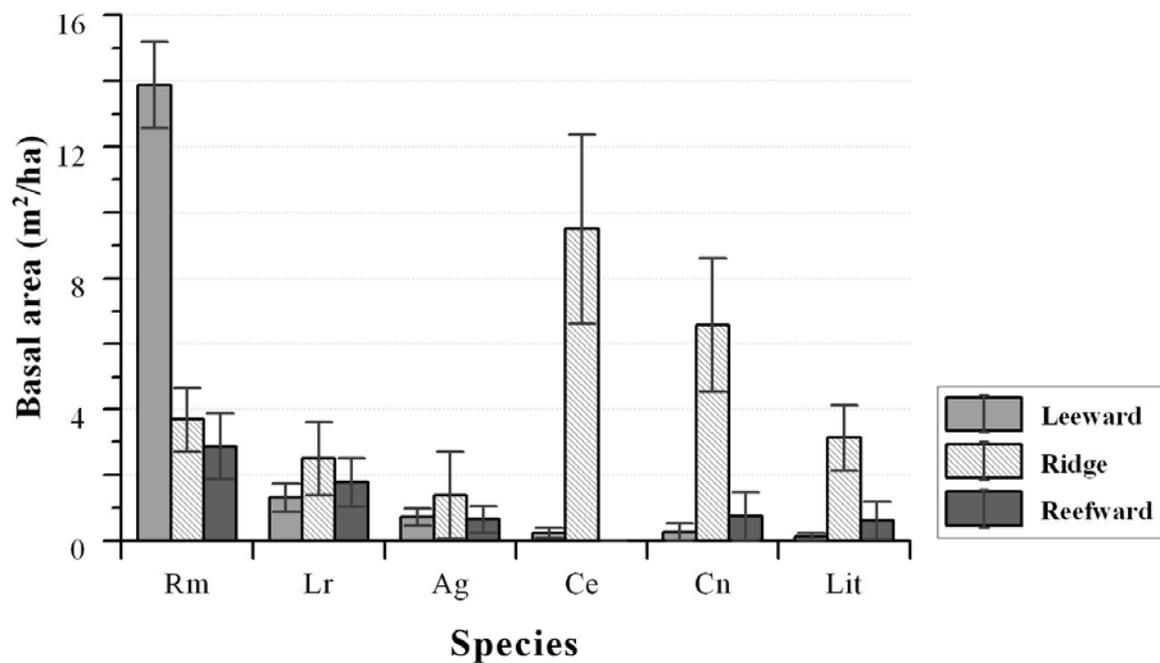


Figure 5.9. Average basal area by vegetation type and exposure from reef, relative to spring high tide with SE bars. Ridge represents the group of plots that were located on substrate above the spring high tide. (Rm = *R. mangle*, Lr = *L. racemosa*, Ag = *A. germinans*, Ce = *C. erectus*, Cn = *C. nucifera*, Lit = littoral).

Average stem diameter and height for all species increased away from the reef crest and towards higher substrate elevation on the cays (Fig. 5.10). There was a gradual decrease of both on the leeward side of the cay with increasing water depth.

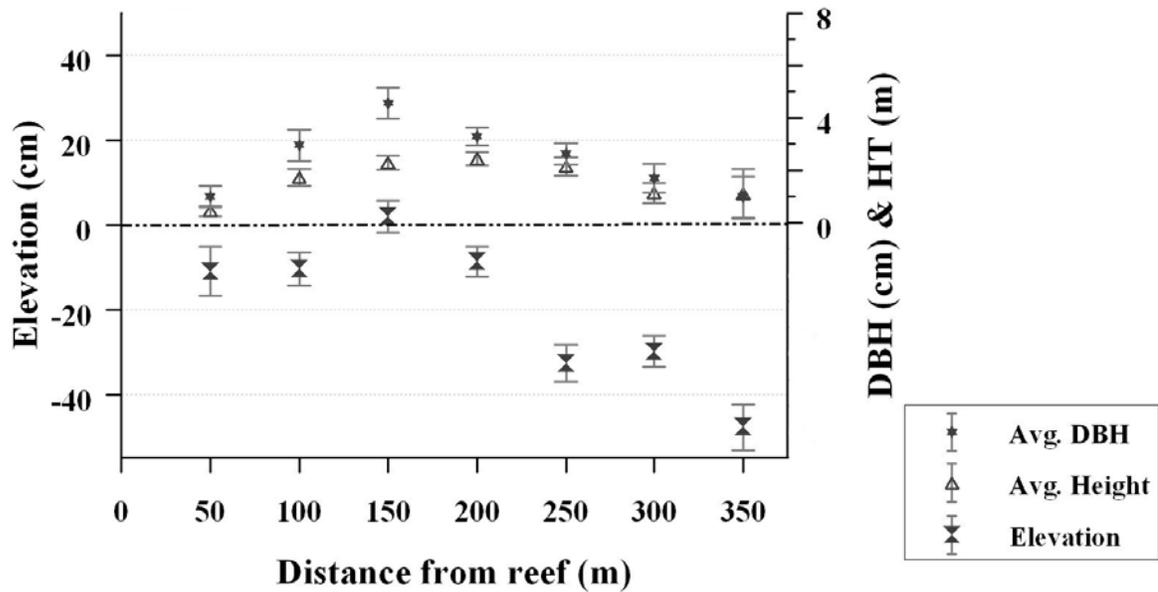


Figure 5.10. Average stem diameter (DBH) and height for all tree species and substrate elevation with SE bars vs. distance from the edge of reef crest. Line across the zero value (y-axis) represents the spring high tide.

For *R. mangle* trees, the average height, and stem diameter increased to the lee of the ridge zone (Appendix O). Basal areas of *R. mangle* increased with distance from the reef and peaked to the lee of the ridge zone (Fig. 5.11). However, a decrease in basal area was observed beyond the 300 m distance. For *R. mangle* seedling density, there was more variability along transects but densities were typically higher to the lee of the ridge zone (Fig. 5.12).

The leeward zone of the northern group of cays with respect to the reef crest (Cockroach Cay-20, -22, and -23) was affected by Hurricane Keith in 2000. The following are the results from the independent-samples t-test for plot average height and stem diameter for all mangrove tree species of the leeward zone northern group of cays with combined leeward

zone of central and southern group of cays (Soldier Cay, Big Calabash Cay, Dead Man Cays-2, -4 and -5). The test indicated that average height was significantly higher for the southern group ($mean = 4.27, SD = 1.51$) than northern group ($mean = 3.25, SD = 1.70$), $t(71) = 2.61$, $p = 0.0112$. For plot average stem diameter, the test indicated non-significance; results for the southern group ($mean = 5.00, SD = 1.70$) and northern group ($mean = 4.38, SD = 2.34$), $t(71) = 1.22$, $p = 0.2272$.

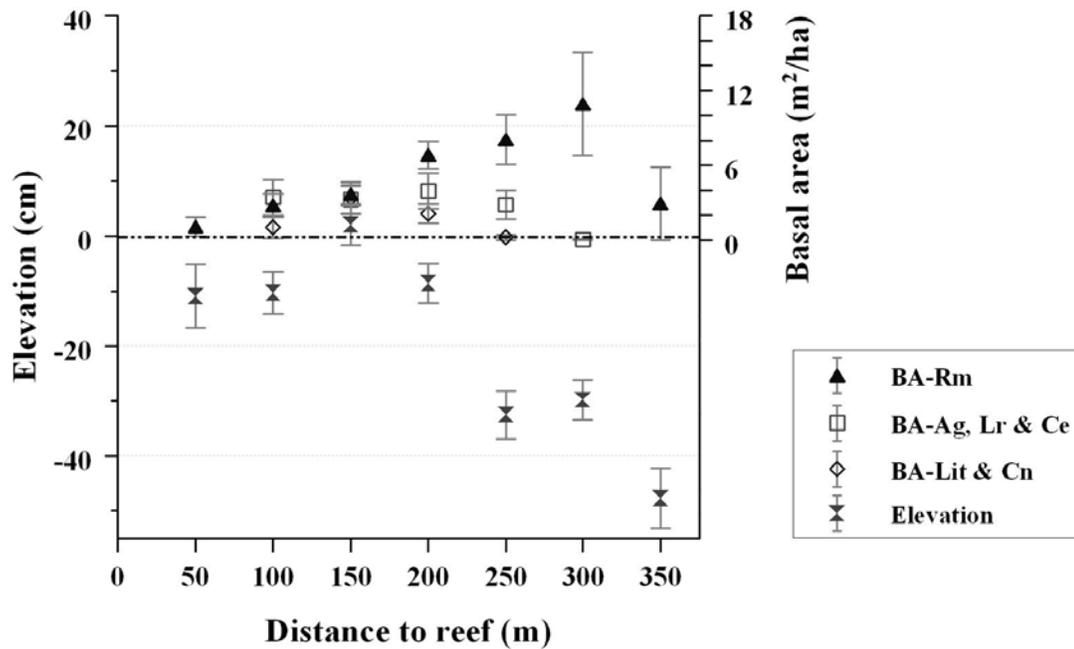


Figure 5.11. Relationship between substrate elevation and basal area (BA) vs. distance from the edge of reef crest with SE bars. Average basal area for *R. mangle* (Rm), combined basal area for *A. germinans* (Ag), *L. racemosa* (Lr), *C. erectus* (Ce), and combined basal area of Littoral forest (Lit) with *C. nucifera* (Cn). Dashed line across the zero value (y-axis) represents the spring high tide.

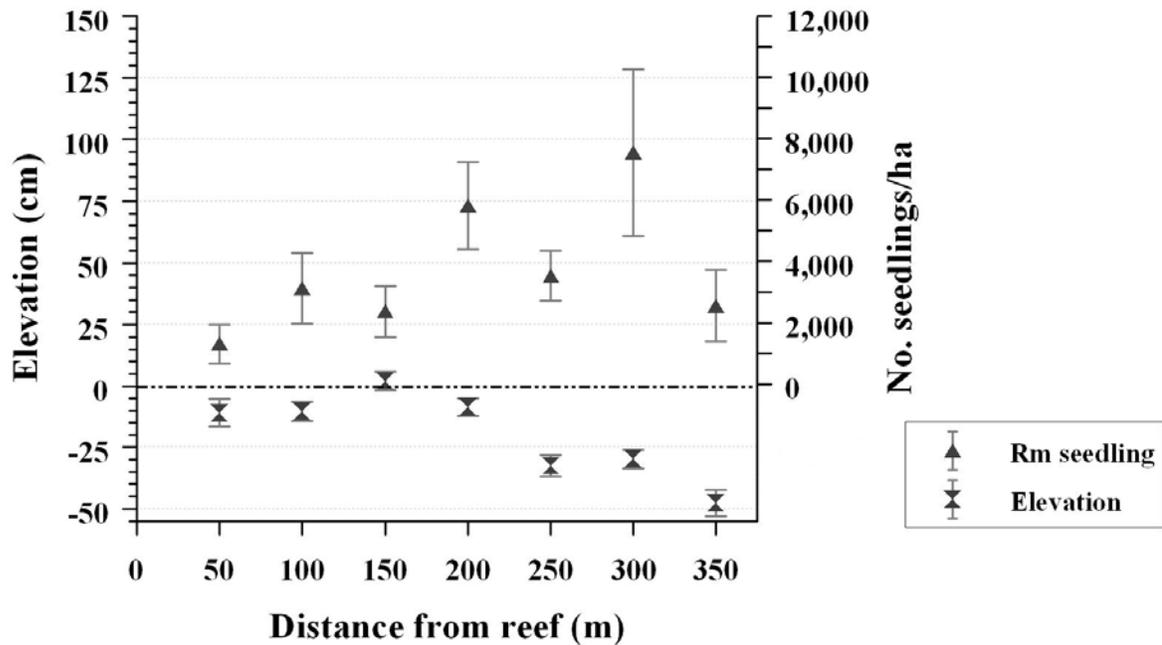


Figure 5.12. Number of live seedlings per ha of *R. mangle* (Rm seedling) and substrate elevation with SE bars vs. distance from the edge of reef crest. Line across the zero value (y-axis) represents the spring high tide.

Rhizophora mangle seedlings occurred at a wider range in elevations below and above the spring high tide than the other mangrove and non-mangrove species (Fig. 5.13). Seedlings of *A. germinans* showed the most restricted elevation range. Some of the vegetation typical of littoral forests was also found establishing very close to the spring high tide as part of the beach strata. In many cases, roots of these seedlings were being undermined by erosion. For the most part *C. nucifera* seedlings were found only on the ridge zone. Salinity decreased with distance from the reef (Fig. 5.14) and was lowest at the ridge zone. Leeward of the ridge zone, salinity increased to values closer to those near the reef.

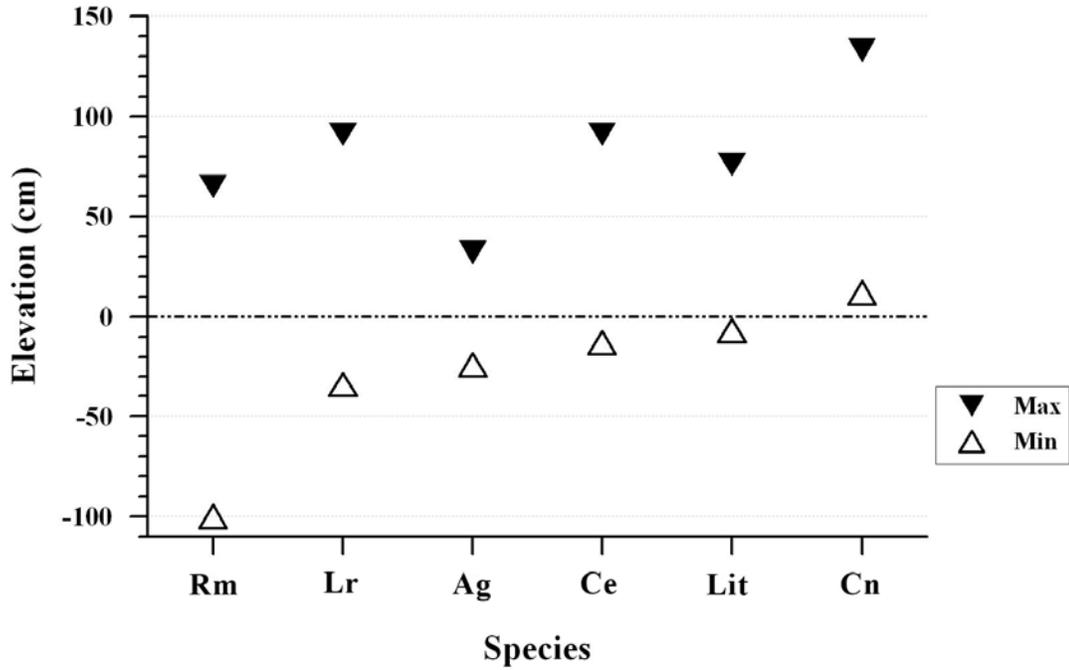


Figure 5.13. Extreme maximum and minimum substrate elevation where seedlings were found. Line across the zero value (y-axis) represents the spring high tide. Rm = *R. mangle*, Lr = *L. racemosa*, Ag = *A. germinans*, Ce = *C. erectus*, Lit = Littoral forest, Cn = *C. nucifera*.

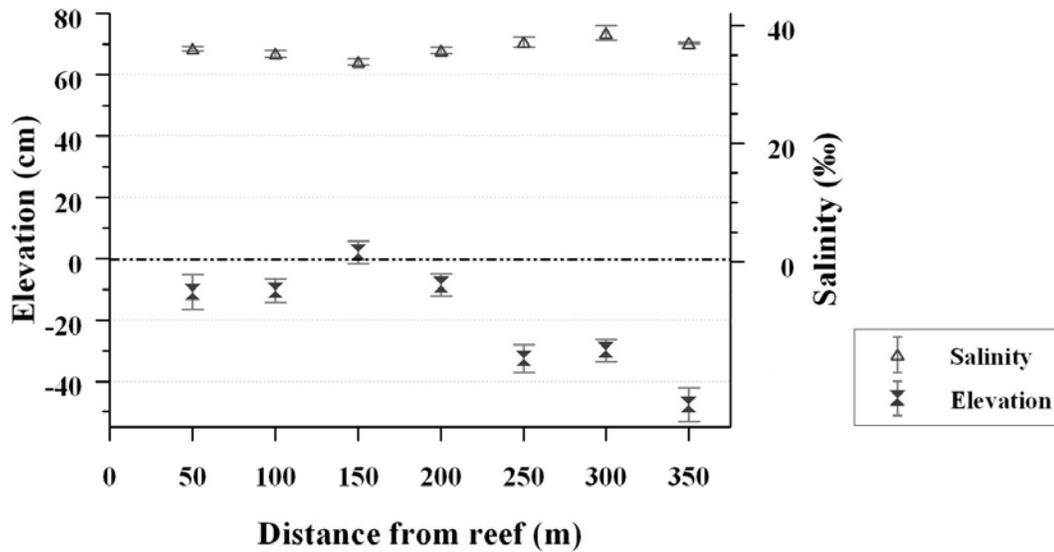


Figure 5.14. Substrate elevation and salinity vs. distance from the edge of the reef crest with SE bars. Dashed line across the zero value (y-axis) represents the spring high tide.

Sediment cores, taken at the center of the plots, along transects, showed a gradient of particle size distribution and origin (coral vs. peat) with distance from the reef (Fig. 5.15). In the reefward zone, coral rubble was the dominant substrate type, while sand increased with distance from the edge of the reef crest. Peat increased from the ridge zone towards the leeward zone. Peat decreased past the 300 m distance as substrate elevations dropped. The elevation of maximum peat accumulation was at 30 to 40 cm below spring high tide, and this was consistent with the elevation at which *R. mangle* basal area was highest. The accumulation of peat in the leeward zone was punctuated by episodic sand burial as was evident from 30 cm substrate cores (Fig. 5.16).

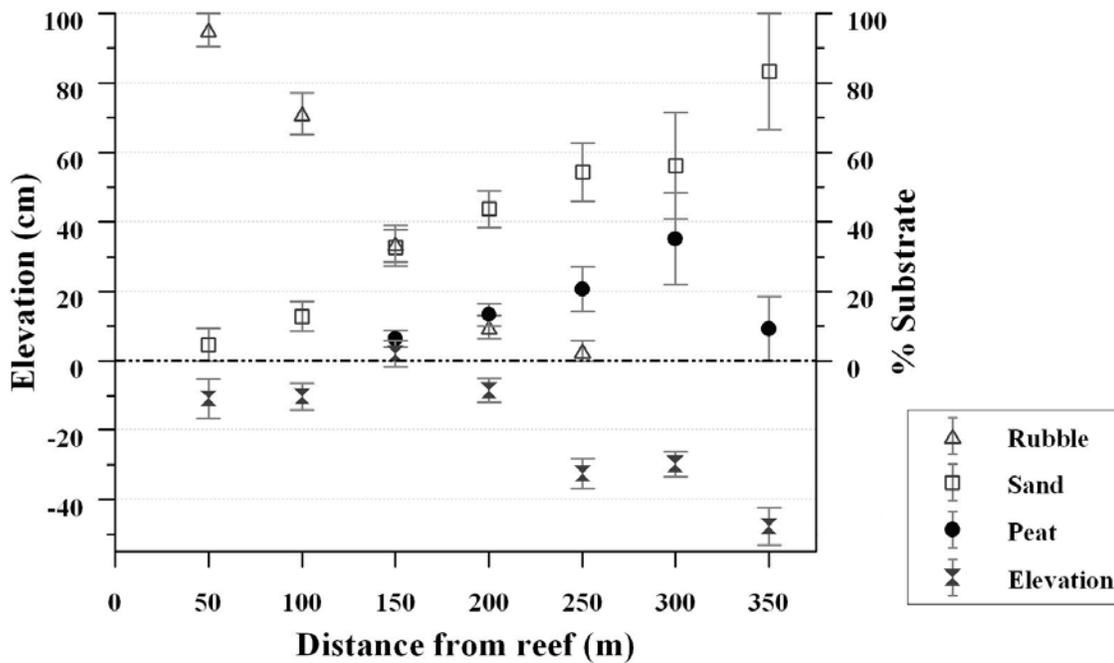


Figure 5.15. Mean percent substrate composition and elevation vs. distance from the edge of reef crest with SE bars. Dashed line across the zero value (y-axis) represents the spring high tide.



Figure 5.16. Substrate cores from Cockroach Cay-23 showing accumulation of mangrove peat on sand, and buried peat layers. Core-A taken 187 m from the reef crest and Core-B taken 284 m from the reef crest.

The three distinct geomorphic habitat zones had different levels of wave exposure and salinity (Table 5.2). The leeward zone with respect to the reef crest experienced stress from high salinity and tidal inundation and was sheltered from the disturbance of wave energy. The ridge zone was exposed to low stress from salinity and tidal inundation in conjunction to low disturbance from wave energy. The reefward zone experienced stress from high salinity and tidal inundation in conjunction with disturbance from wave energy due to its exposed location.

Table 5.2. Cay geomorphic habitat zones and levels of stress from soil salinity and tidal inundation and of disturbance from wave energy.

		Zones		
		Leeward	Ridge	Reefward
Stress	Soil salinity	High	Low	High
	Tidal inundation	High	Low	High
Disturbance	Wave energy	Low	Low	High

Average plot-level basal area and plot-level maximum tree height were negatively correlated with wave energy, frequency of tidal inundation and salinity, and were positively correlated with elevation (Table 5.3). These vegetation parameters were uncorrelated with distance from the reef or large leeward islands. A number of the site parameters were correlated with each other. Salinity increased with tidal inundation and decreased with elevation.

Table 5.3. Pearson correlation among dependent and potential predictor variables, correlation coefficients involving basal area and maximum tree height (all species); r values are given above p-values; significant correlations are in bold font.

Variable	Basal Area	Max Height	Wave	Tidal	Salinity	Elevation	Reef
Wave	-0.3355 <.0001	-0.3372 <.0001					
Tidal	-0.3612 <.0001	-0.3351 <.0001	0.3179 <.0001				
Salinity	-0.3591 <.0001	-0.3862 <.0001	0.0391 0.6116	0.6413 <.0001			
Elevation	0.2996 <.0001	0.3576 <.0001	-0.0381 0.6205	-0.6365 <.0001	-0.5378 <.0001		
Reef	0.0089 0.9083	-0.0076 0.9210	-0.2572 0.0007	0.3156 <.0001	0.2776 0.0002	-0.4063 <.0001	
Island	0.0260 0.7355	-0.0788 0.3058	-0.0564 0.4639	0.1047 0.1731	0.2299 0.0025	0.0958 0.2124	-0.1460 0.0568

Note: Basal Area = Basal area (m²/ha) for all tree species, Max Height = maximum height per plot for all species, Wave = high (1) or low (0) wave energy, Tidal = high (1) or low (0) frequency from tidal inundation, Salinity = measured soil salinity in plot, Elevation = Plot elevation (cm), Reef = Plot distance from reef (m), Island = Plot distance from large islands (m); Correlation is significant at p < 0.05; n = 171.

The model for maximum height of all tree species included elevation (positive effect), wave energy (negative effect), and salinity (negative effect). However, this model explained only 28% of the variation in tree height (Table 5.4). Plot basal area of all tree species was predicted by the same variables, but the regression fit was even weaker (Table 5.5).

Table 5.4. Multiple linear regressions for maximum height for all tree species.

Variable	Parameter Estimate	Standard Error of Parameter	F Value	p-value	Root MSE	R²	n
Intercept	10.0467	1.3175	58.15	< 0.0001			
Wave	-2.3242	0.4778	23.66	< 0.0001			
Salinity	-0.1275	0.0375	11.56	0.0008			
Elevation	0.0184	0.0071	6.82	0.0098			
Tidal	ns	ns	ns	0.1098			
Island	ns	ns	ns	0.2759			
Reef	ns	ns	ns	0.5213			
Model					2.5450	0.2824	171

Note: Maximum height in m. Wave = high or low wave energy, Salinity = plot soil salinity, Elevation = plot elevation (cm), Tidal = high or low frequency from tidal inundation, Island = plot distance to the edge of the large islands (m), Reef = plot distance to the edge of the reef crest (m). ns = non-significant, $\alpha = 0.05$.

Table 5.5. Multiple linear regressions for the square root basal area for all tree species.

Variable	Parameter Estimate	Standard Error of Parameter	F Value	p-value	Root MSE	I²	n
Intercept	6.7303	1.0416	41.75	< 0.0001			
Wave	-2.1872	0.3778	33.52	< 0.0001			
Salinity	-0.0781	0.0296	6.95	0.0092			
Elevation	0.0142	0.0056	6.48	0.0118			
Reef	ns	ns	ns	0.1617			
Island	ns	ns	ns	0.3976			
Tidal	ns	ns	ns	0.6190			
Model	ns	ns	ns		16.3389	0.1804	171

Note: Basal area in m²/ha. Wave = high or low wave energy, Salinity = plot soil salinity, Elevation = plot elevation (cm), Reef = plot distance to the edge of the reef crest (m), Island = plot distance to the edge of the large islands (m), Tidal = high or low frequency from tidal inundation. I² = correlation index squared for square root of dependent variable (basal area). ns = non-significant, $\alpha = 0.05$.

Soil salinity, plot elevation, and plot distance from the edge of the reef crest contributed positively to the presence of mangrove seedlings of any species, while wave energy had a

negative effect (Table 5.6). Elevation was non-significant in the model for *R. mangle* seedling presence (Table 5.7).

Table 5.6. Logistic regression for the presence of one or more seedlings for four mangrove species (*R. mangle*, *A. germinans*, *L. racemosa*, and *C. erectus*).

Variable	Parameter Estimate	Standard Error of Parameter	Wald X²	Pr > X²
Intercept	-8.2211	1.6282	25.4939	< 0.0001
Wave	-0.9681	0.3193	9.1937	0.0024
Salinity	0.2365	0.0471	25.2308	< 0.0001
Elevation	0.0134	0.0056	5.6928	0.017
Reef	0.0070	0.0026	7.0643	0.0079
Tidal	ns	ns	ns	0.3916
Island	ns	ns	ns	0.2676

Note: Wave = high or low wave energy, Salinity = plot soil salinity, Elevation = plot elevation (cm), Reef = plot distance to the edge of the reef crest (m), Tidal = high or low frequency from tidal inundation, Island = plot distance to the edge of the large islands (m). Hosmer-Lemeshow goodness of fit for the model, chi-square = 4.88, 8 df (p=0.77). ns = non-significant, $\alpha = 0.05$, n = 284.

Table 5.7. Logistic regression for the presence of one or more seedlings of *R. mangle*.

Variable	Parameter Estimate	Standard Error of Parameter	Wald X²	Pr > X²
Intercept	-5.0970	1.1289	20.3863	< 0.0001
Wave	-0.6387	0.3006	4.5136	0.0336
Salinity	0.1380	0.0323	18.2634	< 0.0001
Reef	0.0062	0.0025	6.3213	0.0119
Island	ns	ns	ns	0.3372
Elevation	ns	ns	ns	0.2217
Tidal	ns	ns	ns	0.1377

Note: Wave = high or low wave energy, Salinity = plot soil salinity, Reef = plot distance to the edge of the reef crest (m), Island = plot distance to the edge of the large islands (m), Elevation = plot elevation (cm), Tidal = high or low frequency from tidal inundation. Hosmer-Lemeshow goodness of fit for the model, chi-square = 14.39, 8 df (p=0.07). ns = non-significant, $\alpha = 0.05$, n = 284.

In both permanent and temporary plots, *R. mangle* dominated followed by *L. racemosa*, *C. erectus* and *A. germinans*, respectively (Table 5.8). The results from Table 5.8 were superimposed on the triangular ordination graph from Saenger (2002; Fig. 5.17). The full and abbreviated names of the mangrove species from Proserpine, Australian and from Turneffe, Belize, in Figure 5.17 are listed in Appendix P. The mangrove flora at Turneffe was considerably less diverse than Australia. However, species that belong to the same family and share some similar characteristics occurred within the same range in the ordination graph. The Turneffe species were located within the range of competition, stress and disturbance axis of the Australian species. Based on the ordination, *Rhizophora mangle* and *Laguncularia racemosa* were somewhat close to their Australian counterparts (from the same plant families), *Rhizophora stylosa* and *Lumnitzera racemosa*, respectively. *Rhizophora stylosa* had the highest dominance index (3120) in Australia (Saenger 1985) and *R. mangle* had the highest dominance index (7840) in the permanent plots at Turneffe.

Table 5.8. Data from permanent CARICOMP plots, collected in 2002, used for ordination of four mangrove species found on fringing mangrove at three cays Turneffe, Belize (Soldier Cay, Big Calabash Cay and Dead Man Cay-5). Comparative data from circular plots show similar trend on dominance index of four mangrove species found on eight fringing cays of Turneffe, Belize (Cockroach Cay-20, -22, and -23, Soldier Cay, Big Calabash Cay, Dead Man Cay-3, -4, and -5).

Permanent Plots (2002)				
Species	Maximum leaf litter (g/m ² /mo)	Maximum height (m)	Stem Density (stems/900 m ²)	Dominance Index
<i>R. mangle</i>	32	10	784	7840
<i>L. racemosa</i>	41	9	52	468
<i>C. erectus</i>	8	7.4	13	96
<i>A. germinans</i>	8	8.6	6	52
Circular Plots (2008)				
<i>R. mangle</i>	na	9.6	470	4509
<i>L. racemosa</i>	na	11.5	27	314
<i>C. erectus</i>	na	10	27	273
<i>A. germinans</i>	na	11	8	84

Note: Stem density for permanent plots = number of trees per 900 m². Original density for circular plots based on number of trees per 10775 m², but for consistency is expressed here as number of trees per 900 m². na = Leaf litter not available for circular plots. Dominance index = maximum height x stem density.

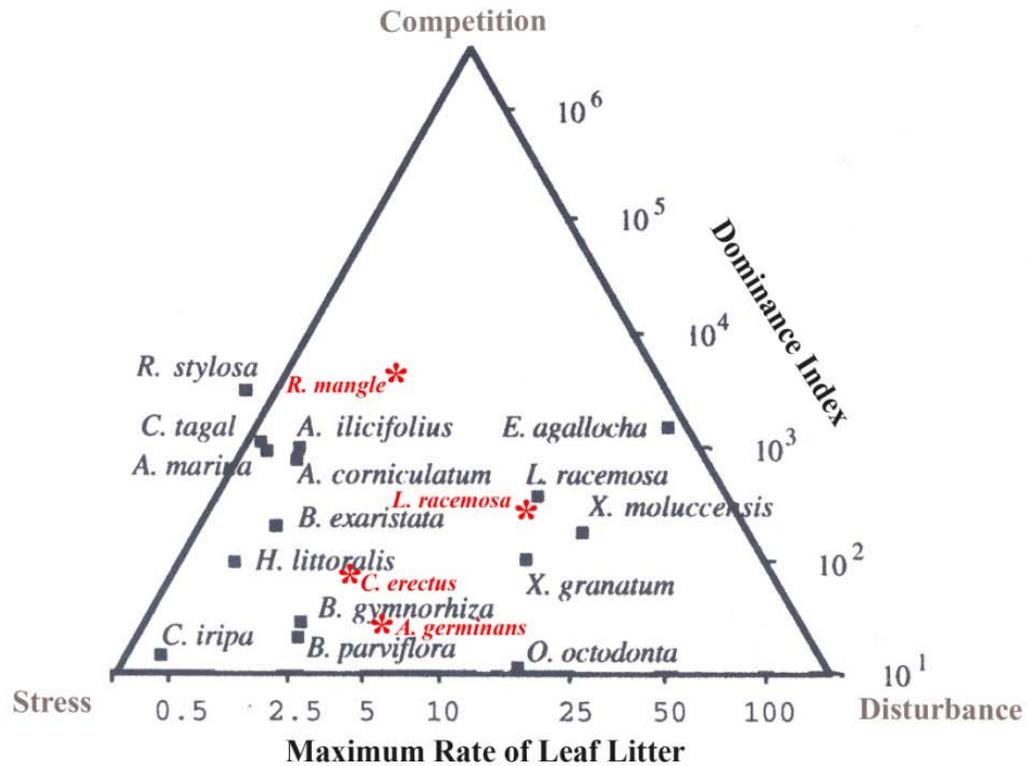


Figure 5.17. Triangular ordination of mangrove species. Distribution of species (squared symbol) were from Proserpine, Australia (data from Saenger 1985); species with asterisk were from Turneffe, Belize. Dominance index derived from the product of maximum height and tree density. Maximum rate of litterfall (Proserpine) derived from *in situ* monthly leaf counts, while maximum rate of litterfall (Turneffe) derived from oven dried litterfall ($\text{g}/\text{m}^2/\text{mo}$). The full and abbreviated names of the mangrove species from Proserpine, Australian and from Turneffe, Belize, used in this graphic are listed in Appendix P. (Redrawn with permission Saenger 2002).

5.1 Discussion

The fringing cays of Turneffe exhibited typical characteristics of mangrove-dominated ecosystems. Mangroves are naturally stressed ecosystems in which high soil salinities increase the cost of obtaining freshwater, tidal inundations remove stored chemical energy in

litter and dissolved organics, disturbance from storm tides and waves cause episodic siltation or erosion, and periodic hurricane or storm winds damage plants and erode sediments (Lugo 1980). According to Lugo (1980), strong environmental gradients act as selective forces determining the distribution and density of species. Depending on species tolerance and the nature of the environmental gradients, this can lead to the development of distinct vegetation zones. Based on substrate condition, exposure to waves and elevation, I identified three geomorphic habitat zones: leeward, ridge and reefward. Vegetation found on the fringing cays has to contend with stress factors (e.g., salinity and tidal inundation) and disturbance (e.g., wave energy). Since these factors differ among the three geomorphic zones (ridge, leeward and reefward) on the Turneffe cays, species dominance in these zones provides insights into the adaptive strategies of local species. Grime (1977) contends that when combinations of high and low stress with high and low disturbance are examined, only three are viable as plant habitats since high disturbance and high stress prevent recovery or reestablishment of vegetation. The combination of low stress with low disturbance produces an environment that favors more competitive plants. In contrast, high stress with low disturbance favors stress-tolerant plants, while low stress with high disturbance favors disturbance-tolerant plants (Grime 1977). These three strategies are at the extremes, and many plants have adapted to habitats with intermediate intensities of stress and disturbance. In view of Grime's plant strategies, I interpreted species strategies at Turneffe as evidenced by their ability to colonize certain zones. Further insights were gained via Saenger's (2002) triangular ordination approach and comparing the Turneffe mangrove species with his Australian mangrove species. For example, *R. mangle* came out as "competitor-stress tolerator" in the ordination.

5.1.1 Ridge zone

The ridge zone, which also included the coral rubble rampart, consisted of cay substrate and vegetation above the spring high tide. The ridge zone was composed of a mixture of substrate types, but for those cays with a well-formed ridge, the dominant substrate was a mixture of sand and coarse coral rubble. Wave energy, particularly the intensified wave energy during storms, was clearly the driving force in the formation and maintenance of the ridge zone. Catastrophic storms are the only mechanism capable of transporting large amounts of coarse sediment from reefs on-to reef flats (Bayliss-Smith 1988). Larcombe and Carter (2004) explain that cyclonic activity on tropical reef shelves contributed sediment by breaking reef structures during cyclone passage across the outer shelf reef tract, and moved carbonate gravel and sand to the back-reef sediment aprons. For the Ontong Java Atoll, Bayliss-Smith (1988) reported a low sediment supply to islands located outside the main zone of hurricane damage to reefs. Within a translating hurricane the wave field is characterized by a swell ahead of the storm, radiating out from the intense wind region to the right of the storm centre (Young 2003). This is caused by the significant asymmetry from higher winds and extended translating fetch to the right of the storm centre (Young 2003). It is expected that the storm surge propagating ahead of the storm is responsible for dislodging and moving material from the reef to the back-reef sediment apron. It is likely that the shingle ramparts and rubble zones at Turneffe were initiated in an episodic way during hurricanes, and were then modified by subsequent routine wave action. The ridge zone for the group of fringing cays at Turneffe spanned from 50 to 250 m from the edge of the reef crest with the greatest area occurring between 100 to 150 m. This distance was consistent with Macintyre et al.'s (1987)

observation that along the Tobacco Reef apron in Belize, very little coarse debris was transported more than 150 m from the reef crest.

While storms and routine wave energy affect the morphologic features present on reef shelves, vegetation can also influence the evolution of these features (e.g., Stutz and Pilkey 2011). The role, if any, that vegetation plays in the initial formation of the ridge zone was not clear from this study. But, vegetation does appear to play a role in the subsequent buildup and consolidation process. In some plots, the trunks of well-established trees were buried up to a meter from the current substrate surface. On Soldier Cay the prop roots of *R. mangle* were buried and survived the buildup of rubble and sand from Hurricane Ivan in 2004. However, as discussed in Chapter 3, during high energy storms (e.g., categories 4 and 5 hurricanes), cay vegetation is severely damaged and in some cases, completely removed along with severe erosion of cay substrate. This was described by Stoddart (1963) and is evident from his aerial photographs of the eastern cays before and after Hurricane Hattie. On the fringing cays there was evidence of a self-reinforcing process of substrate accumulation and vegetation establishment with the formation and stabilization of the ridge zone and protected leeward zone.

The effects of inundation on woody plants vary from catastrophic to beneficial, depending on the plant species and genotype, the intensity, timing, and duration of flooding, and site conditions (Kozlowski 1982; Kozlowski and Pallardy 1997). Tidal inundation usually decreases plant growth as it reduces oxygen concentrations at the root surface, inhibiting water uptake and other primary physiological functions (Gibbs and Greenway 2003). In

coastal ecosystems, inundation is compounded by salinity and the mechanical effects of waves and currents. In mangrove forest and salt marshes, species distribution is closely related to variations in physiography, which also determines patterns of tidal inundation, salinity of the soil, and water table fluctuations (Clarke and Hannon 1969). The substrate above spring high tide (the ridge zone) was dominated by littoral and coral forest at Turneffe. Both *C. erectus* and *C. nucifera* contributed a significant part of the basal area on the ridge zone. Although the groups of plant species on the ridge zone have some tolerance for salt water, they are adapted to colonize zones above high tide. At these higher elevations, the influence of tidal inundation and its effects on salinity and root zone oxygenation are minimized, and there is no exposure to wave energy except during storms. Average height, stem diameter and average plot basal area were at their highest for all tree species in this zone, which suggests that interspecies competition becomes more important in this zone. Based on the regression model for maximum tree height, both exposure to wave energy and salinity had negative effects whilst substrate elevation was positive.

Combined tidal inundation and salinity decreases growth and survival of plants more than either stress alone, and the rate of diameter growth is reduced by prolonged inundation in most flood-intolerant species (Kozlowski 1997). Close to brackish water conditions were observed on various plots located on the ridge zone (according to Meadows et al. 2004 brackish water is in the range of 9 to 18 parts per thousand (ppt.)). It is expected that the non-mangrove species found on the fringing cays must have some tolerance for salt water and especially at the seed and seedling stage (e.g., from overwash and sea spray). Although data on vines, grasses and shrubs was not collected in this study, these plants were widespread on

cays with well-developed ridge zones. On most cays, all four mangrove species were capable of colonizing the ridge zone with *C. erectus* having the highest basal area. Various mangrove propagules and seeds of non-mangrove species were found along the wrack line, which suggests that these drift propagules and seeds are imported and exported between cays and probably from more distant sources. As an example, coconut seed (*C. nucifera*) is buoyant and can colonize coastal areas once these seeds are washed above permanently flooded areas. The concentration of coral and littoral forest along with *C. erectus* on the ridge zone indicated the niche that these species were adapted to colonize. *Cocos nucifera* does not tolerate waterlogging, although it copes with brief incursions of seawater (Foale and Harries 2009). *Cocos nucifera* trees were found at various cay elevations on the ridge zone including areas that are briefly inundated by the tides. Although these trees looked robust, signs of substrate erosion were evident, and the roots were being exposed. However, *C. nucifera* seedlings were found only above the spring high tide. Some of the coconut trees found on these cays may have been reintroduced by people after Hurricane Hattie. However, according to local fishers, the majority of these eastern cays were abandoned after Hurricane Hattie, thus plant recolonization was primarily natural. The composition of plants on the ridge zone suggested that normal tidal transport and sorting was not enough. Higher energy waves from storms washing over cays with well-developed ridge zones would be necessary to explain the presence of species with water transported seed/propagules. Birds could also transport seeds to these parts of the cays (Gillham 1956; Abbott 1980).

The effects of overwash on the fringing cays can be beneficial, stressful or even detrimental, particularly for seedlings that are at a vulnerable life stage. The benefits of overwash are

reworking of the substrate and the chance for viable propagules to be relocated from low to higher elevation zones, which can increase the chances for successful recruitment of littoral species. However, episodic overwash might also stress established littoral plants and benefit mangroves by the infusion of saltwater. I found that *R. mangle* had robust growth on the ridge zone and was competing with other mangrove and non-mangrove species. Robust growth was evident from the extended growth between leaf and leaf scars. Average basal area for *R. mangle* was similar to that of *L. racemosa*, but higher than *A. germinans* and lower than *C. erectus*. Robust growth of *R. mangle* was particularly pronounced in the ridge zone at Soldier Cay where the coral rubble was spread over a larger area and where other factors could also be influencing mangrove growth, such as the deposition of bird guano (Chapter 4). Waves and tides are more likely to overwash the low lying cays that lack a well-developed ridge zone (e.g., Big Calabash Cay and Dead Man Cay-5).

The ridge zone offers protection to the leeward zone from wave energy especially during stormy conditions, buffering waves that make it beyond the reef and trapping sediment and debris (e.g., logs and thrash that wash onto cays). Scars on stems and roots were only present on trees on the ridge zone on the side facing the reef crest. Oceanic debris was found to be concentrated on the ridge zone. Dead marine organisms (e.g., eel, octopus, sand dollars etc.), were found along the wrack line, decomposition of which could be a potential source of nutrients around this zone. Such shore drift of algae and carrion and seabird colonies were two methods described by Polis and Hurd (1996) whereby marine productivity entered the terrestrial food web of islands and coastal areas.

5.1.2 Leeward zone

The leeward zone is to the lee of the ridge zone and included an intertidal and subtidal zone. For some cays, the leeward zone had an abrupt increase in water depth (southern cays) while in others change in depth was gradual (northern cays). The dominant substrate was fine sand, but peat was also present, especially in those areas where mangrove stands were dense. The effect of the ridge zone on incident waves appeared to influence the pattern of leeward *R. mangle* colonization, which has a “teardrop” or tapered shape when viewed from above (Appendix M; CRC-20, -22 and -23). The buffering effect of the ridge zone on wave energy was also apparent from the substrate size distribution and accumulation of peat in the leeward zone.

The accumulation of peat requires the long-term presence of mangrove vegetation and the absence of, or low levels of, wave energy (Mascarenhas et al. 1993; Lidz et al. 2003). Retention of organic matter in mangrove systems is important for vertical accretion and habitat stability (Cahoon and Lynch 1997), particularly on islands built on carbonate platforms that receive little allochthonous input of sediment from river discharge (Ellison and Stoddart 1991; Parkinson et al. 1994). Mangrove peat deposits occur throughout the Caribbean region. Peat cores from Twin Cays, Belize indicated deposits of up to 10 m thick (Macintyre et al. 2004). Some Belizean offshore islands (e.g., Tobacco Range) have been dominated by mangrove communities throughout their entire Holocene history (Macintyre et al. 1995; McKee et al. 2007a). An analysis of peat accumulation in mangroves living on carbonate sediments suggested accretion rates ranging from 1.0 to 3.7 mm/yr (Alongi 2008).

McKee (2011) found Belizean dwarf mangroves to have substrate elevation increases of 1.2 mm/yr and Belizean fringing mangrove to have increases of 8.8 mm/yr, with mangrove roots as the primary contributors to this upward change in substrate elevation. At the Turneffe eastern cays, peat deposition occurred primarily in the leeward zone, and the highest peat accumulation coincided with the highest *R. mangle* basal area and seedling density. Sediment coming from the reef is trapped on the ridge zone making the leeward zone a place of coral sediment deficit.

In cays where peat was the dominant substrate in the leeward zone, peat was over 50 cm in depth (e.g., Cockroach Cays), indicating potential accumulation for 135 to 500 years using Alongi's (2008) accumulation rate estimates. Kumara et al. (2010) found that high density mangroves enhanced rates of sediment accretion and surface elevation, and pointed out that this may be crucial in mangrove ecosystem adaptation to sea-level rise. Since catastrophic hurricanes have a return interval of approximately 80 years in Turneffe (Chapter 3), this suggests that peat deposits persisted through some events. Aerial photos of the cays taken by Stoddart after Hurricane Hattie in 1961 indicated that some vegetation survived, including mangrove trees, so presumably the underlying peat also persisted. Coral sediments washed in from the reef during storms have periodically buried accumulating peat as evidenced by alternating layers of sand and peat in some of the cores (Fig. 5.16). The uppermost layer in these cores was peat, indicating that mangroves were adept at colonizing new substrate and recolonizing disturbed areas.

For most of the cays, monospecific stands of *R. mangle* dominated the leeward side of these cays with respect to the reef crest. *Rhizophora mangle* seedling density, average height, stem diameter, and basal area were higher than the ridge and reefward zones, indicating they were adapted to cope with the conditions in the leeward zone. Since plants in this zone were rooted below the spring high tide, they must cope with the stresses of high soil salinities, tidal inundation and soil anoxia. On other Belizean cays, *R. mangle* has also been observed to form monospecific stands along shorelines and creekbanks where inundation by the tides is frequent (McKee 1995b).

5.1.3 Reefward zone

The reefward zone encompassed an intertidal and subtidal zone. During a spring low tide, a large portion of the reefward zone can be exposed and some low depressions can form pools. The reefward zone was a zone of high stress and disturbance due to continual exposure to tidal inundation and routine wave energy, and exposure to extreme waves and transported debris during storms. Between high-energy storms, there is an opportunity for vegetation to establish in the reefward zone and closer to the reef crest. While I found areas of exposed coral rubble (e.g., elevated above the spring high tide) closer to the reef crest (approximately 50 m), these were all unvegetated. This suggests that routine wave energy limits mangrove establishment, while dissipation with distance from the reef enables plant colonization in the ridge and leeward zone.

Wave energy is refracted on the coral reefs and propagates along the back-reef somewhat parallel to the reef crest. This was evident on the sandy ripples created on the back-reef sediment apron. Laboratory models of fringing reefs show that if a wave breaks close to the reef-edge, very effective energy dissipation occurs (Gourlay 1994). The dissipation of wave energy with distance from the reef was evident from the gradient in substrate composition along the surveyed transects. Based on the cores made on and around the cays, coarse coral rubble was the dominant substrate on the reefward zone. The percentage of coral rubble composition decreased with distance from the reef crest and was practically absent beyond 250 m. Conversely, mangrove peat was practically absent on the reefward zone of the fringing cays even where dense patches of mangroves occurred, presumably because of constant erosion of surface organic matter. Organic particles, due to their low density, tend to erode easily. Substrates in areas with strong flows, are generally composed of coarse particle sizes, lack organic matter and are nutrient-poor (Chambers et al. 1991; Madsen et al. 2001). The average soil salinity in this zone was similar to ocean salinity, presumably due to the constant washing of seawater coming from outside the reef. Mangrove seedlings were more likely in plots with higher salinity but lower wave energy, which were characteristics of the leeward zone with respect to the reef crest.

Average basal area for all tree species was lower on the reefward zone than on the leeward and ridge zones. The average basal area of *L. racemosa* was in the same range as *R. mangle*. However, *L. racemosa* trees were concentrated closer to the border with the ridge zone. *Rhizophora mangle* trees dominated the reefward zone, and seedlings from this species were the only ones found close to the edge of the reef crest, albeit at low densities. Seedling

establishment was limited in this zone. Wind driven waves, in addition to tidal inundation, can destabilize sediment and prevent seedling establishment (Keddy 1983; Bruno 2000).

During storms, considerable amount of oceanic debris is washed in the direction of the fringing cays. Some cays had logs lodged on the vegetation or along the wrack line. Debris swept along the reefward zone has potential to dislodge seedlings found on this zone.

Mangrove trees within this zone were typically small and sometimes isolated from the rest of cay vegetation. The small size could reflect the effects of salinity and limited nutrients on productivity, but presumably also reflects the high loss rate of established trees during storm events. Interestingly, Boizard and Mitchell (2010) found that the seedlings of mangroves growing outside of the mangrove overstory on coral rubble were 3.5 times more strongly anchored than those growing within the mangrove overstory on sand.

The edge of the ridge zone that faces the reefward zone showed the most striking evidence of erosion in progress. This edge was inundated twice daily depending on the tidal cycle.

McKee (1995b) observed that at the highest reaches of the tide, both inundation and salinity stresses were minimized and higher-elevation sites were infrequently flooded over the soil surface, whereas the lower elevation sites near the shoreline were inundated twice daily on mangrove areas at Twin Cays, Belize. Field observations suggest that the tidal fluctuations on the leeward zone were less variable than the reefward zone due to exposure to wind driven waves. At the boundary between the reefward zone and the ridge zone, substrate and vegetation such as *C. nucifera*, littoral and mangrove forest was being undermined by the erosive forces of waves. Analysis based on historical and contemporary aerial photographs and the combined effects of accretion and erosion led to the conclusion that the fringing cays

have shifted away from the reef crest between 1945 and 2006 (Chapter 3). Removal of the natural vegetation from the late 1800's until the mid 1900's could have made the fringing cays highly vulnerable to erosion. Cays with a well-formed ridge zone were targeted for *C. nucifera* plantations and for human habitation. Hurricane Hattie, the only catastrophic hurricane between 1945 and 2008, approached Turneffe from the east. The majority of storms within this period had similar paths. Coupled with that and the erosive effect of storms, the expansion of mangrove on the leeward zone produces a net cay shift away from the reef crest. In many cays, a historical edge of cay vegetation was evident from the presence of mixed organic sand and coral rubble along with dead and decaying roots. Upstanding remnants of conglomerate rock which survived substrate erosion, were noticed by Stoddart (1963), on the eastern side of some of the fringing cays after the passage of Hurricane Hattie and some of these upstanding remnants of conglomerate rock were still visible during the course of this study.

5.1.4 Vegetation strategies

Mangroves are known to be well-adapted for growth in highly stressful habitats (Ball 1988) and can be characterized as stress-tolerators. However, the intensity of stresses in a mangrove forest varies spatially and temporally (Boto and Wellington 1984). Although nutrient availability was not measured on this system, these carbonate based environments are widely considered to be phosphorus-limited (Feller 1995; Feller et al. 2002; Short et al. 1985, 1990) which may be a result of the geochemistry of phosphate and carbonate minerals (Short 1987), since biogenic carbonate sediments commonly bind inorganic phosphate (Berner 1974; De

Kanel and Morse 1978). McKee (1995a) did some experiments with light and nutrient availability and concluded that *R. mangle*, *A. germinans* and *L. racemosa* were also generally 'stress-tolerators'. Slow growth rates and high levels of defensive chemicals exhibited by certain plant species are considered to be characteristics of resource-limited habitats (Grime 1977 and 1979).

Plants with faster growth rates and greater allocation to shoot growth can displace plant species referred as 'stress-tolerators', when both are found in resource-rich habitats (Grime and Campbell 1991). The three habitat zones of the Turneffe fringing cays are an ideal setting to study mangrove and non-mangrove competition and succession. Based on the triangular ordination according to stress, disturbance and competition (c.f. Saenger 1985), some general observations can be made about the mangrove species at Turneffe.

According to Saenger (personal communication), the Proserpine Study site was in the delta of the Proserpine River, Australia and was a relatively sheltered site. The area is subtropical, humid, with a summer rainfall. Saenger's plot was influenced by semidiurnal tides, which during the wet season would be about 50% seawater salinities. The mangrove stand on the Proserpine plot was mixed.

All four mangrove species from Turneffe were within the general distribution of mangroves from Proserpine, Australia. None of the Turneffe mangroves were found to have evolved the strategy of extreme 'competitors' or 'disturbance'. However, *R. mangle* had the highest dominance index, which positioned it closer towards the competition corner than the other

mangrove species. *Laguncularia racemosa* from Turneffe and *Lumnitzera racemosa* from Proserpine, which belong to the same taxonomic family (Combretaceae), were similar in the ordination. Although *C. erectus* is also from this family, it appears to be more 'stress tolerant' along with *A. germinans*. *Rhizophora stylosa* and *Rhizophora mangle* were somewhat close in the ordination and belong to the family Rhizophoraceae.

Using data from multiple mangrove species, Saenger (1985), suggested that none of the mangroves had extreme 'competitor' or 'disturbance tolerator' strategies. Rather, there was a general clustering of mangrove species towards the 'stress tolerator' strategy. However, he also suggested that from a list of 15 mangrove species, four species that are widespread in Australasia appear to have a combined 'competitor/stress-tolerator' strategy, including *Rhizophora stylosa*. This strategy enables plants to persist during unfavorable conditions and to exploit favorable conditions when available (Saenger 2002). *Rhizophora mangle* was the dominant mangrove species on Turneffe and also appears to exhibit the combined 'competitor/stress-tolerator' strategy. *Rhizophora mangle* effectively competed for space with littoral and other mangrove species on the ridge zone and almost exclusively dominated the intertidal and subtidal zones. The seedling density and basal area of *R. mangle* was highest in the leeward zone with respect to the reef crest, a zone with relatively low routine disturbance but significant stresses from inundation.

Although *R. mangle* was not as effective at colonizing the reefward zone compared to the leeward zone, it was the only species found in close proximity to the reef. In the reefward zone, *R. mangle* was exposed to routine wave energy and was damaged during storms.

Established seedlings were reasonably common, even in coarse rubble substrates near the reef; however, mature plants with prop roots were relatively rare, indicating periodic loss of the seedling cohort. This suggests that this species has trouble persisting without a geomorphic barrier. Overall, while the ordination using Saenger's approach suggests that *R. mangle* is a 'competitor-stress-tolerator', its dominance of the leeward zone and presence on the reefward and ridge zones suggests that it is the most disturbance-tolerant of the mangrove species at Turneffe.

Both *Laguncularia racemosa* and *Lumnitzera racemosa* are semi-deciduous, which theoretically places them in the disturbance-tolerance corner (Saenger, personal communication). Although as noted previously, neither of these species was as abundant as *R. mangle* in the reefward zone. The number of canopy leaves in *Lumnitzera racemosa* varies greatly from year to year and presumably reflects environmental conditions (Saenger 1985). By adjusting their photosynthetic surface area, *Lumnitzera racemosa* can regulate growth functions for the coming year (Saenger 1985). *Conocarpus erectus* is fairly distinct from the other two Combretacea species, and tended towards 'stress-tolerator' strategy. *Conocarpus erectus* does not show any tendency to be semi-deciduous (Saenger, personal communication). McKee's seedling experiment (1995b) found that *A. germinans* and *L. racemosa* were less likely to outperform *R. mangle* where resources were limiting. Reforestation experiments conducted in Columbia by Elster (2000) showed that generally, all three mangrove species (*R. mangle*, *A. germinans*, and *L. racemosa*) developed best at sites with low salinities and a water level near the soil surface. In Southern Florida, Ball (1980) observed that maximum growth of both *R. mangle* and *L. racemosa* occurred in intertidal

zones, while both species were stunted and had sparse, poorly formed canopies in drier environments above the mean high-water level. *Rhizophora mangle* basal area was lower than *C. erectus* on the ridge zone, which indicated the increased competitiveness of *C. erectus* in the absence of inundation, although robust growth was observed on the *R. mangle* stands.

Competition between mangrove and other tree species contributed to vegetation zonation on the cays at Turneffe. *Rhizophora mangle* is known for frequently colonizing flooded zones, and this “preference” has been incorporated into the zonation theory for mangrove distribution (Rabinowitz 1978b). Ukpong (1991) found in southeastern Nigeria that mangroves and mangrove associates may be confined to certain salinity ranges, but that there were also overlapping ecological optima along the gradient. He further stated that considering salinity as a stress factor, the ecological optimum is a salinity value at which a species achieves the highest level of competition and adaptation such that other species are (theoretically) excluded from that niche. There is considerable ambiguity concerning the optimal salinity for various aspects of *R. mangle* growth (Pezeshki et al. 1990; Smith and Snedaker 1995; Lopez-Portillo and Ezcurra 1989). Some authors have found that growth and metabolism of many mangrove species decline when salt is withheld (Ball 2002) which suggests a loss of competitive ability under “terrestrial” conditions (Feller et al. 2010). Growth of mangroves is also slowed under high salinity conditions, even though many species can maintain some level of growth (Lovelock et al. 2005).

The mean salinity for the equatorial Atlantic-Caribbean is 36 ppt. (Haug et al. 2001). Mangroves, which colonize the intertidal and subtidal zones, are exposed to ocean level salinities, and in areas of rapid evaporation may experience even higher salinities. On the fringing cays, *R. mangle* seedlings were found in a range of salinities, from 25 to over 50 ppt. Established *R. mangle* trees were found in soil salinities from 23 to over 50 ppt. The northern group of cays had the highest salinities (over 50 ppt.). This was pronounced in peat substrate within the tidal inundated zones and with no or minimal overhead canopy. These leeward zones had formerly supported vegetation, but had been denuded by Hurricane Keith in 2000. The high salinity zones are presumably from surface water evaporation. Even in these highly saline zones, *R. mangle* seedlings were dominant.

Rhizophora mangle propagules also have some adaptive advantages over *A. germinans* and *L. racemosa* for establishment on the cays. In experiments conducted by Rabinowitz (1978b) on mangrove establishment, tidal sorting of mangrove species was attributed to the interacting effects of water depth and propagule size on dispersal and establishment. Sousa et al. (2007) observed from field experiments that contrary to the tidal sorting hypothesis, all three mangrove species established best in the lower intertidal zone, where they were in extended contact with the soil surface during low tides. However, Sousa et al. (2007) did find that, in agreement to the tidal sorting hypothesis, large propagules of *R. mangle* rooted and persisted better in turbulent habitats than did the smaller propagules of other species. This was consistent with patterns observed on the Turneffe fringing cays. Although the density of *R. mangle* seedlings and trees was low on the reefward zone, it was the dominant colonizer in these exposed reefward conditions. Furthermore, from the minimum and maximum

elevations at which seedlings were found, it was evident that *L. racemosa*, *A. germinans*, and *C. erectus* were more restricted in their elevation ranges relative to spring high tide in comparison to *R. mangle*.

McKee (1995b) found that long-term survivorship (2.5 years) was determined by sensitivity to physical and chemical factors such as flooding (*A. germinans* and *L. racemosa*) and salinity (*L. racemosa*) and initial orientation of the seedling axis (*R. mangle*) but she also noted that distributions across the intertidal zone were determined by dispersal and differential establishment abilities. Elster (2000) observed that because of the relatively small propagules of *A. germinans* and *L. racemosa*, these species find it difficult to establish in inundated soils in Columbia. They were carried away by currents and dried out rapidly in direct sun. The recently established seedlings of these species are delicate and are easily broken by wind and waves or moving substrate. Their establishing seedlings have relatively short roots and therefore dry up and die when direct sunlight desiccates the substrate surface where they anchor (Elster 2000). Elster (2000) also observed that *R. mangle* seedlings were capable of surviving total flooding for up to six months. *Rhizophora mangle* can also colonize new areas via lateral expansion from established trees, and is capable of growing in a range of substrate types. These advantages enable it to colonize the various zones across the fringing cays.

It is worth noting that extensive areas for the potential establishment of mangrove propagules were observed on the back-reef between the fringing cays. However, the absence of mangrove seedlings across most of this area underlines the importance of a protective barrier

for successful mangrove establishment. The back-reef sediment apron at the northern fringing cays was also wider than at the southern cays, presumably due to the more exposed conditions in the northern portion of Turneffe.

Plant species with less tolerance to high salinities, tidal inundation and wave energy were found to be concentrated on the ridge zone (e.g., *C. erectus*, coccolith and littoral forest).

Although the vegetation on the ridge zone was not inundated by regular tide cycles, the vegetation is undoubtedly affected by sea spray that tends to have copious amounts of salt. It is in this context that the distance between the coccolith and/or littoral forest stands from the reef becomes important and might play a role in the reduction of sea spray that reaches the ridge zone. Franklin et al. (1999) observed that maritime influence (salt spray and wind desiccation) decreased with increasing distance from the coast and with leewardness.

Ehrenfeld (1990) also found that plant distribution on barrier islands occurred in response to steep environmental gradients that arise with increasing distance from the sea. The coral reefs around Turneffe serve as a barrier that breaks and buffers incoming waves and the wave breakage on the reef crest produces sea spray. This phenomenon was observed with clarity, especially on windy days when a fog-like cloud of sea spray hovered between the reef and the cays. A study on how distance from the reef and sea spray concentration affect the salinity levels on the ridge zone will aid in understanding plant stress and species distribution patterns. During storm surge, both mangrove and non-mangrove species on these cays would suffer from sea spray across the different zones. It would also be interesting to find the effects of saltwater intrusion on vegetation found on substrate above the spring high tide after a storm surge event and to compare with the salinity levels from freshwater input during the

rainy season as opposed to the dry season. This would be particularly interesting considering the diversity of non-mangrove species found on these cays.

Stoddart's photographs taken before and after Hurricane Hattie suggests that the larger islands fared better than the small eastern cays during storm damage from Hurricane Hattie. It also appears from the photographs and surveys that fringing cays with well-developed ridge zones fared better than those without. Although distance to the large islands did not come out as a significant parameter in the models, it is likely that the large islands play an important role during the initial stages of mangrove and non-mangrove vegetation colonization and recolonization on the fringing cays following hurricanes. The fragmentation characteristics of mangrove forest may ultimately dictate the potential for regeneration within landscapes (e.g., Sengupta et al. 2005; Gustafson and Gardner 1996). The recent clearance of mangrove and littoral forest along the edge of the larger islands for resort development is of concern since these forest stands are the closest propagule and seedling source to the fringing cays.

Tomlinson (1986) states that mangroves have little capacity for vegetative reproduction and are dependent on seedling recruitment for forest maintenance and spread. However, *R. mangle* recolonizes via propagules and lateral expansion from surviving plants. Mangrove recolonization after Hurricane Keith (in 2000) was observed on the group of cays to the north (Cockroach Cays-20, -22 and -23), and provided some insights into post-hurricane recovery at Turneffe. Storms predominantly approach Turneffe from the southeast (Chapter 3). However, Hurricane Keith (2000) was an exception and approached Turneffe from the

northwest. Hurricane Keith killed mangrove vegetation in the leeward zone (with respect to the reef), of the Cockroach Cays, yet extensive layers of mangrove peat survived erosion and/or burial. Over a period of eight years mangroves have revegetated nearly all of the areas damaged by that storm (Chapter 3; Fig. 3.22). The rapid vegetation recovery on the northern group of cays was presumably as a result of the survival of vegetation close to and on the ridge zone, which provided propagules for recolonization.

5.2 Conclusion

The coral rubble substrate on the back-reef comes directly from the coral reefs. Storm activity was the primary force that displaced sediment and coral rubble into the back-reef zone. A ridge of sediment material (node) accumulated above the spring high tide at a critical distance from the reef where wave energy dissipates, which can lead to fringing cay formation.

The three geomorphic zones, reefward, ridge, and leeward, provided habitats that differ in stress, and disturbance. The spatial distribution of the plant communities across these zones reflects the different means plants employ to avoid or tolerate the effects of stress, disturbance and interspecies competition. Mangroves promoted cay formation by stabilizing the substrate and trapping incoming sediment. This increased the elevation and area of the ridge zone and enabled littoral plants to establish. Interspecies competition is expected to increase as the ridge zone expands vertically and laterally. However, the ridge zone was still exposed to periodic overwash and fluctuations in salinity from intrusion and salt spray. Well-

formed ridge zones protected the leeward zone from wave energy, and *R. mangle* dominated this sheltered intertidal environment, leading to peat accumulation. The reefward zone was repeatedly scoured and/or buried by sediment. *Rhizophora mangle* seedlings do establish in this zone, but rarely persist to the prop root stage.

Rhizophora mangle can cope with high and varying degrees of salinity and elevation, was able to colonize various substrate types and a range of environments on the fringing cays including high wave energy zones facing the reef. Saenger's ordination approach suggests that *R. mangle* is a 'competitor-stress-tolerator'. *Rhizophora mangle*'s presence in the reefward zones and domination of the fringing cay environment in the absence of human disturbance indicated that it was the most disturbance-tolerant of the local mangrove species. The accumulation of peat (over 30 cm) suggested that mangroves have been thriving in this environment in the long-term. To improve our understanding of mangrove plant strategies and to draw parallels with Grime's ordination, more comprehensive litter data are needed. Additionally, the measurement of parameters such as sedimentation rates, available nutrients and surface temperatures could provide a better understanding of conditions and plant responses in the three zones.

Chapter 6: Conclusion

Fringing cays develop on the back-reef sediment apron in exposed reef environments. They are important contributors to the structural and biological diversity of atoll ecosystems. These are dynamic storm-prone environments. Datasets that document disturbance and long-term recovery of these ecosystems are rare. In this thesis research, I had the opportunity to combine historic aerial photos and field observations taken just before and just after catastrophic Hurricane Hattie in 1961 with contemporary imagery and permanent and temporary plot data. The goal of this thesis research was to examine the fringing cays of eastern Turneffe in order to understand fringing cay geomorphology and vegetation community development, in particular the role of mangroves. Temporal changes in cays and mangroves were documented using historic aerial photographs and satellite imagery (Chapter 3). Stand-level growth and litter production in mangrove-dominated stands were documented using permanent sample plot data (Chapter 4). Contemporary aerial photographs, transects and temporary plots were used to examine spatial patterns in cay geomorphology, mangrove community structure and composition, and vegetation strategies of local mangrove species (Chapter 5).

6.1 Summary of principal findings and implications

6.1.1 Fringing cay dynamics and the impacts of hurricanes and humans (Chapter 3)

- In 157 years (1851-2008), six hurricanes and four tropical storms have made landfall on Turneffe. The return interval for hurricanes on Turneffe was 26 years;
- September and October were the months with the highest frequency of hurricane landfall on Turneffe;
- the northern part of Turneffe was prone to a higher frequency of storms;
- Hurricane Hattie in 1961 was the only catastrophic (Category 5) storm to affect Turneffe directly during the period 1945 to 2008;
- between 1945 to 2006, 11 cays were devegetated and eroded, and four new vegetated cays formed;
- in 2006, cay vegetated area was not significantly different from the 1945 estimates, but a significant part of the vegetated area was below the spring high tide in 2008;
- the fringing cays of Turneffe have changed from coral to mangrove-dominated forest;
- a cay shift away from the reef crest was observed between 1945 and 2006.

6.1.2 Stand-level growth in fringing mangrove (Chapter 4)

- Two of the three cays studied had a significant increase in above-ground biomass between 2002 and 2008;
- this difference may have been in part due to differences in guano deposits and available substrate;
- leaves were the dominant fraction of above-ground and ground surface litter;
- there was a seasonal depositional pattern for both leaf litter and bract-flower-fruit fraction, both fractions peaked between August and October for all three sites;
- there was a significant correlation between mean litter (without guano and miscellaneous) and mean stand height;
- there was a significant correlation between litter (without miscellaneous) and guano at two of the three sites (Soldier Cay and Big Calabash Cay).

6.1.3 Spatial patterns in cay substrate and vegetation (Chapter 5)

- Storm energy was the driving force for displacing coral from the reef to the back-reef, creating a sediment and elevation gradient with potential for plant colonization;
- distance to the reef crest played a predictive role in the location of the ridge zone, which was one of three distinct geomorphic/habitat zones with

successful plant colonization along with the exposed reefward and sheltered leeward zones;

- exposure to wave energy and salinity had a negative effect whilst substrate elevation a positive effect for maximum tree height all species;
- *Rhizophora mangle* was capable of colonizing exposed reefward environments with a wave disturbance regime, although seedling survival was low and growth of established plants was sparse and stunted;
- *Rhizophora mangle* had the widest distribution when compared to the other mangrove species, and was present in the reefward, ridge and leeward zones;
- *Rhizophora mangle* represented the competitor-stress tolerator plant strategy and with the highest dominance index for the Turneffe mangrove species when plotted on the modified triangular ordination by Saenger 1985.

6.1.4 Implications

Not many studies have had the opportunity to assess change at the landscape level before and after a catastrophic disturbance over a period of six decades. The fringing cays on Turneffe provided an ideal place to study long-term vegetation change and recovery in a hurricane prone environment. The absence of permanent human settlements on most of the cays after Hurricane Hattie made it possible to examine the natural recovery and dynamics of this system. This study shows that in the absence of permanent human development and activities, the vegetation on fringing cays have the capacity to recolonize in the same general location following a hurricane.

Fringing cays form on the back-reef sediment apron. A conceptual framework for the formation of vegetated fringing cays and their subsequent devegetation and/or erosion by storms is illustrated on Figure 6.1. Storms are the major driving forces for dislodging and moving coarse coral rubble onto the back-reef. A sediment node is formed at a distance away from the reef crest that is conducive to vegetation colonization. The self reinforcing process of vegetation colonization in conjunction with low intensity storms contributes to sediment stability and cay expansion. High intensity storms have the potential to devegetate and/or erode cays.

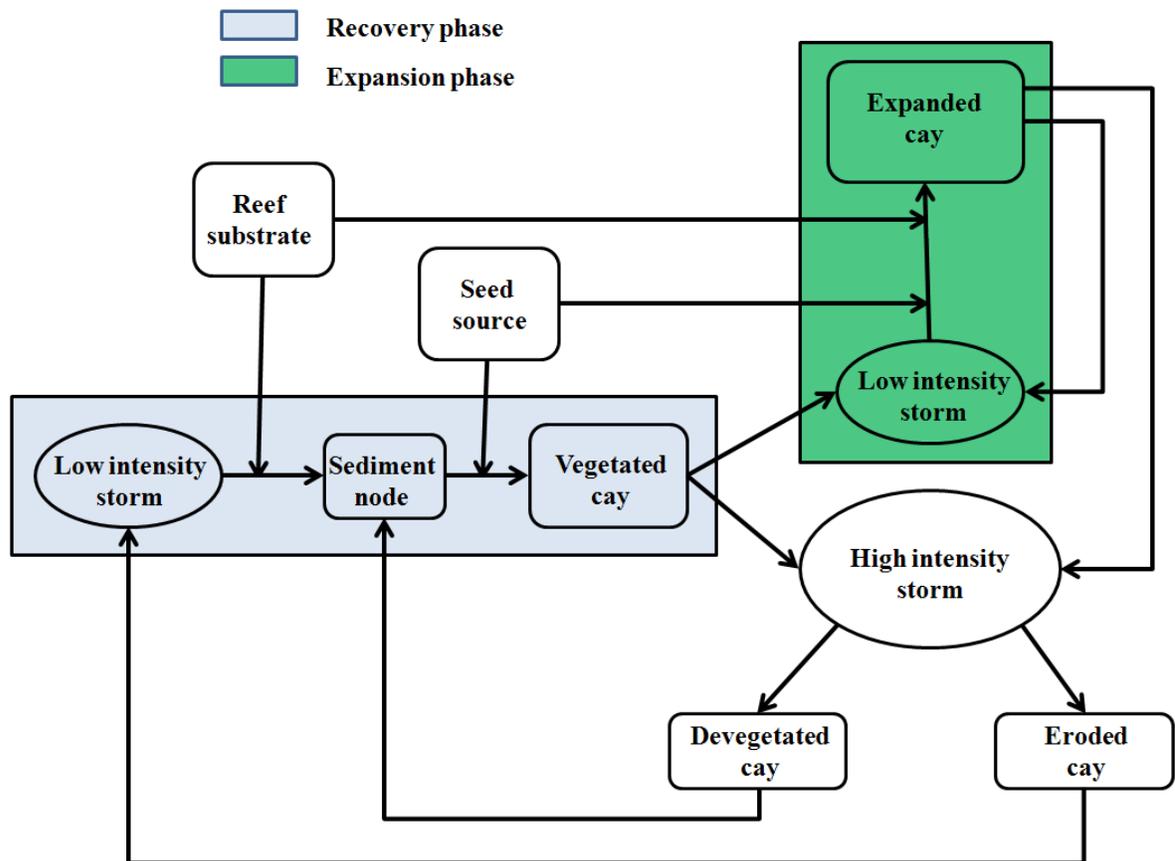


Figure 6.1. Conceptual model for vegetated fringing cay formation and the effect of storm energy on reef sediments and vegetation.

The coral rubble rampart had an area above the spring high tide, creating ridge, sheltered leeward and exposed reefward zones. Each zone had a distinctive environment and vegetation community. Distance to the large islands probably played an important role during the time of early cay vegetation colonization after devegetation from human activities or severe storms (by providing seeds), but was not a predictor of contemporary vegetation attributes. Once vegetation is established on or adjacent to reforming fringing cays it appears these plants are believed to promote further sediment accumulation and stabilization. Removal of mangroves presumably affects the capacity of cays to accrete sediment.

In the years since Hurricane Hattie, mangroves and other native species have recovered naturally on the fringing cays where cocal forest was the dominant vegetation before Hurricane Hattie (e.g., Soldier Cay and Big Calabash Cay). In other circumstances, human assisted recovery of mangroves may be desirable (e.g. Komiyama et al. 1996; Turner and Lewis 1997; Jiménez 1990; and Getter et al. 1984). However, in human assisted recovery (e.g., reforestation projects), the vegetative strategies and differing ranges in which mangrove propagules and seeds can anchor relative to high tide and reef are important factors to consider when restoring and revegetating coastal areas. Special attention must be paid to the different geomorphic zones, and their suitability for recolonization.

Although the natural vegetation had been replaced primarily with coconut palms on most of the fringing cays before the 1961 hurricane, mangrove forest was the dominant vegetation at Turneffe during the course of this study. It appears that a continual human presence and extensive replanting of cocal forest after Hurricane Hattie would have prevented these cays

from recovering to their present state. The fringing cays on Turneffe were resilient yet fragile. Smaller cays were particularly vulnerable to erosion as reflected in the loss of smaller sized cays from the northern group that have eroded since 1945. Human disturbance is an ongoing threat to the existence and character of these cays. Small islands are considered to be less able to withstand locally induced changes, such as vegetation removal by humans or global changes such as a sea level rise (e.g., Bayliss-Smith 1998).

Mangrove forest primary production and accumulated peat contributes to the overall productivity of the atoll ecosystem. The presence of buried mangrove peat deposits in leeward zones of the fringing cays indicates community stability over the very long-term. The leeward zone was the sheltered zone relative to the reef crest. The presence of seagrass, mangrove litter and marine detritus on the cays underscore the connectivity between adjacent reef, seagrass and fringing cay ecosystems. In addition, the seasonal presence of the algal blooms developing near bird colonies suggests the importance of the fringing cays as bird roosting sites.

Storms moved and redistributed sediment along the back-reef. From 2002, when the permanent plots were established and remeasured in 2008, new sediment was found in some of the monitoring sites. Mangrove roots and stems were buried along with the tags used to identify the trees. Mangrove roots were effectively stabilizing the new sediment load, thus increasing the elevation and substrate area. Mangrove trees along the ridge zone (e.g., Soldier Cay) facing the reef were also found with coral fragments wedged between roots and multiple scars were observed on the roots and stems presumably caused by debris during

storm surge. Sediment burial from low energy storms seemed to be within the tolerable range for mangrove survival.

The Turneffe environment supported all four mangrove species but *R. mangle* dominated the reefward and sheltered leeward zones because of certain morphological and physiological advantages. *Rhizophora mangle* can produce copious amounts of propagules that have larger energy reserves and remain viable for a longer period (Elster 2000), which likely provides a competitive advantage over the other mangrove species. *Rhizophora mangle* propagules have been reported to have a higher survival rate during flooding events, and seedlings have a better chance of surviving debris impact or burial (Elster 2000). The unique ability of *R. mangle* trees to expand and colonize new substrate laterally was also advantageous in these environments.

Rhizophora mangle was also able to colonize and persist in the higher elevations of the ridge zone, among littoral competitors. This was likely due to the overwash these cays experience during storm activity. *Rhizophora mangle* propagules could be transported during storm surge to these higher elevations, and the influx of salinity could also reduce the vigor of less salt-tolerant plant species. The triangular ordination based on Saenger (1985) suggested *R. mangle* to be closer to the axis describing a “competitor-stress tolerator”. However, when the stress, competition and disturbance regimes were analyzed within the context of the three zones (sheltered leeward, ridge and reefward zone) of the fringing cays, *R. mangle* was adept at colonizing all three geomorphic habitat zones.

The leeward and reefward zones differed in mangrove establishment patterns. The sheltered leeward zones appear to have high rates of recruitment and vegetative expansion. Isolated mangrove patches (3 m apart) were coalescing into single patches within a period of two years from 2006 to 2008 (e.g., leeward zone of Big Calabash Cay). The sheltered leeward zone characterized by high stress and low disturbance was the “preferred zone” for *R. mangle*. The reefward and ridge zones appear to create an optimal *R. mangle* sheltered environment leeward of the reef crest (leeward zone). The ridge zone and its vegetation promote the survival and expansion of the fringing cays. This was apparent when considering the large expanses of back-reef between the fringing cays on the eastern side of Turneffe, which seemed suitable for mangrove establishment but was not occupied by mangroves.

Fringing cays are dependent on the supply of sediment from the reefs directly to seaward. To survive, the coral reefs must also be able to produce enough material so that the reef can replace what is being lost to the back-reef from storm activity. It is therefore important to understand and maintain the health of these reefs in order to protect fringing cays.

6.2 Recommendations and future research

There were a number of challenges in conducting research in this ecosystem and there are a number of opportunities to extend and refine the approaches used. The use of high resolution satellite imagery (e.g., QuickBird), is highly recommended for future studies that require the georectification of aerial photographs for studies at the scale of the fringing cays. Historical aerial photographs taken by the RAF can be useful for creating digital maps. Unfortunately,

many photographs from the Belmopan, Belize collection were missing from the files in 2007. I would recommend that available photographs be scanned into digital format. Existing photographs should be stored in adequate cabinets and in an air-conditioned room to preserve quality. Missing photographs should be replaced by contacting the relevant departments in the UK that have copies of photographs from past RAF flights. These photographs are a valuable resource for the monitoring and historic reconstruction of coastal areas and can provide important information on spatial and temporal changes.

Monitoring forest stands using permanent plots was an effective way to track change in mangrove forest biomass. However, it was very challenging to track individual mangrove stem growth. When tagging mangrove trees, it is important to use a method that is secure and relatively easy to identify the stem and position where measurements are taken (e.g., stem diameter). Stem diameter measurements of *R. mangle* trees, which tend to form prop roots along the stems and lateral branches, were especially challenging to track over time. A stem marking and identification method that can withstand adverse weather conditions such as high wind, humidity and temperature, periodic and episodic inundation, and partial burial from sediments is important for future measurements if comparisons are to be made at the tree, plot and site level.

Measurements of soil nutrients and physical and chemical parameters in plots would contribute to the understanding of the dynamics of these systems. Though *R. mangle* dominates the vegetation composition in the plots, subsequent re-measurements would provide information on the dynamics of species composition over time. Six years of

observation was a very short time to reveal significant species replacement for long-living organisms such as trees.

The high below-ground to above-ground biomass and high root to shoot ratios in mangroves have been attributed to unstable substratum conditions (Hutchings and Saenger 1987). It would be interesting to find those ratios for carbonate systems since in some mangrove stands the immediate substratum can be lined by tough coral rubble which would be difficult for mangrove roots to penetrate. For example, Boizard and Mitchell (2010) observed a higher percentage of live roots in seedlings were among the peat-canopy location than the rubble-canopy location. However, they also found that seedlings growing on coral rubble and outside of mangrove overstory were 3.5 times more strongly anchored than those growing within the mangrove overstory on sand.

A consecutive two year collection of litterfall would be very useful for productivity estimates, especially if additional parameters like temperature, rainfall and salinity are also measured. To have a better understanding of mangrove plant strategies and to draw parallels with Grime's and Saenger's ordination, more comprehensive mangrove litterfall data is needed. Litterfall sorted at the species level is recommended. Fertilization plots were started on Turneffe in 2002 but due to problems in acquiring the required fertilizer, the experiment was halted. That experiment should be restarted to provide data on patterns of nutrient availability of Turneffe mangrove forests. Long-term monitoring (e.g., CARICOMP permanent plots Chapter 4) can provide the much needed data for the development of a broad coastal management framework and the scientific basis for planning and policy for Turneffe.

Stands of littoral forest were an important component of fringing cay vegetation. Future work on composition of littoral forest on fringing cays would facilitate the understanding of the diversity and colonization by these plants. Most of these non-mangrove species have recolonized these fringing cays naturally after devegetation by humans and Hurricane Hattie. Inventorying the plant communities of the fringing cays, would produce a useful list of potentially plants that could be used for landscaping and reforestation projects along the coast and cays. For example, this information could be useful in places where abandoned shrimp aquaculture farms need to be reclaimed or where property (resorts) devegetated from natural or human disturbances needs to be replanted.

Deeper peat cores and core analysis on the leeward zone with respect to the reef crest of the fringing cays could possibly provide a paleoecological reconstruction of storm and vegetation history of the fringing cays. Core analyses on the larger islands have been carried out, but these apparently lack the clear overwash layers needed for storm analysis (e.g., McCloskey 2009).

6.3 Concluding remarks on mangrove conservation

Mangrove ecosystems tend to be found in developing countries where a substantial portion of the population lives in poverty. Dependence on mangrove forest, particularly subsistence fishing, and coastal protection are often quoted as being vital to the livelihoods of many coastal communities (Valiela et al. 2001). The ecological roles mangroves play along the

coast are specific, in addition mangroves provide income for millions of people, but destruction of these ecosystems can only be explained for shorter economic benefits. The concept that mangroves are wastelands unless developed needs to be changed.

Much effort has been focused on coral reef conservation in Belize, but this is less true for mangrove, littoral forests, and seagrass beds. The Belize Protected Areas map (Belize Land and Survey Department 2011; <http://www.pactbelize.org/ProtectedAreas.aspx>) shows the relatively low percentage of mangroves and littoral forest under protection. It is essential to consider mangroves in conservation and management along with adjacent ecosystems.

It is difficult to put a monetary value on all the services a mangrove forest provides, and even when calculated it can be significantly understated. Cooper et al. (2009) estimated that, in total, the value of reef and mangrove-related fisheries, tourism, and shoreline protection services in Belize is US\$395 to \$559 million per year and that mangrove forests provide an estimated US\$174 to \$249 million of this total. Tourism is of national economic importance for Belize. Turneffe, the nearest atoll to Belize City, its international airport, and the cruise ship industry, will continue to see an increase in visitors based on the current tourism trend.

Allowing clearance of fringing cays for tourism, recreational or other development is ecologically short-sighted. Given the exposure of these small cays to damage during recurrent storms and hurricanes, it also unnecessarily risks human life and property. The increasing population in Belize will continue to put pressure on coastal resources and the incentives for the development and conversion of forest appear more profitable than conservation (e.g., shrimp aquaculture). The challenge for Belize is to reap economic benefits

from its natural resources while preserving their diversity and productivity for future generations.

References

- Abbott, I. (1980). The transition from mainland to island, illustrated by the flora and landbird fauna of headlands, peninsulas and islands near Albany, Western Australia. *Journal of the Royal Society of Western Australia*, 63, 79-92.
- Abbott, I., & Black, R. (1980). Changes in species composition of floras on islets near Perth, Western Australia. *Journal of Biogeography*, 7(4), 399-410.
- Adams, D. E., & Anderson, R. (1980). Species response to a moisture gradient in central Illinois forests. *American Journal of Botany*, 67(3), 381-392.
- Adame, M. F., & Lovelock, C. E. (2011). Carbon and nutrient exchange of mangrove forests with the coastal ocean. *Hydrobiologia*, 663, 23-50.
- Agrios, G. N. (1978). Plant diseases caused by mycoplasma-like organisms. *Plant Pathology* (2nd ed.). New York, USA: Academic Press.
- Aksornkhae, S., & Paphavasit, N. (1993). Effect of sea level rise on the mangrove ecosystem in Thailand. *Malaysian Journal of Tropical Geography*, 24(1-2), 29-34.
- Allaby, A., & Allaby, M. (1999). *'Backreef.'* A dictionary of earth sciences. Retrieved 02/03, 2009, from <http://www.encyclopedia.com/doc/1O13-backreef.html>
- Allaway, W. G., & Ashford, A. E. (1984). Nutrient input by seabirds to the forest on a coral island of the Great Barrier Reef. *Marine Ecology Progress Series*, 19, 297-298.
- Allen, J. A., Ewel, K. C., Keeland, B. D., Tara, T., & Smith, T. J. (2000). Downed wood in Micronesian mangrove forest. *Wetlands*, 20(1), 169-176.
- Alongi, D. M. (2008). Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuarine, Coastal and Shelf Science*, 76(1), 1-13.

- Alves, L. F., Vieira, S. A., Scaranello, M. A., Camargo, P. B., Santos, F. A. M., Joly, C. A., et al. (2010). Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *Forest Ecology and Management*, 260(5), 679.
- Anderson, W. B., & Polis, G. A. (1998). Marine subsidies of island communities in the Gulf of California: Evidence from stable carbon and nitrogen isotopes. *Oikos*, 81(1), 75-80.
- Aronoff, S. (2005). *Remote sensing for GIS managers* (1st ed.). Redlands, California, USA: ESRI Press.
- Ashburner, R., & Quiroz, L. (1996). Lethal yellowing of coconut palms arrives in San Pedro. Retrieved 01/10, 2010, from <http://www.sanpedrosun.com/old/yellopalm.html>
- Auclair, A. N. D., Bouchard, A., & Pajaczkowski, J. (1976). Plant standing crop and productivity relations in a *Scirpus-Equisetum* wetland. *Ecology*, 57(5), 941-952.
- Ball, M. C. (2002). Interactive effects of salinity and irradiance on growth: Implications for mangrove forest structure along salinity gradients. *Trees - Structure and Function*, 16(2), 126-139.
- Ball, M. C. (1988). Ecophysiology of mangroves. *Trees - Structure and Function*, 2(3), 129-142.
- Ball, M. C. (1980). Patterns of secondary succession in a mangrove forest of southern Florida. *Oecologia*, 44(2), 226-235.
- Bardsley, K. N. (1985). The effects of cyclone Kathy on mangrove vegetation. In K. N. Bardsley, J. D. S. Davies & C. D. Woodroffe (Eds.), *Coasts and tidal wetlands of the Australian monsoon region* (Mangrove Monograph, pp. 167-187). Darwin, Australia: Australian National University, North Australia Research Unit.

- Batschelet, E. (1981). *Circular statistics in biology*. London: Academic Press.
- Bayliss-Smith, T. P. (1988). The role of hurricanes in the development of reef islands, Ontong Java Atoll, Solomon Islands. *The Geographical Journal*, 154(3), 377-391.
- Beakbane, A. B., Slater, C. H. W., & Posnette, A. F. (1972). Mycoplasmas in the phloem of coconut, *Cocos nucifera* L., with lethal yellowing disease. *The Journal of Horticultural Science and Biotechnology*, 47(2), 265-556.
- Begon, M., Harper, J. L., & Townsend, C. R. (1990). *Ecology: Individuals, populations, and communities* (2nd ed.). Oxford, UK: Blackwell Scientific Publications.
- Bell, D. T. (1980). Gradient trends in the streamside forest of Central Illinois. *Bulletin of the Torrey Botanical Club*, 107(2), 172-180.
- Bell, D. T., & Del Moral, R. (1977). Vegetation gradients in the streamside forest of Hickory Creek, Will County, Illinois. *Bulletin of the Torrey Botanical Club*, 104(2), 127-135.
- Bellingham, P. J., Tanner, E. V. J., Rich, P. M., & Goodland, T. C. R. (1996). Changes in light below the canopy of a Jamaican montane rainforest after a hurricane. *Journal of Tropical Ecology*, 12(5), 699-722.
- Bennett, E. L., & Reynolds, C. J. (1993). The value of a mangrove area in Sarawak. *Biodiversity and Conservation*, 2(4), 359-375.
- Berlin, C. (1996). Lethal yellowing update.... first the bad news, then the good news. Retrieved 01/10, 2010, from <http://www.sanpedrosun.com/old/yellowing3.html>
- Berner, R. A. (1974). Kinetic models for the early diagenesis of nitrogen, sulfur phosphorus, and silicon in anoxic marine sediments. In E. D. Goldberg (Ed.), *Marine chemistry. The sea - ideas and observations on progress in the study of the seas* (pp. 427-450). New York: John Wiley and Sons, Inc.

- Bertram, G. C. L. (1936). Some aspects of the breakdown of coral at Ghardaqa, Red Sea. *Proceedings of the Zoological Society of London*, 106(4), 1011-1026.
- Bijlsma, L., Ehler, C., N., Klein, R. J. T., Kulshrestha, S. M., McLean, R. F., Mimura, N., et al. (1996). Coastal zones and small islands. In R. T. Watson, M. C. Zinyowera & R. H. Moss (Eds.), *Climate change, 1995: Impacts, adaptations and mitigation of climate change: Scientific-technical analyses* (pp. 289-324). New York, U.S.A.: Cambridge University Press.
- Binkley, D., & Vitousek, P. M. (1989). Soil nutrient availability. In R. W. Pearcy, J. R. Ehleringer, H. A. Mooney & P. W. Rundel (Eds.), *Plant physiological ecology: Field methods and instrumentation* (pp. 75-96). New York, U.S.A.: Chapman and Hall.
- Bird, E. C. F. (1984). *Coasts: An introduction to coastal geomorphology* (3rd ed.). Oxford, UK: Basil Blackwell.
- Blanchard, J., & Prado, G. (1995). Natural regeneration of *Rhizophora mangle* in strip clearcuts in northwest Ecuador. *Biotropica*, 27(2), 160-167.
- Blanchon, P., Jones, B., & Kalbfleisch, W. (1997). Anatomy of a fringing reef around Grand Cayman; storm rubble, not coral framework. *Journal of Sedimentary Research*, 67(1), 1-16.
- Blanchon, P., & Jones, B. (1995). Marine-planation terraces on the shelf around Grand Cayman: A result of stepped Holocene sea-level rise. *Journal of Coastal Research*, 11(1), 1-33.
- Boizard, S., & Mitchell, S. (2010). Resistance of red mangrove (*Rhizophora mangle* L.) seedlings to deflection and extraction. *Trees - Structure and Function*, 25(3), 371-381.

- Boose, E. R., Foster, D. R., & Fluet, M. (1994). Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs*, 64(4), 369-400.
- Bormann, F. H., & Likens, G. E. (1979). *Pattern and process in a forested ecosystem*. New York, U.S.A.: Springer.
- Bosire, J. O., Dahdouh-Guebas, F., Kairo, J. G., Kazungu, J., Dehairs, F., & Koedam, N. (2005). Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya. *Biological Conservation*, 126(2), 287-295.
- Bosman, A. L., Du Toit, J. T., Hockey, P. A. R., & Branch, G. M. (1986). A field experiment demonstrating the influence of seabird guano on intertidal primary production. *Estuarine, Coastal and Shelf Science*, 23(3), 283-294.
- Bosman, A. L., & Hockey, P. A. R. (1986). Seabird guano as a determinant of rocky intertidal community structure. *Marine Ecology Progress Series*, 32(2-3), 247-257.
- Boto, K. G., & Wellington, J. T. (1984). Soil characteristics and nutrient status in a northern Australian mangrove forest. *Estuaries*, 7(1), 61-69.
- Bouillon, S., Borges, A. V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N. C., et al. (2008). Mangrove production and carbon sinks: A revision of global budget estimates. *Global Biogeochemical Cycles*, 22, 1-12.
- Bowden, R. D., Castro, M. S., Melillo, J. M., Steudler, P. A., & Aber, J. D. (1993). Fluxes of greenhouse gases between soils and the atmosphere in a temperate forest following a simulated hurricane blowdown. *Biogeochemistry*, 21(2), 61-71.
- Brander, R. W., Kench, P. S., & Hart, D. (2004). Spatial and temporal variations in wave characteristics across a reef platform, Warraber Island, Torres Strait, Australia. *Marine Geology*, 207, 169-184.

- Brown, S., & Lugo, A. E. (1984). Biomass of tropical forests: A new estimate based on forest volumes. *Science*, 223(4642), 1290-1293.
- Bruno, J. F. (2000). Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora*. *Ecology*, 81(5), 1179-1192.
- Buckley, R. C. (1982). Soils and vegetation of central Australian sandridges. IV. Soils. *Australian Journal of Ecology*, 7(2), 187-200.
- Buckley, R. C. (1981). Soils and vegetation of central Australian sandridges. III. Sandridge vegetation of the Simpson Desert. *Australian Journal of Ecology*, 6(4), 405-422.
- Bunt, J. S. (1982). Studies of mangrove litter fall in tropical Australia. In B. F. Clough (Ed.), *Mangrove ecosystem in Australia* (pp. 223-237). Canberra, Australia: Australian National University Press.
- Burke, R. B. (1982). Reconnaissance study of the geomorphology and benthic communities of the outer barrier reef platform, Belize. In K. Rützler, & I. G. Macintyre (Eds.), *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize* (pp. 509-526). Washington, D.C.: Smithsonian Institution Press.
- Cablk, M. E., Kjerfve, B., Michener, W. K., & Jensen, J. R. (1994). Impacts of Hurricane Hugo on a coastal forest: Assessment using Landsat TM data. *Geocarto International*, 9(2), 15-24.
- Cahoon, D. R., Hensel, P., Rybczyk, J., & Perez, B. C. (2002). Hurricane Mitch: Impacts on mangrove sediment elevation dynamics and long-term mangrove sustainability. (Open File Report 03-184). U.S.A.: USGS.

- Cahoon, D. R., & Lynch, J. C. (1997). Vertical accretion and shallow subsidence in a mangrove forest of southwestern Florida, U.S.A. *Mangroves and Salt Marshes*, 1(3), 173-186.
- CARICOMP Program. (1997). Structure and productivity of mangrove forests in the greater Caribbean region. *Proceedings of the 8th Interantional Coral Reef Symposium, Panama*. pp. 669-672.
- Castañeda-Moya, E., Rivera-Monroy, V. H., & Twilley, R. R. (2006). Mangrove zonation in the dry life zone of the Gulf of Fonseca, Honduras. *Estuaries and Coasts*, 29(5), 751-764.
- Chabreck, R. H., & Palmisano, A. W. (1973). The effects of Hurricane Camille on the marshes of the Mississippi River Delta. *Ecology*, 54(5), 1118-1123.
- Chale, F. M. M. (1996). Litter production in an *Avicennia germinans* (L.) stearn forest in Guyana, South America. *Hydrobiologia*, 330(1), 47-53.
- Chambers, P. A., Prepas, E. E., Hamilton, H. R., & Bothwell, M. L. (1991). Current velocity and its effect on aquatic macrophytes in flowing waters. *Ecological Applications*, 1(3), 249-257.
- Chazdon, R. L. (2003). Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, 6(1-2), 51-71.
- Chen, R., & Twilley, R. R. (1999). Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida. *Estuaries*, 22(4), 955-970.
- Cherrington, E. A., Hernandez, B. E., Trejos, N. A., Smith, O. A., Anderson, E. R., Flores, A. I., et al. (2010). Technical report: Identification of threatened and resilient mangroves

in the Belize Barrier Reef system. Panama: Water Center for the Humid Tropics of Latin America and the Caribbean (CATHALAC).

Chi, F. (2003). Long term effect of hurricane disturbance and recovery based on vegetation coverage, biomass and productivity estimates of the Turneffe mangrove forest in Belize. (Thesis). University of Bremen, Germany. pp. 1- 75.

Christensen, B. (1982). Management and utilization of mangroves in Asia and the Pacific. (Paper 3). Rome: Food and Agriculture Organization of the United Nations.

Cintrón, G., & Schaeffer-Novelli, Y. (1985). Características y desarrollo estructural de los manglares de Norte y Sur América. *Ciencia Interamericana*, 25, 4-15.

Cintrón, G., & Schaeffer-Novelli, Y. (1984). Methods for studying mangrove structure. In S. C. Snedaker, & J. G. Snedaker (Eds.), *The mangrove ecosystem: Research methods* (pp. 91-113). Paris, France: UNESCO.

Cintrón, G., Lugo, A. E., Pool, D. J., & Morris, G. (1978). Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica*, 10(2), 110-121.

Clarke, L. D., & Hannon, N. J. (1969). The mangrove swamp and salt marsh communities of the Sydney District: II. The Holocoenotic complex with particular reference to physiography. *Journal of Ecology*, 57(1), 213-234.

Clarke, P. J., & Kerrigan, R. A. (2002). The effects of seed predators on the recruitment of mangroves. *The Journal of Ecology*, 90(4), 728-736.

Clarke, P. J., & Allaway, W. G. (1993). The regeneration niche of the grey mangrove (*Avicennia marina*): Effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia*, 93(4), 548-556.

- Clough, B. F., Dixon, P., & Dalhaus, O. (1997). Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Australian Journal of Botany*, 45(6), 1023-1031.
- Clough, B. F., & Scott, K. (1989). Allometric relationships for estimating above-ground biomass in six mangrove species. *Forest Ecology and Management*, 27(2), 117-127.
- Clough, B. F., & Attiwill, P. M. (1982). Primary productivity of mangroves. In B. F. Clough (Ed.), *Mangrove ecosystems in Australia - structure, function and management* (pp. 213-222). Townsville, Australia: Australian Institute of Marine Science.
- Cole, D. W., & Rapp, M. (1981). Elemental cycling in forest ecosystems. In D. E. Reichle (Ed.), *Dynamic properties of forest ecosystems* (pp. 341-407). New York, U.S.A.: Cambridge University Press.
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, 199(4335), 1302-1310.
- Conner, W. H., Day, J. W., Baumann, R. H., & Randall, J. M. (1989). Influence of hurricanes on coastal ecosystems along the northern Gulf of Mexico. *Wetlands Ecology and Management*, 1(1), 45-56.
- Cooper, E., Burke, L., & Bood, N. (2009). Belize's coastal capital: The economic contribution of Belize's coral reefs and mangroves. Washington D.C., U.S.A.: WRI Working paper. World Resources Institute.
- Cooper-Ellis, S., Foster, D. R., Carlton, G., & Lezberg, A. (1999). Forest response to catastrophic wind: Results from an experimental hurricane. *Ecology*, 80(8), 2683-2696.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., et al. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253-260.

- Dahdouh-Guebas, F., & Koedam, N. (2006). Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): Solutions to ambiguous field situations and description of the PCQM + protocol. *Forest Ecology and Management*, 228(1-3), 1-18.
- Dahdouh-Guebas, F., Jayatissa, L. P., Di Nitto, D., Bosire, J. O., Lo Seen, D., & Koedam, N. (2005). How effective were mangroves as a defence against the recent tsunami? *Current Biology*, 15(12), R443-R447.
- Danielsen, F., Sørensen, M. K., Olwig, M. F., Selvam, V., Parish, F., Burgess, N. D., et al. (2005). The Asian tsunami: A protective role for coastal vegetation. *Science*, 310(5748), 643-643.
- Davis, J. H. J. (1940). The ecology and geologic role of mangroves in Florida. (Papers from Tortugas Lab 32, No. 517). Washington: Carnegie Institute of Washington.
- Davis, R. A. J. (1996). *Coasts*. New Jersey, U.S.A.: Prentice Hall.
- Davis, R. A. J., & Hayes, M. O. (1984). What is a wave-dominated coast? *Marine Geology*, 60(1-4), 313-329.
- Day, J. W. Jr., Coronado-Molina, C., Vera-Herrera, F. R., Twilley, R., Rivera-Monroy, V. H., Alvarez-Guillen, H., et al. (1996). A 7 year record of above-ground net primary production in a southeastern Mexican mangrove forest. *Aquatic Botany*, 55(1), 39-60.
- Day, J. W. Jr., Conner, W. H., Ley-Lou, F., Day, R. H., & Navarro, A. M. (1987). The productivity and composition of mangrove forests, Laguna de Términos, México. *Aquatic Botany*, 27(3), 267-284.
- De Kanel, J., & Morse, J. W. (1978). The chemistry of orthophosphate uptake from seawater on to calcite and aragonite. *Geochimica et Cosmochimica Acta*, 42(9), 1335-1340.

- De Lange, W. P., & De Lange, P. J. (1994). An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. *resinifera*) in New Zealand. *Journal of Coastal Research*, 10(3), 539-548.
- Delgado, P., Hensel, P. F., Jiménez, J. A., & Day, J. W. (2001). The importance of propagule establishment and physical factors in mangrove distributional patterns in a Costa Rican estuary. *Aquatic Botany*, 71(3), 157-178.
- Diamond, J. M. (2005). *Collapse: How societies choose to fail or succeed*. New York, U.S.A.: Viking.
- Díaz, J. M., Sánchez, J. A., Garzón-Ferreira, J., & Zea, S. (1996). Morphology and marine habitats of two southwestern Caribbean atolls: Albuquerque and Courtown. *Atoll Research Bulletin*, 435, 1-33.
- Dick, T. M., & Osunkoya, O. O. (2000). Influence of tidal restriction floodgates on decomposition of mangrove litter. *Aquatic Botany*, 68(3), 273-280.
- Dixon, C. (1991). Yucatan after the wind: Human and environmental impact of Hurricane Gilbert in the central and eastern Yucatan Peninsula. *GeoJournal*, 23(4), 337-345.
- Doyle, T. W., Michot, T. C., Day, R. H., & Wells, C. J. (2002). History and ecology of mangroves in the Dry Tortugas. (No. FS 047-02). Lafayette, U.S.A.: U.S. Geological Survey National Wetlands Research Center.
- Doyle, T. W., Smith, T. J. III., & Robblee, M. B. (1995). Wind damage effects of Hurricane Andrew on mangrove communities along the southwest coast of Florida, U.S.A. *Journal of Coastal Research*, (SI-21), 159-168.
- Dronkers, J. (2005). *Dynamics of coastal systems*. Singapore: World Scientific Publishing Co.

- Duarte, C. M., Geertz-Hansen, O., Tampanya, U., Terrados, J., Fortes, M. D., Kamp-Nielsen, L., et al. (1998). Relationship between sediment conditions and mangrove *Rhizophora apiculata* seedling growth and nutrient status. *Marine Ecology Progress Series*, 175, 277-283.
- Duarte, C. M., & Cebrian, J. (1996). The fate of marine autotrophic production. *Limnology and Oceanography*, 41(8), 1758-1766.
- Duke, N. C. (2001). Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. *Wetlands Ecology and Management*, 9(3), 257-269.
- Duke, N. C., Ball, M. C., & Ellison, J. C. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters*, 7(1), 27-47.
- Duke, N. C. (1992). Mangrove floristics and biogeography. In A. I. Robertson, & D. M. Alongi (Eds.), *Tropical mangrove ecosystems* (pp. 63-100). Washington D.C., U.S.A.: American Geophysical Union.
- Duryea, M. L., Blakeslee, G. M., Hubbard, W. G., & Vasquez, R. A. (1996). Wind and trees: A survey of homeowners after Hurricane Andrew. *Journal of Arboriculture*, 22(1), 44-50.
- Ehrenfeld, J. G. (1990). Dynamics and processes of barrier island vegetation. *Reviews in Aquatic Sciences*, 2, 437-480.
- Ellison, A. M. (2000). Mangrove restoration: Do we know enough? *Restoration Ecology*, 8(3), 219-229.
- Ellison, J. C. (1998). Impacts of sediment burial on mangroves. *Marine Pollution Bulletin*, 37, 420-426.

- Ellison, A. M., & Farnsworth, E. J. (1997). Simulated sea level change alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). *Oecologia*, 112(4), 435-446.
- Ellison, A. M., & Stoddart, D. R. (1991). Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *Journal of Coastal Research*, 7, 151-165.
- Ellison, J. C. (1994). Climate change and sea level rise impacts on mangrove ecosystems (A Marine Conservation and Development Report No. vii). Gland, Switzerland: IUCN.
- Elster, C. (2000). Reasons for reforestation success and failure with three mangrove species in Colombia. *Forest Ecology and Management*, 131(1-3), 201-214.
- Emanuel, K. A. (2005). *Divine wind: The history and science of hurricanes*. New York, U.S.A.: Oxford University Press.
- Emery, K. O., Tracy, J. I., & Ladd, L. S. (1949). Submarine geology and topography in the northern Marshalls. *Transactions - American Geophysical Union*, 30, 55-58.
- Everham, E. M. III, & Brokaw, N. V. L. (1996). Forest damage and recovery from catastrophic wind. *Botanical Review*, 62(2), 113-185.
- Ezekiel, M., & Fox, K. A. (1959). *Methods of correlation and regression analysis, linear and curvilinear*. New York, U.S.A.: John Wiley and Sons.
- Feller, I. C., Lovelock, C. E., Berger, U., McKee, K. L., Joye, S. B., & Ball, M. C. (2010). Biocomplexity in mangrove ecosystems. *Annual Review of Marine Science*, 2(1), 395-417.

- Feller, I. C., Lovelock, C. E., & Piou, C. (2009). Growth and nutrient conservation in *Rhizophora mangle* in response to fertilization along latitudinal and tidal gradients. *Smithsonian Contributions to Marine Science*, 38, 345-358.
- Feller, I. C., Whigham, D. F., McKee, K. L., & Lovelock, C. E. (2003). Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia*, 134(3), 405-414.
- Feller, I. C. (2002). The role of herbivory by wood-boring insects in mangrove ecosystems in Belize. *Oikos*, 97(2), 167-176.
- Feller, I. C., McKee, K. L., Whigham, D. F., & O'Neill, J. P. (2002). Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry*, 62(2), 145-175.
- Feller, I. C., Whigham, D. F., O'Neill, J. P., & McKee, K. L. (1999). Effects of nutrient enrichment on within-stand cycling in a mangrove forest. *Ecology*, 80, 2193-2205.
- Feller, I. C., & Mathis, W. N. (1997). Primary herbivory by wood-boring insects along an architectural gradient of *Rhizophora mangle*. *Biotropica*, 29(4), 440-451.
- Feller, I. C. (1995). Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecological Monographs*, 65(4), 477-505.
- Ferwerda, J., Ketner, P., & McGuinness, K. (2007). Differences in regeneration between hurricane damaged and clear-cut mangrove stands 25 years after clearing. *Hydrobiologia*, 591(1), 35-45.
- Field, C. D. (1998). Rehabilitation of mangrove ecosystems: An overview. *Marine Pollution Bulletin*, 37(8-12), 383-392.

- Flood, P. G. (1986). Sensitivity of coral cays to climatic variations, southern Great Barrier Reef, Australia. *Coral Reefs*, 5(1), 13-18.
- Flores-Verdugo, F., González-Farías, F., Ramírez-Flores, O., Amezcua-Linares, F., Yáñez-Arancibia, A., Alvarez-Rubio, M., et al. (1990). Mangrove ecology, aquatic primary productivity, and fish community dynamics in the Teacapán-Agua Brava lagoon-estuarine system (Mexican Pacific). *Estuaries and Coasts*, 13(2), 219-230.
- Flores-Verdugo, F. J., Day, J. W., & Briseño-Dueñas, R. (1987). Structure, litter fall, decomposition, and detritus dynamics of mangroves in a Mexican coastal lagoon with an ephemeral inlet. *Marine Ecology Progress Series*, 35, 83-90.
- Foale, M., & Harries, H. (2009). Farm and forestry production and marketing profile for coconut (*Cocos nucifera*). In C. R. Elevitch (Ed.), *Specialty crops for pacific island agroforestry* (pp. 1-24). Holualoa, Hawai'i: Permanent Agriculture Resources.
- Foster, D. R., Fluet, M., & Boose, E. R. (1999). Human or natural disturbance: Landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications*, 9(2), 555-572.
- Foster, D. R., Knight, D. H., & Franklin, J. F. (1998). Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems*, 1(6), 497-510.
- Foster, D. R., Aber, J. D., Melillo, J. M., Bowden, R. D., & Bazzaz, F. A. (1997). Forest response to disturbance and anthropogenic stress. *Bioscience*, 47(7), 437-445.
- Foster, D. R., & Boose, E. R. (1995). Hurricane disturbance regimes in temperate and tropical forest ecosystems. In M. P. Coutts, & J. Grace (Eds.), *Wind and trees* (pp. 305-339). Cambridge, UK: Cambridge University Press.

- Foster, D. R. (1988a). Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hampshire, U.S.A. *Journal of Ecology*, 76(1), 105-134.
- Foster, D. R. (1988b). Species and stand response to catastrophic wind in central New England, U.S.A. *Journal of Ecology*, 76(1), 135-151.
- Frank, W. M. (1977). The structure and energetics of the tropical cyclone. I. Storm structure. *Monthly Weather Review*, 105(9), 1119-1135.
- Franklin, J., Drake, D. R., Bolick, L. A., Smith, D. S., & Motley, T. J. (1999). Rain forest composition and patterns of secondary succession in the Vava'u Island group, Tonga. *Journal of Vegetation Science*, 10(1), 51-64.
- Franz, E. H., & Bazzaz, F. A. (1977). Simulation of vegetation response to modified hydrologic regimes: A probabilistic model based on niche differentiation in a floodplain forest. *Ecology*, 58(1), 176-183.
- Froede, C. R. (2008). Changes to Dauphin Island, Alabama, brought about by Hurricane Katrina (August 29, 2005). *Journal of Coastal Research*, Supplement 24(4C), 110-117.
- Fromard, F., Puig, H., Mougin, E., Marty, G., Betoulle, J. L., & Cadamuro, L. (1998). Structure, above-ground biomass and dynamics of mangrove ecosystems: New data from French Guiana. *Oecologia*, 115(1-2), 39-53.
- Fujimoto, K. (2004). Below-ground carbon sequestration of mangrove forest in the Asia-Pacific region. In M. Vannuci (Ed.), *Mangrove management and conservation, present and future* (pp. 138-146). New York, U.S.A.: United Nations University Press.

- Gammage, S. (1997). Estimating the returns to mangrove conversion: Sustainable management or short term gain? (Discussion Paper 97-02). London, UK: International Institute for Environment and Development, Environmental Economics Programme.
- Garcia, E., & Holtermann, K. (1998). Calabash Caye, Turneffe Islands Atoll, Belize. In B. Kjerfve (Ed.), CARICOMP – Caribbean coral reef, seagrass and mangrove sites. Coastal region and small island papers 3 (pp. 67-77). Paris, France: UNESCO.
- Gardner, T. A., Côté, I. M., Gill, . A., Grant, A., & Watkinson, A. R. (2005). Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. *Ecology*, 86(1), 174-184.
- Gerritsen, J., & Patten, B. C. (1985). System theory formulation of ecological disturbance. *Ecological Modelling*, 29(1-4), 383-397.
- Getter, C. D., Cintrón, G., Dicks, B., Lewis, R. R., & Seneca, E. D. (1984). The recovery and restoration of salt marshes and mangroves following an oil spill. In J. Cairns Jr., & A. Buikema Jr. (Eds.), *Restoration of habitats impacted by oil spills* (pp. 65-113). Boston, U.S.A.: Butterworth Publishers.
- Gibbs, J., & Greenway, H. (2003). Review: Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. *Functional Plant Biology*, 30(3), 353-353.
- Gibson, D. J. (2002). *Methods in comparative plant population ecology*. Oxford, UK: Oxford University Press.
- Gill, A. M., & Tomlinson, P. B. (1977). Studies on the growth of red mangrove (*Rhizophora mangle* L.) 4. The adult root system. *Biotropica*, 9(3), 145-155.

- Gillham, M. E. (1956). Ecology of the Pembrokeshire Islands: V. Manuring by the colonial seabirds and mammals, with a note on seed distribution by gulls. *Journal of Ecology*, 44(2), 429-454.
- Gischler, E. (2003). Holocene lagoonal development in the isolated carbonate platforms off Belize. *Sedimentary Geology*, 159(1-2), 113-132.
- Gischler, E., & Lomando, A. J. (2000). Isolated carbonate platforms of Belize, Central America: Sedimentary facies, late quaternary history and controlling factors. Geological Society, London, Special Publications, 178(1), 135-146.
- Gischler, E., & Hudson, J. H. (1998). Holocene development of three isolated carbonate platforms, Belize, Central America. *Marine Geology*, 144(4), 333-347.
- Gischler, E., & Lomando, A. J. (1997). Holocene cemented beach deposits in Belize. *Sedimentary Geology*, 110(3-4), 277-297.
- Gischler, E. (1994). Sedimentation on three Caribbean atolls: Glovers Reef, Lighthouse Reef and Turneffe Islands, Belize. *Facies*, 31(1), 243-254.
- Golley, F. B. (1969). Caloric value of wet tropical forest vegetation. *Ecology*, 50(3), 517-519.
- Golley, F. B., Odum, H. T., & Wilson, R. F. (1962). The structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology*, 43(1), 9-19.
- Golovkin, A. N. (1967). The effects of colonial seabirds on the development of phytoplankton. *Oceanology*, 7, 521-529.
- Goodban, J. W. D. (1952). A report on the coconut industry of British Honduras. British Honduras: Director of Agriculture, British Honduras. Belmopan, Belize: Belize Archives and Records Service.

- Gordon, D. M. (1988). Disturbance to mangroves in tropical-arid western Australia: Hypersalinity and restricted tidal exchange as factors leading to mortality. *Journal of Arid Environments*, 15, 117-145.
- Gosselink, J. (1984). The ecology of delta marshes of coastal Louisiana: A community profile (No. FWS/OBS-84-09). Louisiana, U.S.A.: Louisiana State University, Baton Rouge, Center for Wetland Resources.
- Gourlay, M. R. (1994). Wave transformation on a coral reef. *Coastal Engineering*, 23(1-2), 17-42.
- Gourlay, M. R. (1988). Coral cays: Products of wave action and geological processes in a biogenic environment. *Proceedings of the 6th International Coral Reef Symposium, Australia*. pp. 491-496.
- Gourlay, M. R. (1987). Some potential problems associated with boat harbours and marine structures on coral reefs. *Fringing Reef Workshop: Science Industry and Management, Magnetic Island, Australia*. pp. 214-225.
- Green, D. R., Cummins, R., Right, R., & Miles, J. (1993). A methodology for acquiring information on vegetation succession from remotely sensed imagery. In R. Haines-Young, D. R. Green & S. Cousins (Eds.), *Landscape ecology and geographic information systems* (pp. 111-128). Bristol, P.A., U.S.A.: Taylor and Francis, Inc.
- Greer, J. E., & Kjerfve, B. (1982). Water currents adjacent to Carrie Bow Cay, Belize. In K. Rützler, & I. G. Macintyre (Eds.), *The atlantic barrier reef ecosystem at Carrie Bow Cay, Belize. I. Structure and communities* (pp. 53-58). Washington, D.C., U.S.A.: Smithsonian Institution Press.

- Grime, J. P. (2001). Plant strategies, vegetation processes, and ecosystem properties (2nd ed.). New York, U.S.A.: John Wiley and Sons Ltd.
- Grime, J. P., & Campbell, B. D. (1991). Growth rate, habitat productivity, and plant strategy as predictors of stress response. In H. A. Mooney, W. E. Winner & E. J. Pell (Eds.), Responses of plants to multiple stresses (pp. 143-159). New York, U.S.A.: Academic Press.
- Grime, J. P. (1979). Plant strategies and vegetation processes. New York, U.S.A.: John Wiley and Sons Ltd.
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111(982), 1169-1194.
- Grime, J. P. (1974). Vegetation classification by reference to strategies. *Nature*, 250(5461), 26-31.
- Grove, S. J., Turton, S. M., & Siegenthaler, D. T. (2000). Mosaics of canopy openness induced by tropical cyclones in lowland rain forests with contrasting management histories in northeastern Australia. *Journal of Tropical Ecology*, 16, 883-894.
- Gustafson, E. J., & Gardner, R. H. (1996). The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, 77(1), 94-107.
- Harcombe, P. A., Harmon, M. E., & Greene, S. E. (1990). Changes in biomass and production over 53 years in a coastal *Picea sitchensis*-*Tsuga heterophylla* forest approaching maturity. *Canadian Journal of Forest Research*, 20(10), 1602-1610.
- Harmon, M. E., & Hua, C. (1991). Coarse woody debris dynamics in two old-growth ecosystems. *Bioscience*, 41(9), 604-610.

- Harper, J. L. (1977). *Population biology of plants*. London, UK: Academic Press.
- Harris, S. W., & Marshall, W. H. (1963). Ecology of water-level manipulations on a northern marsh. *Ecology*, 44(2), 331-343.
- Harrison, N., Cordova, I., Richardson, P., & Dibonito, R. (1999). Detection and diagnosis of lethal yellowing. In C. Oropeza, J. L. Verdeil, G. R. Ashburner, R. Cardena & J. M. Santamaria (Eds.), *Current advances in coconut biotechnology* (pp. 183-196). Dordrecht, Netherlands: Kluwer Academic Publishers.
- Haslett, S. K. (2000). *Coastal systems*. London, UK: Routledge, Taylor and Francis Group.
- Haug, G. H., Tiedemann, R., Zahn, R., & Ravelo, A. C. (2001). Role of Panama uplift on oceanic freshwater balance. *Geology*, 29(3), 207-210.
- Hendry, M., & Digerfeldt, G. (1989). Palaeogeography and palaeoenvironments of a tropical coastal wetland and offshore shelf during Holocene submergence, Jamaica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 73, 1-10.
- Hensel, P., & Proffitt, C. E. (2002). Hurricane Mitch: Acute impacts on mangrove forest structure and an evaluation of recovery trajectories: Executive summary. (Open File 03-182). U.S.A.: USGS.
- Hiraishi, T., & Harada, K. (2003). Greenbelt tsunami prevention in south-Pacific region. (No. 42) Report of the Port and Airport Research Institute, 42(2), 1-23.
- Hodgson, G., & Dixon, J. A. (1988). *Logging versus tourism in Palawan: An environmental and economic analysis*. Honolulu, Hawaii, U.S.A.: Environment and Policy Institute, East-West Center.
- Hook, D. D., Buford, M., A., & Williams, T. M. (1991). Impact of Hurricane Hugo on the south Carolina coastal plain forest. *Journal of Coastal Research*, 8, 291-300.

- Houghton, R. A. (2007). Balancing the global carbon budget. *Annual Review of Earth and Planetary Sciences*, 35(1), 313-347.
- Hoyt, J. H. (1967). Barrier island formation. *Geological Society of America Bulletin*, 78(9), 1125-1136.
- Huggett, R. J. (1995). *Geoecology: An evolutionary approach*. New York, U.S.A.: Routledge.
- Hughes, M. L., McDowell, P. F., & Marcus, W. A. (2006). Accuracy assessment of georectified aerial photographs: Implications for measuring lateral channel movement in a GIS. *Geomorphology*, 74(1-4), 1-16.
- Hutchings, P. A., & Saenger, P. (1987). *Ecology of mangroves*. St. Lucia, Australia: University of Queensland Press.
- Iwasa, Y., & Roughgarden, J. (1984). Shoot/root balance of plants: Optimal growth of a system with many vegetative organs. *Theoretical Population Biology*, 25(1), 78-105.
- James, N. P., Ginsburg, R. N., Marszalek, D. S., & Choquette, P. W. (1976). Facies and fabric specificity of early subsea cements in shallow Belize (British Honduras) reefs. *Journal of Sedimentary Research*, 46(3), 523-544.
- Jarvinen, B. R., Neumann, C. J., & Davis, M. A. S. (1984). A tropical cyclone data tape for the north Atlantic basin, 1886-1983: Contents, limitations, and uses (NOAA Technical Memorandum, NWS NHC No. 22). Coral Gables, Florida: NOAA.
- Jennerjahn, T., & Ittekkot, V. (2002). Relevance of mangroves for the production and deposition of organic matter along tropical continental margins. *Naturwissenschaften*, 89(1), 23-30.

- Jiménez, J. A. (1990). The structure and function of dry weather mangroves on the Pacific coast of Central America, with emphasis on *Avicennia bicolor* forests. *Estuaries and Coasts*, 13(2), 182-192.
- Jiménez, J. A., & Soto, R. (1985). Patrones regionales en la estructura y composición florística de los manglares de la costa pacífica de Costa Rica. *Revista De Biología Tropical*, 33, 25-37.
- Jordan, C. F. (1985). *Nutrient cycling in tropical forest ecosystems: Principles and their application in management and conservation*. New York, U.S.A.: Wiley.
- Jorgensen, J. R., Wells, C. G., & Metz, L. J. (1975). The nutrient cycle: Key to continuous forest production. *Journal of Forestry*, 73(7), 400-403.
- Kamaludin, H. (1993). The changing mangrove shorelines in Kuala Kurau, peninsular Malaysia. *Sedimentary Geology*, 83(3-4), 187-197.
- Karr, J. R., & Freemark, K. E. (1985). Disturbance and vertebrates: An integrative perspective. In S. T. A. Pickett, & P. S. White (Eds.), *The ecology of natural disturbance and patch dynamics* (pp. 153-168). New York, U.S.A.: Academic Press.
- Kasawani, I., Kamaruzaman, J., & Nurun-Nadirah, M. I. (2007). A study of forest structure, diversity index and above-ground biomass. 5th WSEAS International Conference on Environment, Ecosystems and Development, Tenerife, Spain. pp. 269-276.
- Kathiresan, K., & Bingham, B. L. (2001). *Biology of mangroves and mangrove ecosystems*. Advances in marine biology. London, UK: Academic Press.
- Keddy, P. A. (1984). Quantifying a within-lake gradient of wave energy in Gillfillan Lake, Nova Scotia. *Canadian Journal of Botany*, 62(2), 301-309.

- Keddy, P. A. (1983). Shoreline vegetation in Axe Lake, Ontario: Effects of exposure on zonation patterns. *Ecology*, 64(2), 331-344.
- Keddy, P. A. (1982). Quantifying within-lake gradients of wave energy: Interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. *Aquatic Botany*, 14(0), 41-58.
- Keim, B. D., Muller, R. A., & Stone, G. W. (2007). Spatiotemporal patterns and return periods of tropical storm and hurricane strikes from Texas to Maine. *Journal of Climate*, 20(14), 3498-3509.
- Kempes, C. P., West, G. B., Crowell, K., & Girvan, M. (2011). Predicting maximum tree heights and other traits from allometric scaling and resource limitations. *PLoS ONE*, 6(6), 1-10.
- Kench, P. S., McLean, R. F., & Nichol, S. L. (2005). New model of reef-island evolution: Maldives, Indian Ocean. *Geology*, 33(2), 145-148.
- Kerekes, J. J. (1994). Preface. In J. J. Kerekes (Ed.), *Aquatic birds in the trophic web of lakes* (pp. viii). Dordrecht, The Netherlands: Kluwer Academic Publishers.
- King, D. M. (1991). Costing out restoration. *Restoration and Management Notes*, 9(1), 15-21.
- Kjerfve, B., Ogden, J. C., Garzón-Ferreira, J., Jordán-Dahlgreen, E., De Meyer, K., Penchaszadeh, P., et al. (1998). CARICOMP: A caribbean network of marine laboratories, parks and reserves for coastal monitoring and scientific collaboration. In B. Kjerfve (Ed.), *CARICOMP – Caribbean coral reef, seagrass and mangrove sites. coastal region and small island papers 3* (pp. 1-16). Paris, France: UNESCO.

- Kjerfve, B., Rützler, K., & Kierspe, G. H. (1982). Tides at Carrie Bow Cay, Belize. In K. Rützler, & I. G. Macintyre (Eds.), *The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize 1. structure and communities* (pp. 47-51). Washington, D.C. U.S.A.: Smithsonian Institution Press.
- Kobara, S., & Heyman, W. D. (2010). Sea bottom geomorphology of multi-species spawning aggregation sites in Belize. *Marine Ecology Progress Series*, 405, 243-254.
- Koch, M. S., & Snedaker, S. C. (1997). Factors influencing *Rhizophora mangle* L. seedling development in Everglades carbonate soils. *Aquatic Botany*, 59(1-2), 87-98.
- Kölliker, M., & Richner, H. (2004). Navigation in a cup: Chick positioning in great tit, *Parus major*, nests. *Animal Behaviour*, 68(4), 941-948.
- Koltes, K. H., Tschirky, J. J., & Feller, I. C. (1998). *Carrie Bow Cay, Belize*. (No. 3). Paris, France: United Nations Educational, Scientific and Cultural Organization (UNESCO).
- Komiyama, A., Santiean, T., Higo, M., Patanaponpaiboon, P., Kongsangchai, J., & Ogino, K. (1996). Microtopography, soil hardness and survival of mangrove (*Rhizophora apiculata* BL.) seedlings planted in an abandoned tin-mining area. *Forest Ecology and Management*, 81(1-3), 243-248.
- Kozak, A., & Smith, J. H. G. (1993). Standards for evaluating taper estimating systems. *The Forestry Chronicle*, 69(4), 438-444.
- Kozlowski, T. T. (1997). *Responses of woody plants to flooding and salinity*. Tree Physiology Monograph No. 1. Victoria, B.C., Canada: Heron Publishing.
- Kozlowski, T. T., & Pallardy, S. G. (1997). *Growth control in woody plants*. San Diego California, U.S.A.: Academic Press.

- Kozlowski, T. T., Kramer, P. J., & Pallardy, S. G. (1991). *The physiological ecology of woody plants*. San Diego, U.S.A.: Academic Press.
- Kozlowski, T. T. (1982). Water supply and tree growth. Part II. Flooding. *Forestry Abstracts*, 43(3), 145-161.
- Kramer, P. A., & Kramer, P. R. (2002). *Ecoregional conservation planning for the Mesoamerican Caribbean Reef*. Washington, D.C., U.S.A.: World Wildlife Fund.
- Krauss, K. W., Lovelock, C. E., McKee, K. L., Lopez-Hoffman, L., Ewe, S. M. L., & Sousa, W. P. (2008). Environmental drivers in mangrove establishment and early development: A review. *Aquatic Botany*, 89, 105-27.
- Krauss, K. W., Doyle, T., Twilley, R. T., Rivera-Monroy, V., & Sullivan, J. (2006). Evaluating the relative contributions of hydroperiod and soil fertility on growth of south Florida mangroves. *Hydrobiologia*, 569(1), 311-324.
- Krauss, K. W., Allen, J. A., & Cahoon, D. R. (2003). Differential rates of vertical accretion and elevation change among aerial root types in Micronesian mangrove forests. *Estuarine, Coastal and Shelf Science*, 56(2), 251-259.
- Kuehl, R. O. (1994). *Statistical principles of research design and analysis*. Belmont, California, U.S.A.: Duxbury Press.
- Kumara, M. P., Jayatissa, L. P., Krauss, K. W., Phillips, D. H., & Huxham, M. (2010). High mangrove density enhances surface accretion, surface elevation change, and tree survival in coastal areas susceptible to sea-level rise. *Oecologia*, 164, 545-553.
- Lal, P. N. (1990). *Conservation or conversion of mangroves in Fiji*. Honolulu, Hawaii, U.S.A.: Environment and Policy Institute, East-West Center.

- Lambers, H., Chapin III, F. S., & Pons, T. L. (1998). *Plant physiological ecology*. New York, U.S.A.: Springer.
- Larcombe, P., & Carter, R. M. (2004). Cyclone pumping, sediment partitioning and the development of the Great Barrier Reef shelf system: A review. *Quaternary Science Reviews*, 23(1-2), 107-135.
- Lidz, B. H., Reich, C. D., & Shinn, E. A. (2003). Regional quaternary submarine geomorphology in the Florida Keys. *Geological Society of America Bulletin*, 115(7), 845-866.
- Lieth, H., & Whittaker, R. H. (1975). In H. Lieth & R. H. Whittaker. (Eds.), *Primary productivity of the biosphere*. New York, U.S.A.: Springer-Verlag.
- Lindeboom, H. J. (1984). The nitrogen pathway in a penguin rookery. *Ecology*, 65(1), 269-277.
- Lirman, D. (2000). Fragmentation in the branching coral *Acropora palmata* (Lamarck): Growth, survivorship, and reproduction of colonies and fragments. *Journal of Experimental Marine Biology and Ecology*, 251(1), 41-57.
- Littler, M. M., & Littler, D. S. (1990). Productivity and nutrient relationships in psammophytic versus epilithic forms of Bryopsidales (Chlorophyta): Comparisons based on a short-term physiological assay. *Hydrobiologia*, 204-205(1), 49-55.
- Lodge, D. J., Scatena, F. N., Asbury, C. E., & Sanchez, M. J. (1991). Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. *Biotropica*, 23(4-A), 336-342.

- Longuet-Higgins, M. S., & Stewart, R. W. (1962). Radiation stress and mass transport in gravity waves, with application to "surfbeats". *Journal of Fluid Mechanics*, 13, 481-504.
- Lopez-Portillo, J., & Ezcurra, E. (1989). Response of three mangroves to salinity in two geofoms. *Functional Ecology*, 3(3), 355-361.
- Lopez-Portillo, J., & Ezcurra, E. (1985). Litter fall of *Avicennia germinans* L. in a one-year cycle in a mudflat at the Laguna de Mecoacan, Tabasco, Mexico. *Biotropica*, 17(3), 186-190.
- Lovelock, C. E., Ball, M. C., Choat, B., Engelbrecht, B. M. J., Holbrook, N. M., & Feller, I. C. (2006). Linking physiological processes with mangrove forest structure: Phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. *Plant, Cell and Environment*, 29(5), 793-802.
- Lovelock, C. E., Feller, I. C., McKee, K. L., & Thompson, R. (2005). Variation in mangrove forest structure and sediment characteristics in Bocas del Toro, Panama. *Caribbean Journal of Science*, 41(3), 456-464.
- Lovelock, C. E., Feller, I. C., McKee, K. L., Engelbrecht, B. M. J., & Ball, M. C. (2004). The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Functional Ecology*, 18(1), 25-33.
- Lowe, R. J., Falter, J. L., Bandet, M. D., Pawlak, G., Atkinson, M. J., Monismith, S. G., et al. (2005). Spectral wave dissipation over a barrier reef. *Journal of Geophysical Research*, 110(C04001), 1-16.
- Lugo, A. E. (1999). Ecological aspects of catastrophes in Caribbean islands. *Acta Cientifica*, 2, 24-31.

- Lugo, A. E. (1997). Old-growth mangrove forests in the United States. *Conservation Biology*, 11(1), 11-20.
- Lugo, A. E. (1990). Fringe wetlands. In A. E. Lugo, M. Brinson & S. Brown (Eds.), *Forested wetlands: Ecosystems of the world 15* (pp. 143-169). New York, U.S.A.: Elsevier Science Publishing.
- Lugo, A. E., Brown, S., & Chapman, J. (1988). An analytical review of production rates and stemwood biomass of tropical forest plantations. *Forest Ecology and Management*, 23(2-3), 179-200.
- Lugo, A. E., Sanchez, M. J., & Brown, S. (1986). Land use and organic carbon content of some subtropical soils. *Plant and Soil*, 96(2), 185-196.
- Lugo, A. E., Applefield, M., Pool, D. J., & McDonald, R. B. (1983). The impact of Hurricane David on the forests of Dominica. *Canadian Journal of Forest Research*, 13(2), 201-211.
- Lugo, A. E. (1980). Mangrove ecosystems: Successional or steady state? *Biotropica*, 12(Supp. 2), 65-72.
- Lugo, A. E., & Snedaker, S. C. (1975). Properties of a mangrove forest in southern Florida. *Proceedings of International Symposium on Biology and Management of Mangroves*, Honolulu, Hawaii. pp. 170-212.
- Lugo, A. E., & Snedaker, S. C. (1974). The ecology of mangroves. *Annual Review of Ecology and Systematics*, 5(1), 39-64.
- Lugo-Fernández, A., Hernández-Ávila, M. L., & Roberts, H. H. (1994). Wave-energy distribution and hurricane effects on Margarita Reef, southwestern Puerto Rico. *Coral Reefs*, 13(1), 21-32.

- Lynch, J. F. (1991). Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. *Biotropica*, 23(4a), 488-496.
- MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Woodstock, Oxfordshire, UK: Princeton University Press.
- Macintyre, I. G., Toscano, M. A., Lighty, R. G., & Bond, G. B. (2004). Holocene history of the mangrove islands of Twin Cays, Belize, Central America. *Atoll Research Bulletin*, 510, 1-14.
- Macintyre, I. G., Littler, M. M., & Littler, D. S. (1995). Holocene history of Tobacco Range, Belize, Central America. *Atoll Research Bulletin*, 430, 1-18.
- Macintyre, I. G., Graus, R. R., Reinthal, P. N., Littler, M. M., & Littler, D. S. (1987). The barrier reef sediment apron: Tobacco Reef, Belize. *Coral Reefs*, 6(1), 1-12.
- MacKie, E. (1963). Appendix XXII.2. Some Maya pottery from Grand Bogue Point, Turneffe Islands, British Honduras. In D. R. Stoddart, *Effects of Hurricane Hattie on the British Honduras Reefs and Cays, October 30–31, 1961* (pp. 131-135). *Atoll Research Bulletin*, 95.
- Madsen, J. D., Chambers, P. A., James, W. F., Koch, E. W., & Westlake, D. F. (2001). The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia*, 444(1), 71-84.
- Marchand, C., Baltzer, F., Lallier-Vergès, E., & Albéric, P. (2004). Pore-water chemistry in mangrove sediments: Relationship with species composition and developmental stages (French Guiana). *Marine Geology*, 208(2-4), 361-381.
- Mascarenhas, A., Paropakari, A. L., & Prakash Babu, C. (1993). On the possibility of allochthonous peat on the inner shelf off Karwar. *Current Science*, 64, 684-687.

- Mason, E. (2008). Influences of silviculture, genetics and environment on *radiata* pine corewood properties results from recent studies and a future direction. *New Zealand Journal of Forestry*, 53(2), 26-31.
- Massel, S. R., Furukawa, K., & Brinkman, R. M. (1999). Surface wave propagation in mangrove forests. *Fluid Dynamics Research*, 24(4), 219-249.
- Matthijs, S., Tack, J., Van Speybroeck, D., & Koedam, N. (1999). Mangrove species zonation and soil redox state, sulphide concentration and salinity in Gazi Bay (Kenya), a preliminary study. *Mangroves and Salt Marshes*, 3(4), 243-249.
- Maust, B. E., Espadas, F., Talavera, C., Aguilar, M., Santamaria, J. M., & Oropeza, C. (2003). Changes in carbohydrate metabolism in coconut palms infected with the lethal yellowing phytoplasma. *Phytopathology*, 93(8), 976-981.
- Mazda, Y., Wolanski, E., King, B., Sasa, A., Ohtsuka, D., & Magi, M. (1997). Drag force due to vegetation in mangrove swamps. *Mangroves and Salt Marshes*, 1, 93-199.
- McCloskey, T.A. (2009). Proxy records of paleohurricanes for the western and southern Caribbean. (Thesis). Louisiana State University and Agricultural and Mechanical College, U.S.A. pp. 1-702
- McGill, J. (1996). Turneffe Islands development guidelines, part one: Terrestrial (No. CZM/iczm-904). Belize City, Belize: Belize Coastal Zone Management Unit.
- McKee, K. L. (2011). Biophysical controls on accretion and elevation change in Caribbean mangrove ecosystems. *Estuarine, Coastal and Shelf Science*, 91(4), 475-483.
- McKee, K. L., Cahoon, D. R., & Feller, I. C. (2007a). Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. *Global Ecology and Biogeography*, 16(5), 545-556.

- McKee, K. L., Rooth, J. E., & Feller, I. C. (2007b). Mangrove recruitment after forest disturbance is facilitated by herbaceous species in the Caribbean. *Ecological Applications*, 17(6), 1678-1693.
- McKee, K. L. (1995a). Interspecific variation in growth, biomass partitioning, and defensive characteristics of neotropical mangrove seedlings: Response to light and nutrient availability. *American Journal of Botany*, 82(3), 299-307.
- McKee, K. L. (1995b). Seedling recruitment patterns in a Belizean mangrove forest: Effects of establishment ability and physico-chemical factors. *Oecologia*, 101(4), 448-460.
- McKee, K. L. (1993). Soil physicochemical patterns and mangrove species distribution-reciprocal effects? *Journal of Ecology*, 81(3), 477-487.
- Meadows, D. G., Caballero, J. P., Kruse, S. E., & Vacher, H. L. (2004). Variation of salinity in brackish-water lenses of two Florida Keys. *Journal of Coastal Research*, 20(2), 386-400.
- Meerman, J. C. (2006). Mangrove and conservation value assessment at northern Turneffe. Belmopan, Belize: Belize Forest Department, Ministry of Natural Resources.
- Mergen, F. (1954). Mechanical aspects of wind-breakage and windfirmness. *Journal of Forestry*, 52(2), 119-125.
- Mertley, J., Chub, A., & Jarrah, R. (1987). Growing coconuts in Belize. Belmopan, Belize: Agricultural Information Unit, Ministry of Agriculture. Belmopan, Belize: Belize Archives and Records Service.
- Michener, W. K., Blood, E. R., Bildstein, K. L., Brinson, M. M., & Gardner, L. R. (1997). Climate change, hurricanes and tropical storms, and rising sea level in coastal wetlands. *Ecological Applications*, 7(3), 770-801.

- Middleton, B. A., & McKee, K. L. (2001). Degradation of mangrove tissues and implications for peat formation in Belizean island forests. *The Journal of Ecology*, 89(5), 818-828.
- Minty, C., Murray, M., & Zisman, M. (1995). Turneffe terrestrial resource reconnaissance (No. 2 Technical Report Series). Belize City, Belize. Coral Cay Conservation and University College of Belize, MRC.
- Mooney, H. A. (1972). The carbon balance of plants. *Annual Review of Ecology and Systematics*, 3, 315-346.
- Morgan, J. L., Gergel, S. E., & Coops, N. C. (2010). Aerial Photography: A rapidly evolving tool for ecological management. *BioScience*, 60(1), 47-59.
- Morrissey, D., Beard, C., Morrison, M., Craggs, R., & Lowe, M. (2007). The New Zealand mangrove: Review of the current state of knowledge. (No. 325). New Zealand: Auckland Regional Council.
- Mumby, P. J., & Hastings, A. (2008). The impact of ecosystem connectivity on coral reef resilience. *Journal of Applied Ecology*, 45(3), 854-862.
- Mumby, P. J., Edwards, A. J., Arias-González, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., et al. (2004). Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, 427, 533-536.
- Munk, W. H., & Sargent, M. C. (1948). Adjustment of Bikini Atoll to ocean waves. *Transactions, American Geophysical Union*, 29(6), 855-860.
- Murray, M. R., Zisman, S. A., Furley, P. A., Munro, D. M., Gibson, J., Ratter, J., et al. (2003). The mangroves of Belize: Part 1. Distribution, composition and classification. *Forest Ecology and Management*, 174(1-3), 265-279.

- Murray, M. R., Zisman, S. A., & Minty, C. D. (1999). Soil-plant relationships and a revised vegetation classification of Turneffe Atoll, Belize. *Atoll Research Bulletin*, 464, 1-31.
- Murray, D. R. (1986). *Seed dispersal*. Orlando, Florida, U.S.A.: Academic Press.
- Nathan, R. (2001). Dispersal biogeography. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (pp. 127-152). San Diego, California, U.S.A.: Academic Press.
- Neumann, C. J., Cry, G. W., Caso, E. L., & Jarvinen, B. R. (1981). *Tropical cyclones of the north Atlantic Ocean, 1871-1980*. Washington, D.C., U.S.A.: National Oceanic and Atmospheric Administration, National Weather Service.
- Newton, A. C. (2007). *Forest ecology and conservation: A handbook of techniques*. New York, U.S.A.: Oxford University Press.
- Nickerson, N., & Thibodeau, F. (1985). Association between pore water sulfide concentrations and the distribution of mangroves. *Biogeochemistry*, 1(2), 183-192.
- Nielsen, N., & Nielsen, J. (2002). Vertical growth of a young back barrier salt marsh, Skallingen, SW Denmark. *Journal of Coastal Research*, 18(2), 287-299.
- NOAA. (2010a). Atlantic Oceanographic and Meteorological Laboratory - Hurricane Research Division. Retrieved 03/01, 2010, from <http://www.aoml.noaa.gov/hrd/hurdat/DataByYearandStorm.htm>
- NOAA. (2010b). National Hurricane Center – Glossary of NHC terms. Retrieved 05/15, 2010, from <http://www.nhc.noaa.gov/aboutgloss.shtml#1>
- NOAA CoRIS. (2009). NOAA's Coral Reef Information System - Glossary of terminology. Retrieved 03/15, 2009, from http://www8.nos.noaa.gov/coris_glossary/

- Nye, P. H. (1961). Organic matter and nutrient cycles under moist tropical forest. *Plant and Soil*, 13(4), 333-346.
- Oliver, J. (1982). The geographic and environmental aspects of mangrove communities: Climate. In B. F. Clough (Ed.), *Mangrove ecosystems in Australia – structure, function and management* (pp. 19-30). Canberra, Australia: ANU Press.
- Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44(2), 322-331.
- Onuf, C. P., Teal, J. M., & Valiela, I. (1977). Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. *Ecology*, 58, 514-526.
- Orson, R., Panageotou, W., & Leatherman, S. P. (1985). Response of tidal salt marshes of the U.S. Atlantic and gulf coasts to rising sea levels. *Journal of Coastal Research*, 1(1), 29-37.
- Osborne, K., & Smith, T. J. III. (1990). Differential predation on mangrove propagules in open and closed canopy forest habitats. *Vegetatio*, 89(1), 1-6.
- Ovington, J. D. (1961). Some aspects of energy flow in plantations of *Pinus sylvestris* L. *Annals of Botany*, 25(1), 12-20.
- Paine, R. T., Tegner, M. J., & Johnson, E. A. (1998). Compounded perturbations yield ecological surprises. *Ecosystems*, 1(6), 535-545.
- Paine, R. T., & Levin, S. A. (1981). Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecological Monographs*, 51(2), 145-178.
- Parkinson, R. W., De Laune, R. D., & White, J. R. (1994). Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean region. *Journal of Coastal Research*, 10(4), 1077-1086.

- Parrish, J. D. (1989). Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series*, 58, 143-160.
- Patterson, W. A. I., & Foster, D. R. (1990). Tabernacle pines. *Journal of Forestry*, 88(12), 23-25.
- Pearce, D. W. (2001). The economic value of forest ecosystems. *Ecosystem Health*, 7(4), 284-296.
- Peckol, P. M., Curran, H. A., Floyd, E. Y., Robbart, M. L., Greenstein, B. J., & Buckman, K. L. (2003). Assessment of selected reef sites in northern and south-central Belize, including recovery from bleaching and hurricane disturbances (stony corals, algae and fish). In J. C. Lang (Ed.), *Status of coral reefs in the western Atlantic* (pp. 146-171). Washington, D.C., U.S.A.: Smithsonian Institution, *Atoll Research Bulletin* 496.
- Peet, R. K. (1981). Changes in biomass and production during secondary forest succession. In D. C. West, H. H. Shugart & C. B. Botkin (Eds.), *Forest succession: Concepts and application* (pp. 324-338). New York, U.S.A.: Springer-Verlag.
- Perry, D. M. (1988). Effects of associated fauna on growth and productivity in the red mangrove. *Ecology*, 69(4), 1064-1075.
- Peterson, C. J., & Pickett, S. T. A. (1991). Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. *Forest Ecology and Management*, 42(3-4), 205-217.
- Pezeshki, S. R., DeLaune, R. D., & Patrick, W. H. J. (1990). Differential response of selected mangroves to soil flooding and salinity: Gas exchange and biomass partitioning. *Canadian Journal of Forest Research*, 20(7), 869-874.

- Phillips, O. L., Malhi, Y., Higuchi, N., Laurance, W. F., Núñez, P. V., Vásquez, R. M., et al. (1998). Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science*, 282(5388), 439-442.
- Pickett, S. T. A., & White, P. S. (1985). *The ecology of natural disturbance and patch dynamics*. Orlando, Florida, U.S.A.: Academic Press.
- Pierce, G. (1981). The influence of flood frequency on wetlands of the Allegheny river flood plain in Cattaraugus Co., New York. *Wetlands*, 1(1), 87-104.
- Piou, C., Feller, I. C., Berger, U., & Chi, F. (2006). Zonation patterns of Belizean offshore mangrove forests 41 years after a catastrophic hurricane disturbance. *Biotropica*, 38(3), 365-374.
- Pitman, R., Bastrup-Birk, A., Breda, N., & Rautio, P. (2010). *Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests: Sampling and analysis of litterfall. (Part XIII No. 13)*. Hamburg, Germany: UNECE ICP Forests Programme Coordinating Centre.
- Pittman, S. J., & McAlpine, C. A. (2003). Movements of marine fish and decapod crustaceans: Process, theory and application. *Advances in Marine Biology*, 44, 205-294.
- Platt, S. G., Meerman, J. C., & Rainwater, T. R. (1999). Diversity, observations, and conservation of the herpetofauna of Turneffe, Lighthouse, and Glovers Atolls, Belize. *British Herpetological Society Bulletin*, 66, 1-13.
- Polis, G. A., & Hurd, S. D. (1996). Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist*, 147(3), 396-423.

- Pool, D. J., Snedaker, S. C., & Lugo, A. E. (1977). Structure of mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica. *Biotropica*, 9(3), 195-212.
- Pool, D. J., Lugo, A. E., & Snedaker, S. C. (1975). Litter production in mangrove forests of southern Florida and Puerto Rico. *Proceedings of the International Symposium on Biology and Management of Mangroves*, University of Florida, Gainesville, Florida, U.S.A. pp. 213-237.
- Powell, G. V. N., Fourqurean, J. W., Kenworthy, W. J., & Zieman, J. C. (1991). Bird colonies cause seagrass enrichment in a subtropical estuary: Observational and experimental evidence. *Estuarine, Coastal and Shelf Science*, 32(6), 567-579.
- Pringle, J. S. (1982). Floristic observations on South Water and Carrie Bow Cays, Stann Creek District, Belize, in 1979-1980. *Atoll Research Bulletin*, 259, 1-12.
- Putz, F. E., & Chan, H. T. (1986). Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. *Forest Ecology and Management*, 17(2-3), 211-230.
- Rabinowitz, D. (1978a). Dispersal properties of mangrove propagules. *Biotropica*, 10(1), 47-57.
- Rabinowitz, D. (1978b). Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. *Journal of Biogeography*, 5(2), 113-133.
- Regent Realty Limited. (2008). Regent Realty Limited – Buying Property. Retrieved 06/25, 2008, from <http://www.regentrealtybelize.com/>
- Robertson, P. A., Weaver, G. T., & Cavanaugh, J. A. (1978). Vegetation and tree species patterns near the Northern Terminus of the Southern Floodplain Forest. *Ecological Monographs*, 48(3), 249-267.

- Romero, L. M., Smith, T. J. III., & Fourqurean, J. W. (2005). Changes in mass and nutrient content of wood during decomposition in a south Florida mangrove forest. *Journal of Ecology*, 93(3), 618-631.
- Rooker, J. R., & Dennis, G. D. (1991). Diel, lunar, and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science*, 49, 684-698.
- Rosati, J. D. (2009). Barrier island migration over a consolidating substrate. (Thesis). Louisiana State University and Agricultural and Mechanical College, U.S.A. pp. 1-230.
- Rose, M. D., & Polis, G. A. (1998). The distribution and abundance of coyotes: The effects of allochthonous food subsidies from the sea. *Ecology*, 79(3), 998-1007.
- Ross, M. S., Ruiz, P. L., Sah, J. P., Reed, D. L., Walters, J., & Meeder, J. F. (2006). Early post-hurricane stand development in fringe mangrove forests of contrasting productivity. *Plant Ecology*, 185(2), 283-297.
- Ross, M. S., , R., P. L., Telesnicki, G. J., & Meeder, J. F. (2001). Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (U.S.A.). *Wetlands Ecology and Management*, 9(1), 27-37.
- Roth, L. C. (1992). Hurricanes and mangrove regeneration: Effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. *Biotropica*, 24(3), 375-384.
- Saatchi, S. S., Houghton, R. A., Dos Santos Alvalà, R. C., Soares, J. V., & Yu, Y. (2007). Distribution of aboveground live biomass in the Amazon Basin. *Global Change Biology*, 13(4), 816-837.
- Saenger, P. (2002). *Mangrove ecology, silviculture, and conservation*. Dordrecht, The Netherlands: Kluwer Academic Publishers.

- Saenger, P., & Snedaker, S. (1993). Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia*, 96(3), 293-299.
- Saenger, P. (1985). An initial attempt to assess life strategies in Australian mangroves. In K. N. Bardsley, J. D. S. Davies & C. D. Woodroffe (Eds.), *Coasts and tidal wetlands of the Australian monsoon region (NARU Mangrove Monographs, pp. 187-200)*. Darwin, Australia: Australian National University, North Australia Research Unit.
- Saenger, P., Hegerl, E. J., & Davie, J. D. S. (1983). Global status of mangrove ecosystems. *The Environmentalist*, 3(Supp. 3), 1-88.
- Sayer, E. J., Powers, J. S., & Tanner, E. V. J. (2007). Increased litterfall in tropical forests boosts the transfer of soil CO₂ to the atmosphere. *PLoS ONE*, 2(12), e1299-e1304.
- Scatena, F. N., Moya, S., Estrada, C., & China, J. D. (1996). The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica*, 28(4-A), 424-440.
- Scatena, F. N., & Larsen, M. C. (1991). Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica*, 23(4-A), 317-323.
- Schaeffer-Novelli, Y., Cintrón-Molero, G., Adaime, R. R., & de Camargo, T. M. (1990). Variability of mangrove ecosystems along the Brazilian coast. *Estuaries and Coasts*, 13(2), 204-218.
- Schott, T., Landsea, C., Hafele, G., Lorens, J., Taylor, A., Thurm, H., et al. (2009). The Saffir-Simpson hurricane wind scale. Retrieved 06/05, 2009, from <http://www.nhc.noaa.gov/sshws.shtml>

- Schwartz, M. L. (1971). The multiple causality of barrier islands. *The Journal of Geology*, 79(1), 91-94.
- Scoffin, T. P., Stoddart, D. R., McLean, R. F., & Flood, P. G. (1978). The recent development of the reefs in the northern province of the Great Barrier Reef. *Philosophical Transactions of the Royal Society of London. Biological Sciences, Series B*, 284(999), 129-139.
- Sedberry, G. R., & Carter, J. (1993). The fish community of a shallow tropical lagoon in Belize, Central America. *Estuaries*, 16, 198-215.
- Semeniuk, V. (1994). Predicting the effect of sea-level rise on mangroves in northwestern Australia. *Journal of Coastal Research*, 10, 1050-1076.
- Sengupta, R., Middleton, B., Yan, C., Zuro, M., & Hartman, H. (2005). Landscape characteristics of *Rhizophora mangle* forests and propagule deposition in coastal environments of Florida (USA). *Landscape Ecology*, 20(1), 63-72.
- Sheaves, M. (2005). Nature and consequences of biological connectivity in mangrove systems. *Marine Ecology Progress Series*, 302, 293-305.
- Sherman, R. E., Fahey, T. J., & Martinez, P. (2003). Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems*, 6(4), 384-398.
- Sherman, R. E., Fahey, T. J., & Howarth, R. W. (1998). Soil-plant interactions in a neotropical mangrove forest: Iron, phosphorus and sulfur dynamics. *Oecologia*, 115(4), 553-563.
- Shinn, E. (1963). Spur and groove formation on the Florida reef tract. *Journal of Sedimentary Research*, 33(2), 291-303.

- Short, F. T. (1987). Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. *Aquatic Botany*, 27(1), 41-57.
- Short, F. T., Davis, M. W., Gibson, R. A., & Zimmermann, C. F. (1985). Evidence for phosphorus limitation in carbonate sediments of the seagrass *Syringodium filiforme*. *Estuarine, Coastal and Shelf Science*, 20(4), 419-430.
- Simard, M., Zhang, K., Rivera-Monroy, V. H., Ross, M. S., Ruiz, P. L., Castañeda-Moya, E., et al. (2006). Mapping height and biomass of mangrove forests in Everglades National Park with SRTM elevation data. *Photogrammetric Engineering and Remote Sensing*, 72(3), 299-311.
- Simpson, R. H., & Riehl, H. (1981). *The hurricane and its impact*. Baton Rouge, Louisiana, U.S.A.: Louisiana State University Press.
- Slim, F. J., Gwada, P. M., Kodjo, M., & Hemminga, M. A. (1996). Biomass and litterfall of *Ceriops tagal* and *Rhizophora mucronata* in the mangrove forest of Gazi Bay, Kenya. *Marine and Freshwater Research*, 47(8), 999-1007.
- Smith, S. M., & Snedaker, S. C. (1995). Salinity responses in two populations of viviparous *Rhizophora mangle* L. seedlings. *Biotropica*, 27(4), 435-440.
- Smith, T. J. I., & Whelan, K. R. T. (2006). Development of allometric relations for three mangrove species in south Florida for use in the Greater Everglades ecosystem restoration. *Wetlands Ecology and Management*, 14(5), 409-419.
- Smithsonian Institution. (2008). Smithsonian Marine Science Network - Real Time Environmental Monitoring Program. Carrie Bow Cay Marine Laboratory, Belize - Archives. Retrieved 10/18, 2008, from http://nmnhmp.riocan.com/arc_vision.php

- Snedaker, S. C. (1993). Impact on mangroves. In G. A. Maul (Ed.), *Climatic change in the Intra-Americas sea* (pp. 282-305). London, UK: Edward Arnold.
- Sousa, W. P., Kennedy, P. G., Mitchell, B. J., & Ordóñez, L. B. M. (2007). Supply-side ecology in mangroves: Do propagule dispersal and seedling establishment explain forest structure? *Ecological Monographs*, 77(1), 53-76.
- Spalding, M., Kainuma, M., & Collins, L. (2010). *World atlas of mangroves*. London, UK: Earthscan.
- Spaninks, F., & Van Beukering, P. (1997). Economic valuation of mangrove ecosystems: Potential and limitations. (No. 14). London, UK: CREED Working Paper Series.
- Sprugel, D. G. (1985). Natural disturbance and ecosystem energetics. In S. T. A. Pickett, & P. S. White (Eds.), *The ecology of natural disturbance and patch dynamics* (pp. 335-352). Orlando, Florida, U.S.A.: Academic Press.
- Stapp, P., Polis, G. A., & Sanchez Pinero, F. (1999). Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature*, 401(6752), 467-469.
- Sternberg, L., Teh, S., Ewe, S., Miralles-Wilhelm, F., & DeAngelis, D. (2007). Competition between hardwood hammocks and mangroves. *Ecosystems*, 10(4), 648-660.
- Steyer, G. D. (1988). Litter dynamics and nitrogen retranslocation in three types of mangrove forests in Rookery Bay, Florida. (Thesis). University of Southwestern Louisiana, U.S.A.
- Stoddart, D. R., McLean, R. F., Scoffin, T. P., & Gibbs, P. E. (1978). Forty-five years of change on low wooded islands, Great Barrier Reef. *Philosophical Transactions of the Royal Society of London. Biological Sciences, Series B*, 284(999), 63-80.

- Stoddart, D. R., & Steers, J. A. (1977). The nature and origin of coral reef islands. In O. A. Jones, & R. Endean (Eds.), *Biology and geology of coral reefs. IV. Geology II* (pp. 59-105). London, UK: Academic Press.
- Stoddart, D. R. (1971). Coral reefs and islands and catastrophic storms. In J. A. Steers (Ed.), *Applied coastal geomorphology* (pp. 155-197). London, UK: Macmillan and Co. Ltd.
- Stoddart, D. R. (1969). Effects of Hurricane Hattie on the British Honduras reefs and cays re-survey of 1965. *Atoll Research Bulletin*, 131, 1-25.
- Stoddart, D. R. (1965). British Honduras cays and the low wooded island problem. *Transactions of the Institute of British Geographers*, 36, 131-147.
- Stoddart, D. R. (1963). Effects of Hurricane Hattie on the British Honduras reefs and cays, October 30-31, 1961. *Atoll Research Bulletin*, 95, 1-142.
- Stoddart, D. R. (1962). Three Caribbean atolls: Turneffe Island, Lighthouse Reef and Glover's Reef, British Honduras. *Atoll Research Bulletin*, 87, 1-137.
- Stutz, M. L., & Pilkey, O. H. (2011). Open-ocean barrier islands: Global influence of climatic, oceanographic, and depositional settings. *Journal of Coastal Research*, 27(2), 207-222.
- Sukardjo, S. (1987). Natural regeneration status of commercial mangrove species (*Rhizophora apiculata* and *Bruguiera gymnorrhiza*) in the mangrove forest of Tanjung Bungin, Banyuasin District, South Sumatra. *Forest Ecology and Management*, 20(3-4), 233-252.
- Tam, N. F. Y., Wong, Y. S., Lan, C. Y., & Wang, L. N. (1998). Litter production and decomposition in a subtropical mangrove swamp receiving wastewater. *Journal of Experimental Marine Biology and Ecology*, 226(1), 1-18.

- Tanner, W. F. (1961). Mainland beach changes due to Hurricane Donna. *Journal of Geophysical Research*, 66(7), 2265-2266.
- Teas, H. J. (1979). Silviculture with saline water. In A. Hollaender (Ed.), *The biosaline concept: An approach to the utilization of underexploited resources* (pp. 117-161). New York, U.S.A.: Plenum Press.
- Thom, B. G. (1982). Mangrove ecology - a geomorphological perspective. In B. F. Clough (Ed.), *Mangrove ecosystems in Australia: Structure, function and management* (pp. 3-17). Canberra, Australia: Australian Institute of Marine Science in association with Australian National University Press.
- Tomlinson, B. P. (1986). *The botany of mangroves*. New York, U.S.A.: Cambridge University Press.
- Torrescano, N., & Islebe, G. A. (2006). Tropical forest and mangrove history from southeastern Mexico: A 5000 yr pollen record and implications for sea level rise. *Vegetation History and Archaeobotany*, 15(3), 191-195.
- Tunncliffe, V. (1981). Breakage and propagation of the stony coral *Acropora cervicornis*. *Proceedings of the National Academy of Sciences*, 78(4), 2427-2431.
- Turneffe Islands Coastal Advisory Committee (2003). *Turneffe Islands Development Guidelines 2003*. Report from: Coastal Zone Management Authority and Institute.
- Turner, M. G., & Dale, V. H. (1998). Comparing large, infrequent disturbances: What have we learned? *Ecosystems*, 1(6), 493-496.
- Turner, R. E., & Lewis, R. R. (1997). Hydrologic restoration of coastal wetlands. *Wetlands Ecology and Management*, 4(2), 65-72.

- Twilley, R. R., & Rivera-Monroy, V. H. (2005). Developing performance measures of mangrove wetlands using simulation models of hydrology, nutrient biogeochemistry, and community dynamics. *Journal of Coastal Research*, (SI-40), 79-93.
- Twilley, R. R., Pozo, M., Garcia, V. H., Rivera-Monroy, V. H., Zambrano, R., & Boderó, A. (1997). Litter dynamics in riverine mangrove forests in the Guayas River estuary, Ecuador. *Oecologia*, 111(1), 109-122.
- Twilley, R. R. (1995). Properties of mangrove ecosystems related to the energy signature of coastal environments. In C. A. S. Hall (Ed.), *Maximum power: The ideas and applications of H. T. Odum* (pp. 43-62). Colorado, U.S.A.: Colorado University Press.
- Twilley, R. R., Chen, R. H., & Hargis, T. (1992). Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air, and Soil Pollution*, 64(1), 265-288.
- Twilley, R. R. (1985). The exchange of organic carbon in basin mangrove forests in a southwest Florida estuary. *Estuarine, Coastal and Shelf Science*, 20(5), 543-557.
- Twilley, R. W., Lugo, A. E., & Patterson-Zucca, C. (1986). Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology*, 67(3), 670-683.
- Ukpong, I. E. (1991). The performance and distribution of species along soil salinity gradients of mangrove swamps in southeastern Nigeria. *Plant Ecology*, 95(1), 63-70.
- UNDP (2010). Climate risk management. Retrieved 03/15, 2010, from <http://www.undp.org/cpr/documents/disaster/3Disaster%20Risk%20Reduction%20-%20Climate%20Risk%20Management.pdf>

- Valentine, J. F., Heck Jr., K., Blackmon, D., Goecker, M. E., Christian, J., Kroutil, R. M., et al. (2008). Exploited species impacts on trophic linkages along reef-seagrass interfaces in the Florida Keys. *Ecological Applications*, 18(6), 1501-1515.
- Valiela, I., Bowen, J. L., & York, J. K. (2001). Mangrove forests: One of the world's threatened major tropical environments. *BioScience*, 51(10), 807-815.
- Van de Plassche, O. (Ed.). (1986). *Sea-level research: A manual for the collection and evaluation of data*. Norwich, UK: Geo Books.
- Vermeer, D. E. (1963). Effects of Hurricane Hattie, 1961, on the cays of British Honduras. *Zeitschrift fuer Geomorphologie*, 7(4), 332-354.
- Vilarrúbia, T. V. (2000). Zonation pattern of an isolated mangrove community at Playa Medina, Venezuela. *Wetlands Ecology and Management*, 8(1), 9-17.
- Vladi Private Islands. (2008). Vladi Private Islands – Islands for sale. Retrieved 06/25, 2008, from <http://www.vladi-private-islands.de/islandsforsale.html>
- Wafar, S., Untawale, A. G., & Wafar, M. (1997). Litter fall and energy flux in a mangrove ecosystem. *Estuarine, Coastal and Shelf Science*, 44(1), 111-124.
- Waide, R. B., & Lugo, A. E. (1992). A research perspective on disturbance and recovery of a tropical mountain forest. In J. G. Goldammer (Ed.), *Tropical forests in transition: Ecology of natural and anthropogenic disturbance processes* (pp. 173-190). Basel, Switzerland: Birkhauser Verlag.
- Walker, B. H., & Wehrhahn, C. F. (1971). Relationships between derived vegetation gradients and measured environmental variables in Saskatchewan wetlands. *Ecology*, 52(1), 85-95.

- Whitehead, D. R., & Jones, C. E. (1969). Small islands and the equilibrium theory of insular biogeography. *Evolution*, 23(1), 171-179.
- Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation* (2nd ed.). Oxford, UK: Oxford University Press.
- Whittaker, R. J. (1995). Disturbed island ecology. *Trends in Ecology and Evolution*, 10(10), 421-425.
- Williams, W. T., Bunt, J. S., & Duke, N. C. (1981). Mangrove litter fall in north-eastern Australia. II. Periodicity. *Australian Journal of Botany*, 29(5), 555-563.
- Wood, R. (1999). *Reef evolution*. Oxford, UK: Oxford University Press.
- Wood, R. L., Tomlinson-Reid, S. & Reid, A. M. (1988). The field guide to Ambergris Caye, Belize, C. A., including other atolls. *Botany of Ambergris Caye, Belize*. Retrieved 04/20, 2009, from <http://ambergriscaye.com/fieldguide/botany.html>
- Woodroffe, C. D. (2002). *Coasts: Form, process and evolution*. Cambridge, UK: Cambridge University Press.
- Woodroffe, C. D., McLean, R. F., Smithers, S. G., & Lawson, E. M. (1999). Atoll reef-island formation and response to sea-level change: West Island, Cocos (Keeling) islands. *Marine Geology*, 160(1-2), 85-104.
- Woodroffe, C. D. (1995). Response of tide-dominated mangrove shorelines in northern Australia to anticipated sea-level rise. *Earth Surface Processes and Landforms*, 20, 65-86.
- Woodroffe, C. (1992). Mangrove sediments and geomorphology. In A. Robertson, & D. M. Alongi (Eds.), *Tropical mangrove ecosystems* (pp. 7-41). Washington, D.C.: American Geophysical Union.

- Woodroffe, C. D., Bardsley, K. N., Ward, P. J., & Hanley, J. R. (1988). Production of mangrove litter in a macrotidal embayment, Darwin Harbour, N.T., Australia. *Estuarine, Coastal and Shelf Science*, 26(6), 581-598.
- Woodroffe, C. D. (1985). Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus. *Estuarine, Coastal and Shelf Science*, 20(3), 265-280.
- Woodroffe, C. D. (1982). Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera*. *New Zealand Journal of Marine and Freshwater Research*, 16(2), 179-188.
- Wright, A. C. S., Romney, D. H., Arbuckle, R. H., & Vial, V. E. (1959). Land in British Honduras, report of the British Land Use Survey Team. (No. 24). London, UK: Her Majesty's Stationery Office.
- Young, I. R. (2003). A review of the sea state generated by hurricanes. *Marine Structures*, 16, 201-218.
- Zar, J. H. (1996). *Biostatistical analysis* (3rd ed.). New Jersey, U.S.A.: Prentice Hall.
- Zimmerman, J. K., Willig, M. R., Walker, L. R., & Whendee, L. S. (1996). Introduction: Disturbance and Caribbean ecosystems. *Biotropica*, 28(4), 414-423.

Appendices

Appendix A. Fringing cay vegetated area for 2006.

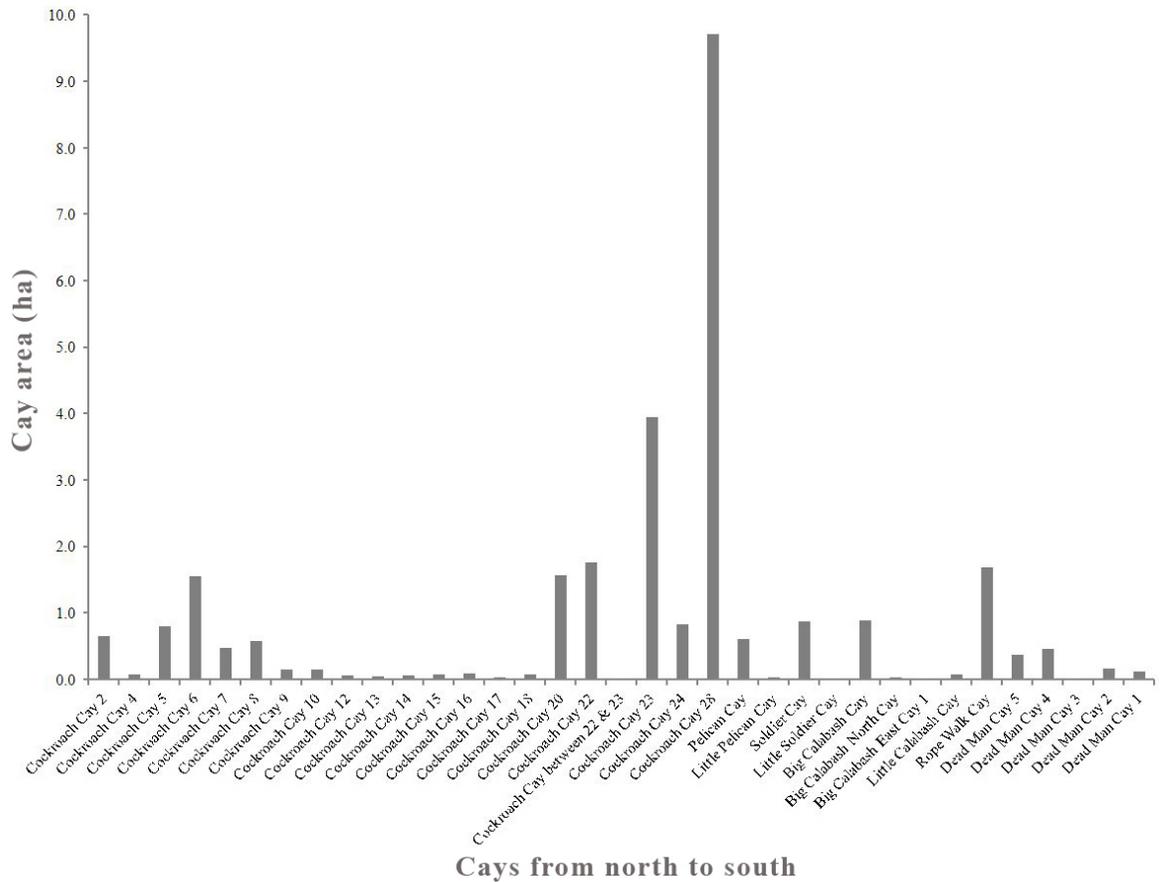


Figure A.1. Cay vegetated area based on 2006 photo-mosaic. Cays arranged from a north to south direction.

Appendix B. Vegetated area of fringing cays before and after Hurricane Hattie.

Table B.1. List of fringing cays with estimated vegetated areas in hectares calculated from georectified photo-mosaics. 1960 photos were pre-Hurricane Hattie and 1961 photos were post-Hurricane Hattie.

Cay	1945	1960¹	1961	1975¹	2006
Dog Flea Cay	0.202	NA	0	NA	0
Cockroach Cay 2	1.030	NA	0.317	NA	0.653
Cockroach Cay between 2 & 3	0.035	NA	0.010	NA	0
Cockroach Cay 3	0.150	NA	0.019	NA	0
Cockroach Cay 4	0.462	NA	0.098	NA	0.073
Cockroach Cay 5	0.616	NA	0.122	NA	0.806
Cockroach Cay 6	1.762	1.035	0.036	NA	1.554
Cockroach Cay 7	0.583	NA	0.269	NA	0.473
Cockroach Cay 8	0.785	NA	0.380	NA	0.581
Cockroach Cay 9	0.098	NA	0.049	NA	0.152
Cockroach Cay 10	0.184	NA	0.038	NA	0.148
Cockroach Cay 11	0.029	NA	0.018	NA	0
Cockroach Cay 12	0.412	NA	0.156	NA	0.064
Cockroach Cay 13	0.245	NA	0.167	NA	0.046
Cockroach Cay 14	0.337	NA	0.222	NA	0.064
Cockroach Cay 15	0.113	NA	0.063	NA	0.084
Cockroach Cay 16	0.245	NA	0.042	NA	0.094
Cockroach Cay 17	0.116	0.134	0.041	NA	0.037
Cockroach Cay 18	0.151	0.197	0.051	NA	0.075
Cockroach Cay 19	0.036	0.088	0.009	NA	0
Cockroach Cay 20	1.371	1.558	0.391	NA	1.573
Cockroach Cay 21	0.052	0.088	0.026	NA	0
Cockroach Cay 22	1.299	1.453	0.726	NA	1.758
Cockroach Cay between 22 & 23	NE	NE	NE	NA	0.009
Cockroach Cay 23	2.917	3.247	2.586	NA	3.955
Cockroach Cay 24	1.152	1.334	0.413	NA	0.830
Cockroach Cay 25	0.041	0.039	0.011	NA	0
Cockroach Cay 26	0.100	0.078	0.040	NA	0
Cockroach Cay 27	0.048	0.028	0.017	NA	0

Table B.1. Continued

Cay	1945	1960	1961	1975	2006
Cockroach Cay 28	5.934	5.484	4.786	NA	9.711
Pelican Cay	0.528	0.582	0.236	NA	0.606
Little Pelican Cay	NE	NE	NE	NE	0.031
Little Black Bird Cay	0.086	0.086	0	NA	0
Soldier Cay	0.582	0.154	0.005	0.498	0.881
Little Soldier Cay	NE	NE	NE	0	0.006
Big Calabash Cay	0.613	0.242	0.124	0.334	0.886
Big Calabash North Cay	NE	NE	NE	NE	0.033
Big Calabash East Cay 1	0.018	0.109	0.001	0.011	0.017
Big Calabash East Cay 2	0.017	0.024	0	0	0
Little Calabash Cay	0.279	0.053	0.001	0.122	0.074
Rope Walk Cay	1.033	1.057	0.527	NA	1.695
Dead Man Cay 5	0.592	0.639	0.416	NA	0.368
Dead Man Cay 4	0.572	0.690	0.426	NA	0.463
Dead Man Cay 3	0.055	0.072	0.032	NA	0.002
Dead Man Cay 2	0.442	0.479	0.143	NA	0.174
Dead Man Cay 1	0.326	0.335	0.012	NA	0.116
Sum	25.649		13.025		28.092
Average	0.611		0.310		0.611
Max	5.934		4.786		9.711
Min	0.017		0		0

¹ NA = aerial photograph coverage not available (incomplete set of photos) from 1960 and 1975 and NE = cay non-existent at that time (1945, 1960, 1961 and 1975).

Appendix C. Fringing cay coordinates from 1945 and 2006 photo-mosaic.

Table C.1. Coordinates (UTM Zone 16N) of centroids of the cay vegetated polygons from the 1945 and 2006 photo-mosaic.

Cay	Easting – X (1945)	Northing - Y (1945)	Easting - X (2006)	Northing - Y (2006)
Cockroach Cay 2	418791.3072	1934948.4610	418796.9150	1934941.7530
Cockroach Cay 4	418373.1190	1934657.8720	418370.4779	1934659.7880
Cockroach Cay 5	418176.4822	1934541.8910	418158.1129	1934549.8090
Cockroach Cay 6	417955.8255	1934452.8440	417954.2937	1934455.7640
Cockroach Cay 7	416850.6036	1933517.5870	416835.6351	1933525.7700
Cockroach Cay 8	416788.2401	1933451.6780	416781.8780	1933461.6470
Cockroach Cay 9	416738.5186	1933348.7480	416730.6850	1933352.5900
Cockroach Cay 10	416730.3331	1933303.1660	416724.3538	1933310.2490
Cockroach Cay 12	416597.8509	1933150.9170	416606.9894	1933161.9550
Cockroach Cay 13	416516.9051	1933001.8580	416526.2358	1933014.8290
Cockroach Cay 14	416377.3805	1932744.8900	416368.2031	1932748.6710
Cockroach Cay 15	416178.2482	1932405.7860	416173.6908	1932406.0150
Cockroach Cay 16	416132.1848	1932355.0520	416133.3250	1932355.9830
Cockroach Cay 17	416096.9352	1932265.9810	416096.1250	1932273.1710
Cockroach Cay 18	416044.6380	1932203.9110	416044.3148	1932205.3550
Cockroach Cay 20	415831.0421	1931969.1140	415807.4593	1931983.3670
Cockroach Cay 22	415573.4283	1931650.2310	415535.8304	1931662.4470
Cockroach Cay 23	415416.1596	1931427.6100	415386.1205	1931454.2520
Cockroach Cay 24	415330.2856	1931132.7670	415293.7163	1931112.4100
Cockroach Cay 28	414807.6428	1930824.7090	414796.0768	1930837.6190
Pelican Cay	413923.6273	1924017.0080	413904.7798	1924015.7800
Soldier Cay	416214.7552	1915690.3840	416191.5649	1915667.7890
Big Calabash Cay	414477.9826	1911137.2510	414457.5621	1911132.7730
Big Calabash East Cay 1	414589.0357	1911139.4340	414570.7341	1911129.7600
Little Calabash Cay	414114.6043	1910882.4980	414112.4534	1910909.8560
Little Rope Walk Cay	408235.3445	1903572.8270	408236.3699	1903568.5010
Dead Man Cay 5	408207.5005	1901782.5410	408165.4350	1901788.3310
Dead Man Cay 4	408099.0415	1901494.8390	408084.0752	1901505.5370
Dead Man Cay 3	408036.9508	1901425.9980	408016.4135	1901438.8150
Dead Man Cay 2	407949.3327	1901277.4040	407922.5218	1901290.7870
Dead Man Cay 1	407885.4351	1901123.1030	407874.2800	1901128.2550

Appendix D. Fringing cay area above and below spring high tide.

Table D.1. Cay area relative to spring high tide. Area measured in hectares. List of cays based on 2006 photo-mosaic and from survey work in 2007-2008.

Cay	Area above high tide¹	Area below high tide²	Total area³
Dog Flea Cay			
Cockroach Cay 2	0.661	0.093	0.754
Cockroach Cay between 2 & 3*			
Cockroach Cay 3			
Cockroach Cay 4	0.070	0.009	0.079
Cockroach Cay 5	0.419	0.405	0.823
Cockroach Cay 6	1.125	0.479	1.605
Cockroach Cay 7	0.183	0.344	0.526
Cockroach Cay 8	0.226	0.405	0.631
Cockroach Cay 9	0.009	0.155	0.164
Cockroach Cay 10	0.026	0.135	0.162
Cockroach Cay 11			
Cockroach Cay 12	0.011	0.065	0.076
Cockroach Cay 13	0	0.055	0.055
Cockroach Cay 14	0.019	0.061	0.080
Cockroach Cay 15	0.013	0.084	0.096
Cockroach Cay 16	0	0.131	0.131
Cockroach Cay 17	0	0.040	0.040
Cockroach Cay 18	0	0.084	0.084
Cockroach Cay 19			
Cockroach Cay 20	0.521	1.103	1.623
Cockroach Cay 21			
Cockroach Cay 22	0.505	1.325	1.830
Cockroach Cay between 22 & 23	0	0.009	0.009
Cockroach Cay 23	0.871	3.300	4.172
Cockroach Cay 24	0.201	1.001	1.202
Cockroach Cay 25			
Cockroach Cay 26			
Cockroach Cay 27			
Cockroach Cay 28	1.460	8.325	9.786

Table D.1. Continued

Cay	Area above high tide¹	Area below high tide²	Total area³
Pelican Cay	0.271	0.366	0.637
Little Pelican Cay	0.000	0.031	0.031
Little Black Bird Cay			
Soldier Cay	0.827	0.295	1.121
Little Soldier Cay	0	0.005	0.005
Big Calabash Cay	0.197	0.724	0.922
Big Calabash North Cay	0	0.036	0.036
Big Calabash East Cay 1	0	0.017	0.017
Big Calabash East Cay 2			
Little Calabash Cay	0.081	0.017	0.098
Little Rope Walk Cay	0.807	1.023	1.830
Dead Man Cay 5	0.122	0.270	0.392
Dead Man Cay 4	0.378	0.104	0.481
Dead Man Cay 3	0	0.002	0.002
Dead Man Cay 2	0.201	0.015	0.216
Dead Man Cay 1	0.103	0.060	0.163
Mean	0.266	0.588	0.854
Max	1.460	8.325	9.786
Min	0	0.002	0.002

¹ Area above high tide = vegetated area and bare substrate above spring high tide.

² Area below high tide = vegetated area below spring high tide.

³ Total area = vegetated area of above and below spring high tide plus area of bare substrate above spring high tide.

Appendix E. List of hurricanes and tropical storms.

Table E.1. List of hurricanes and tropical storms with landfall on the mainland coast of Belize based on center of lowest pressure. List based on the NOAA database 1851 to 2008 (Atlantic Oceanographic and Meteorological Laboratory - Hurricane Research Division).

Hurricane/Cat	Year	Category by Belize	Landfall	Wind Speed (km/h) ¹	Translation Speed (km/h)	Storm Heading (deg) ²
Number 3 / Cat. 1	1864	Cat. 1	North	130	25	280
Number 7 / Cat. 2	1892	Cat. 2	North	160	20	295
Number 2 / Cat. 2	1893	Cat. 1	North	150	24	300
Number 8 / Cat. 3	1906	Cat. 1	North	130	3	335
		Trop.				
Number 8 / Cat. 1	1916	Storm	North	85	18	265
Number 2 / Cat. 2	1918	Cat. 1	South	106	42	275
		Trop.				
Number 1 / Cat. 1	1921	Storm	North	85	20	300
Number 5 / Cat. 3	1931	Cat. 3	North	205	31	280
		Trop.				
Number 7 / Cat. 3	1932	Storm	North	75	18	265
		Trop.				
Number 2 / Cat. 1	1934	Storm	North	75	1	315
Number 4 / Cat. 3	1941	Cat. 1	South	80	22	280
Number 10 / Cat. 2	1942	Cat. 2	North	160	20	265
Number 10 / Cat. 2	1945	Cat. 1	South	130	22	265
		Trop.				
Flossy / Cat. 1	1956	Depression	North	45	12	320
Abby / Cat. 2	1960	Cat. 1	South	120	22	275
Anna / Cat. 3	1961	Cat. 1	South	130	14	290
Hattie / Cat. 5	1961	Cat. 4	South	220	18	245
Francelia / Cat. 3	1969	Cat. 2	South	160	5	270
		Trop.				
Edith / Cat. 5	1971	Storm	North	110	20	315
Fifi / Cat. 2	1974	Cat. 2	South	165	12	285
Greta / Cat. 4	1978	Cat. 2	South	175	24	290
		Trop.				
Gert / Cat. 2	1993	Storm	North	65	18	345
Keith / Cat. 4	2000	Cat. 3	North	185	3	240
Iris / Cat. 4	2001	Cat. 4	South	230	35	260
		Trop.				
Felix / Cat. 5	2007	Depression	South	35	20	300

Table E.1. Continued

Tropical Storm	Year	Category by Belize	Landfall	Wind Speed (km/h)¹	Translation Speed (km/h)	Storm Heading (deg)²
Number 5	1898	Trop. Storm	North	75	16	275
Number 11	1898	Trop. Storm	North	85	22	290
		Trop.				
Number 1	1917	Depression	North	55	14	305
Number 1	1924	Trop. Storm	North	75	24	280
Number 3	1931	Trop. Storm	South	75	11	285
Number 8	1932	Trop. Storm	North	75	11	300
Number 17	1933	Trop. Storm	South	65	18	280
Number 5	1938	Trop. Storm	North	75	20	340
Number 6	1940	Trop. Storm	North	75	24	315
Number 4	1942	Trop. Storm	North	65	12	265
Number 10	1943	Trop. Storm	South	75	27	250
Number 6	1945	Trop. Storm	North	75	24	265
Gilda	1954	Trop. Storm	South	110	12	285
		Trop.				
Number 12	1964	Depression	North	45	16	300
		Trop.				
Chloe	1971	Depression	North	45	11	270
Laura	1971	Trop. Storm	South	110	11	225
		Trop.				
Frieda	1977	Depression	North	35	14	270
Hermine	1980	Trop. Storm	North	110	22	305
		Trop.				
Katrina	1999	Depression	North	45	25	325
Chantal	2001	Trop. Storm	North	110	16	280
Arthur	2008	Trop. Storm	North	75	9	300

Note: The coast of Belize from 3 km north of the Mullins River to the Rio Hondo River on the Mexico-Belize border is referred to as the North section. The remainder of the coast falls in the South section. ¹ Wind speed and storm translation speed based on the closest reported readings to mainland coast of Belize. ² Storm heading calculated from the closest pair of coordinate points to the mainland. Storm heading in degrees azimuth, clockwise from north (example – a 270 ° storm heads from east to west).

Appendix F. Aerial photographs of before and after Hurricane Hattie 1961.

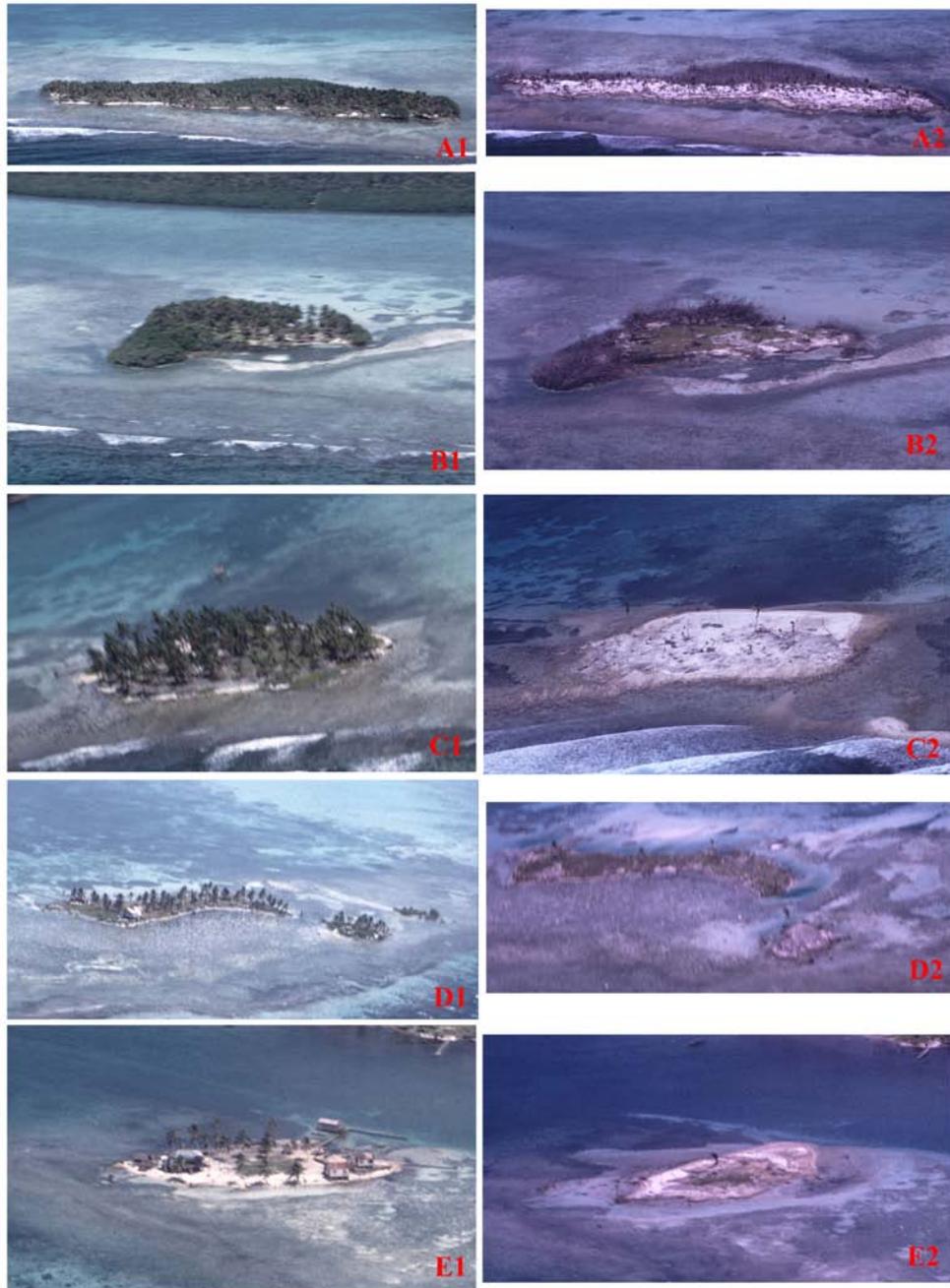


Figure F.1. Oblique aerial photographs of fringing cays before and after Hurricane Hattie 1961. Photos to the left taken in 1960 those to the right in 1962. Photo A = Cockroach Cay-20, B = Pelican Cay, C = Soldier Cay, D = Big Calabash Cay, E = Little Calabash Cay. Photo taken during Stoddart's survey of 1960-62 before and after Hurricane Hattie 1961. (Photo credit, Stoddart).

Appendix G. List of fringing cays from eastern Turneffe.

Table G.1. List of fringing cays and vegetation status identified from 1945, 1960 (pre-Hurricane Hattie), 1961 and 1962 (post-Hurricane Hattie), and 2008 aerial photographs and ground surveys.

Name of cay	Vegetation Status 1945	Vegetation Status 1960	Vegetation Status 1961	Vegetation Status 2008
Dog Flea Cay	P	P	A	A
Cockroach Cay 2	P	P	P	P
Cockroach Cay between 2 & 3	P	P	P	A
Cockroach Cay 3	P	P	P	A
Cockroach Cay 4	P	P	P	P
Cockroach Cay 5	P	P	P	P
Cockroach Cay 6	P	P	P	P
Cockroach Cay 7	P	P	P	P
Cockroach Cay 8	P	P	P	P
Cockroach Cay 9	P	P	P	P
Cockroach Cay 10	P	P	P	P
Cockroach Cay 11	P	P	P	A
Cockroach Cay 12	P	P	P	P
Cockroach Cay 13	P	P	P	P
Cockroach Cay 14	P	P	P	P
Cockroach Cay 15	P	P	P	P

Table G.1. Continued

Name of cay	Vegetation Status 1945	Vegetation Status 1960	Vegetation Status 1961	Vegetation Status 2008
Cockroach Cay 16	P	P	P	P
Cockroach Cay 17	P	P	P	P
Cockroach Cay 18	P	P	P	P
Cockroach Cay 19	P	P	P	A
Cockroach Cay 20	P	P	P	P
Cockroach Cay 21	P	P	P	A
Cockroach Cay 22	P	P	P	P
Cockroach Cay between 22 & 23	A	A	A	NV
Cockroach Cay 23	P	P	P	P
Cockroach Cay 24	P	P	P	P
Cockroach Cay 25	P	P	P	A
Cockroach Cay 26	P	P	P	A
Cockroach Cay 27	P	P	P	A
Cockroach Cay 28	P	P	P	P
Pelican Cay	P	P	P	P
Little Pelican Cay	A	A	A	NV
Little Black Bird Cay	P	P	A	A
Soldier Cay	P	P	P	P
Little Soldier Cay	A	A	A	NV

Table G.1. Continued

Name of cay	Vegetation Status 1945	Vegetation Status 1960	Vegetation Status 1961	Vegetation Status 2008
Big Calabash Cay	P	P	P	P
Big Calabash North Cay	A	A	A	NV
Big Calabash East Cay 1	P	P	P	P
Big Calabash East Cay 2	P	P	A	A
Little Calabash Cay	P	P	P	P
Rope Walk Cay	P	P	P	P
Dead Man Cay 5	P	P	P	P
Dead Man Cay 4	P	P	P	P
Dead Man Cay 3	P	P	P	P
Dead Man Cay 2	P	P	P	P
Dead Man Cay 1	P	P	P	P
Total number of cays	42	42	39	35
Number of vegetated cays lost after Hurricane Hattie since 1945			3	
Number of vegetated cays lost between 1945 to 2006				11
Number of new vegetated cays since 1945		0	0	4

Note: P = vegetation present, A = vegetation absent and NV = new vegetation. For the vegetation status 1961 and 1962 post-Hurricane Hattie, the vegetation present accounts for both live and dead standing vegetation.

Appendix H. Presence and absence of coconut palms relative to 1960 and 1961 cay area.

Table H.1. Presence and absence of *Cocos nucifera* based on 1960 and 1962 oblique aerial photographs. Cay vegetated area based on photo-mosaics from before and after Hurricane Hattie 1961.

Cay	Cay ID 1945	Cn P/A 1960	Cn P/A 1962	Veg Area 1960 ha	Veg Area 1961 (ha)
Dog Flea Cay	1	P	A	NA	0.0000
Cockroach Cay 2	2	P	A	NA	0.3171
Cockroach Cay b/w 2 & 3	3	A	A	NA	0.0099
Cockroach Cay 3	4	P	A	NA	0.0193
Cockroach Cay 4	5	P	A	NA	0.0982
Cockroach Cay 5	6	P	P	NA	0.1220
Cockroach Cay 6	7	P	P	1.035	0.0356
Cockroach Cay 7	8	P	P	NA	0.2687
Cockroach Cay 8	9	P	P	NA	0.3799
Cockroach Cay 9	10	A	A	NA	0.0491
Cockroach Cay 10	11	P	P	NA	0.0380
Cockroach Cay 11	12	A	A	NA	0.0181
Cockroach Cay 12	13	P	P	NA	0.1556
Cockroach Cay 13	14	P	P	NA	0.1666
Cockroach Cay 14	15	P	P	NA	0.2216
Cockroach Cay 15	16	P	P	NA	0.0626
Cockroach Cay 16	17	P	P	NA	0.0425
Cockroach Cay 17	18	A	A	0.134	0.0409
Cockroach Cay 18	19	A	A	0.197	0.0513
Cockroach Cay 19	20	A	A	0.088	0.0090
Cockroach Cay 20	21	P	P	1.558	0.3905
Cockroach Cay 21	22	A	A	0.088	0.0264
Cockroach Cay 22	23	P	P	1.453	0.7256
Cockroach Cay 23	24	P	P	3.247	2.5860
Cockroach Cay 24	25	P	P	1.334	0.4135
Cockroach Cay 25	26	A	A	0.039	0.0111
Cockroach Cay 26	27	A	A	0.078	0.0398
Cockroach Cay 27	28	A	A	0.028	0.0170
Cockroach Cay 28	29	P	P	5.484	4.7861

Table H.1. Continued

Cay	Cay ID	Cn P/A	Cn P/A	Veg Area	Veg Area
	1945	1960	1962	1960 ha	1961 (ha)
Pelican Cay	30	P	A	0.582	0.2358
Little Black Bird Cay	31	P	A	0.086	0.0000
Soldier Cay	32	P	P	0.154	0.0049
Big Calabash Cay	33	P	P	0.242	0.1244
Big Calabash East Cay 1	34	P	P	0.109	0.0004
Big Calabash East Cay 2	35	P	A	0.024	0.0000
Little Calabash Cay	36	P	A	0.053	0.0005
Rope Walk Cay	37	P	P	1.057	0.5269
Dead Man Cay 5	38	P	A	0.639	0.4159
Dead Man Cay 4	39	P	P	0.690	0.4265
Dead Man Cay 3	40	P	A	0.072	0.0319
Dead Man Cay 2	41	P	P	0.479	0.1426
Dead Man Cay 1	42	P	P	0.335	0.0117

¹ Cn = *Cocos nucifera*, P/A denotes presence or absence of Cn. NA = Not Available (due to unavailable vertical aerial photograph coverage).

Appendix I. Presence and absence of coconut palms relative to 2006 cay area.

Table I.1. Presence and absence of *Cocos nucifera*, dominant vegetation type based on 2006 aerial photographs and 2007 – 2008 field surveys.

Cay	Cn P/A 2008¹	Dominant Vegetation 2008²	Vegetation Area 2006
Dog Flea Cay	A	None*	0
Cockroach Cay 2	P	L	0.653
Cockroach Cay b/w 2 & 3	A	None	0
Cockroach Cay 3	A	None	0
Cockroach Cay 4	P	L	0.073
Cockroach Cay 5	P	M	0.806
Cockroach Cay 6	P	L	1.554
Cockroach Cay 7	P	M	0.473
Cockroach Cay 8	P	M	0.581
Cockroach Cay 9	A	M	0.152
Cockroach Cay 10	P	M	0.148
Cockroach Cay 11	A	None	0
Cockroach Cay 12	P	M	0.064
Cockroach Cay 13	A	M	0.046
Cockroach Cay 14	A	M	0.064
Cockroach Cay 15	A	M	0.084
Cockroach Cay 16	P	M	0.094
Cockroach Cay 17	A	M	0.037
Cockroach Cay 18	A	M	0.075
Cockroach Cay 19	A	None	0
Cockroach Cay 20	P	M	1.573
Cockroach Cay 21	A	None	0
Cockroach Cay 22	P	M	1.758
Cockroach Cay b/w 22 & 23	A	M	0.009
Cockroach Cay 23	P	M	3.955
Cockroach Cay 24	A	M	0.83
Cockroach Cay 25	A	None	0
Cockroach Cay 26	A	None	0
Cockroach Cay 27	A	None	0
Cockroach Cay 28	P	M	9.711

Table I.1. Continued

Cay	Cn P/A 2008¹	Dominant Vegetation 2008²	Vegetation Area 2006
Pelican Cay	P	M	0.606
Little Pelican Cay	A	M	0.031
Little Black Bird Cay	A	None	0
Soldier Cay	P	M	0.881
Little Soldier Cay	A	M	0.006
Big Calabash Cay	P	M	0.886
Big Calabash North Cay	A	M	0.033
Big Calabash East Cay 1	A	M	0.017
Big Calabash East Cay 2	A	None	0
Little Calabash Cay	P	Cn	0.074
Rope Walk Cay	P	M	1.695
Dead Man Cay 5	P	M	0.368
Dead Man Cay 4	P	Cn/M	0.463
Dead Man Cay 3	A	M	0.002
Dead Man Cay 2	P	L/Cn	0.174
Dead Man Cay 1	P	L/M	0.116

¹ Cn = *Cocos nucifera*, P/A denotes presence or absence of Cn.

² Vegetation types are: L = Littoral, Mixed = littoral and mangrove; Cn = *Cocos nucifera*, M = Mangrove. * None under the Dominant Vegetation category means cay was found to be devegetated. Cay vegetated area in hectares based on 2006 photo-mosaic.

Appendix J. Fringing cay area damaged from Hurricane Keith 2000.

Table J.1. Estimated damage of cay vegetation area from Hurricane Keith 2000 (survey from 2003, 2006 and 2008).

Area of damaged vegetation (ha)			
Cay	2003	2006	2008
Cockroach Cay 20	0.357	0.004	0.003
Cockroach Cay 22	0.627	0.119	0.107
Cockroach Cay 23	1.302	0.057	0.040

Periphery of cay vegetation (ha)			
	2003	2006	2008
Cockroach Cay 20	1.470	1.535	1.609
Cockroach Cay 22	1.625	1.710	1.808
Cockroach Cay 23	3.522	3.731	3.922

Note: Area of damaged vegetation was estimated by walking with a GPS unit around the edge of dead and alive forest. Area of cay vegetation was estimated by walking with GPS unit around the periphery of the cay.

Appendix K. Permanent plot summary 2002.

Table K.1. Summary of permanent plots established in 2002 at Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5) with 3 plots per site (A, B and C).

Site	Plot	S/Ha	Height		DBH		Biomass ^a	Biomass ^b	
			Mean	Max	Mean	Max			
SC	A	4000	5.2	10.0	7.8	19.0	9.9	9.8	
	B	3700	4.1	8.2	6.3	18.4	5.1	5.1	
	C	10600	4.0	8.0	5.4	14.6	11.0	11.0	
	Site								
			Mean	4.5		6.5		8.7	8.6
		SE	0.2		0.4		1.0	1.0	
BCC	A	9400	4.8	8.2	5.3	19.8	11.3	11.1	
	B	9400	4.7	8.6	5.5	14.6	11.4	11.3	
	C	6700	4.6	9.0	5.7	21.5	8.8	8.6	
	Site								
			Mean	4.7		5.5		10.5	10.3
		SE	0.0		0.1		0.5	0.5	
DMC-5	A	12700	4.2	5.9	3.9	7.3	6.1	6.1	
	B	16700	3.2	5.0	3.8	6.5	6.1	6.1	
	C	12300	3.1	4.8	3.7	5.9	4.1	4.2	
	Site								
			Mean	3.5		3.8		5.4	5.4
		SE	0.2		0.0		0.4	0.4	

Note: S/Ha = stems per ha. Height measured in m and DBH in cm. Above-ground biomass (Biomass^a) was estimated using allometric equation from Cintrón and Shaeffer-Novelli (1984) for *R. mangle* species; for species *A. germinans*, *L. racemosa* and *C. erectus* allometric equations from Fromard et al. (1998) was used. Above-ground biomass (Biomass^b) was estimated using allometric equation from Cintrón and Shaeffer-Novelli (1984) for all species. SE = standard error of the mean.

Appendix L. Permanent plot summary 2008.

Table L.1. Summary of permanent plots re-measured in 2008 at Soldier Cay (SC), Big Calabash Cay (BCC), and Dead Man Cay-5 (DMC-5) with 3 plots per site (A, B and C).

Site	Plot	S/Ha	Height		DBH		Biomass ^a	Biomass ^b	
			Mean	Max	Mean	Max			
SC	A	4400	6.6	11.4	8.8	20.1	15.7	15.6	
	B	4800	6.2	9.6	7.5	19.0	11.3	11.3	
	C	9000	5.4	9.3	5.6	14.9	12.1	12.1	
	Site								
			Mean	6.1		7.3		13.0	13.0
		SE	0.2		0.5		0.8	0.8	
BCC	A	10000	4.7	8.9	5.3	19.9	11.2	11.3	
	B	9500	4.7	9.0	5.5	16.1	12.7	12.0	
	C	6200	4.6	9.7	5.8	24.5	9.9	9.1	
	Site								
			Mean	4.7		5.5		11.3	10.8
		SE	0.0		0.1		0.5	0.5	
DMC-5	A	13500	5.7	8.2	4.5	8.6	11.0	11.0	
	B	17600	4.8	7.4	4.3	8.0	11.5	11.5	
	C	14400	4.1	7.2	4.2	10.3	7.9	8.2	
	Site								
			Mean	4.9		4.3		10.1	10.2
		SE	0.3		0.1		0.6	0.6	

Note: S/Ha = stems per ha. Height measured in m and DBH in cm. Above-ground biomass (Biomass^a) was estimated using allometric equation from Cintrón and Shaeffer-Novelli (1984) for *R. mangle* species; for species *A. germinans*, *L. racemosa* and *C. erectus* allometric equations from Fromard et al. (1998) was used. Above-ground biomass (Biomass^b) was estimated using allometric equation from Cintrón and Shaeffer-Novelli (1984) for all species. SE = standard error of the mean.

Appendix M. Fringing cays from eastern Turneffe.

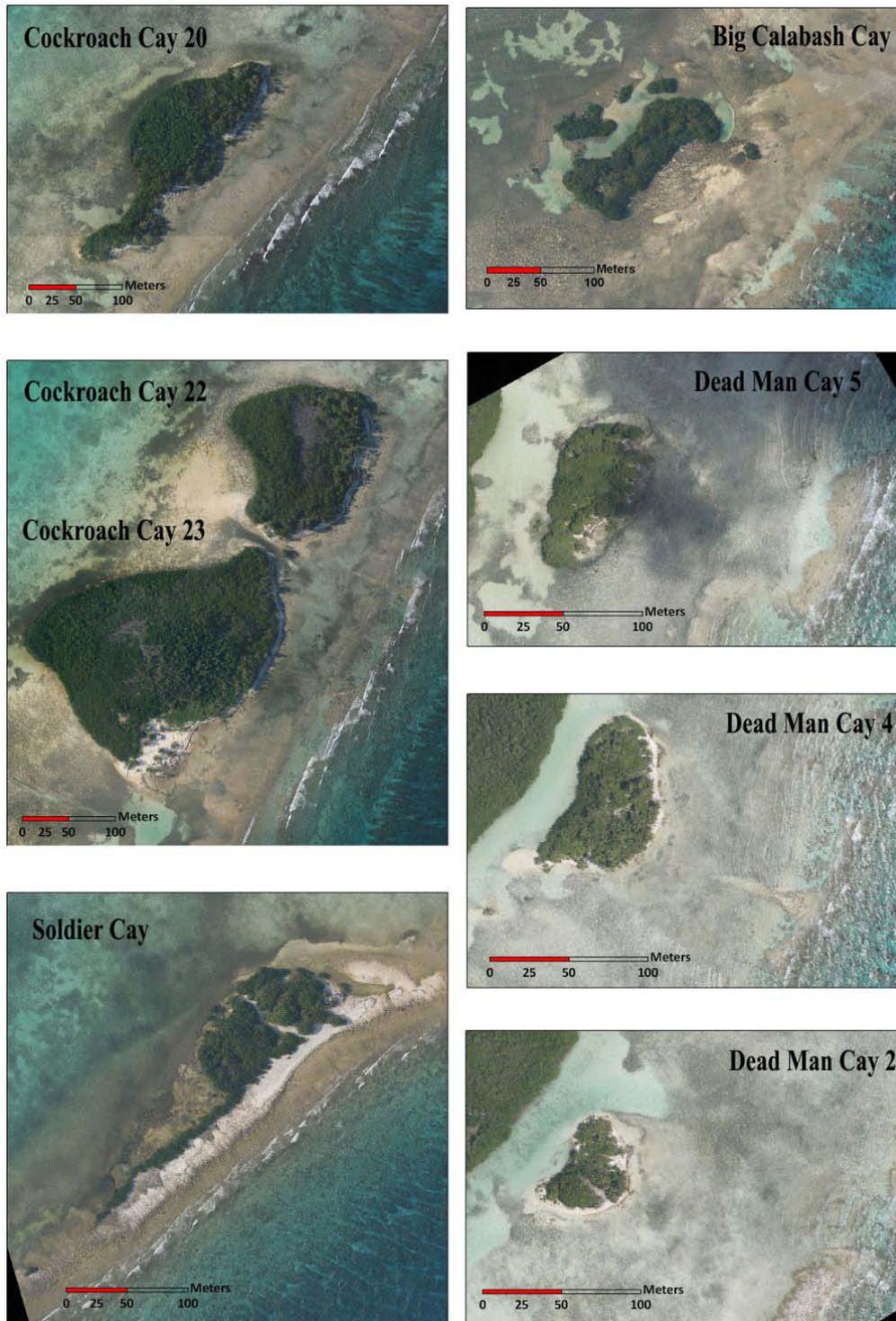


Figure M.1. Eight fringing cays on eastern Turneffe selected for temporary plot establishment.

Appendix N. Adapting the water-level method to measure substrate elevation.



Figure N.1. A 15 m length clear tube with a 1 cm inside diameter was used along with two graduated telescoping poles, and GPS, to measure substrate elevation.

A 15 m length clear tube with a 1 cm inside diameter was used along with two graduated telescoping poles. The entire tube was filled with water and air bubbles were removed from the tube. To test the level of accuracy both ends of the tube were held together at eye sight against a stable object (tree) and observed for approximately one minute. The water's meniscus on both ends of the tube had to be leveled. Any variations in the water's meniscus

level during that minute could be attributed to air bubbles in the tube or a knot in the tube and was corrected. Rubber stoppers were used to plug the ends of the tube to prevent the water from spilling during transportation on the field.

A GPS unit was attached to the telescoping pole to record x and y coordinates at each interval. The telescoping pole at 1.3 m was used as the benchmark height above ground and for subsequent reference height measurements. Person A (PA) with one pole and GPS unit remained at the point of commencement (benchmark) of a transect (e.g., spring tide high-water mark). Person B (PB) extended the tube along the transect following a bearing from PA to a designated distance depending on the terrain's surface. PA held one end of the tube against the pole at 1.3 m level (benchmark) and PB held the other end of the tube against the other pole. The end of the tube at PB was slowly raised or lowered against the pole, if higher than 1.3 m then the pole was extended to compensate for the increase in height. PB would then wait for the stop signal from PA which indicated that the water's meniscus was level at the 1.3 m benchmark of the graduated pole. PB recorded the height indicated at the pole which was in level with the water's meniscus. PB tied a ribbon to mark the station location, and the PA advanced to this position, while PB moved to the next measuring location along the transect. This process was repeated to the end of each transect.

In flooded zones a water depth using the graduated pole and the time was also recorded. The distance between PA and PB was measured using a hypsometer and transponder device. GPS coordinates of the pole's location were recorded at each station. For all strip lines that went across the cays, the spring tide high water mark on the cays was always used as the point of

commencement (benchmark). The spring high tide water mark was either visible or was previously marked as described in Chapter 3. Elevation of benchmark, or datum height was taken as zero at the spring tide high water mark.

The following equation was used to calculate relative elevation after successive measurements from the benchmark (point of commencement).

$$E_r = E_p + (E_s - E_c)$$

(E_r = Relative elevation, E_p = Previous elevation, E_s = Standard elevation (1.3 m), E_c = Current elevation).

Appendix O. Relationship between distance from the edge of reef crest, elevation, plot average stem diameter and plot average height of *Rhizophora mangle*.

This relationship was measured in a group of eight cays from eastern Turneffe (Cockroach Cay-20, -22 and -23; Soldier Cay; Big Calabash Cay; Dead Man Cay-2, -4 and -5). Distance from the edge of reef crest was partitioned into 50 m distance classes. Stem diameter and height measured along transects from circular field plots (n = 296). Both stem diameter and height followed a similar trend away from the edge of the reef crest.

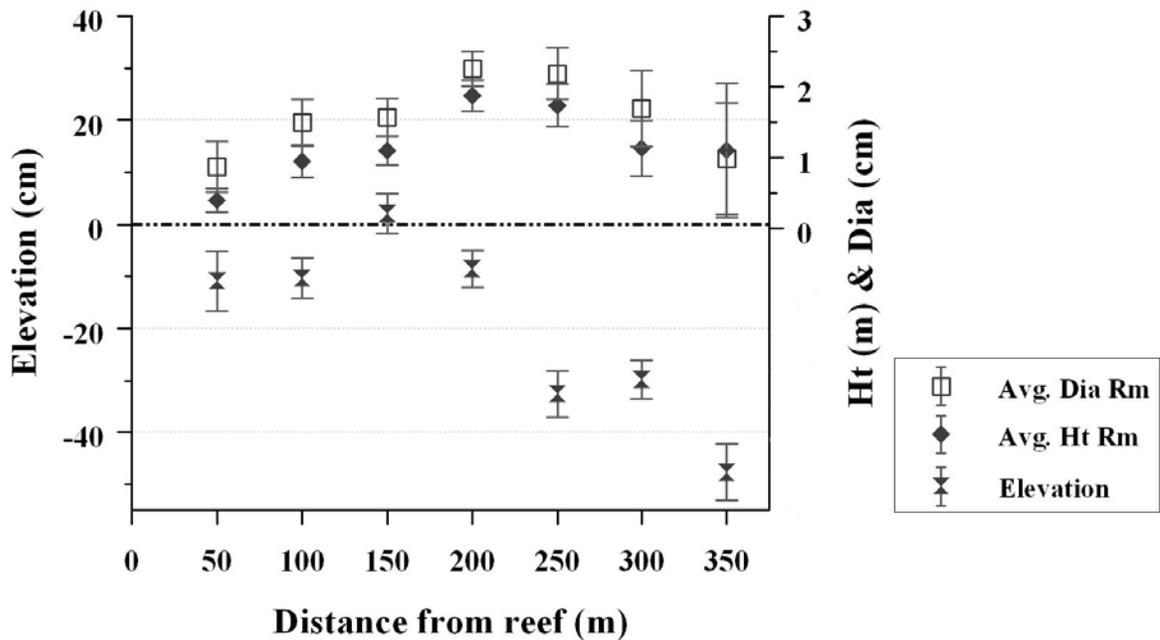


Figure O.1. Elevation, average height and average stem diameter vs. distance from the edge of the reef crest for *R. mangle* trees with SE error bars. Dashed line across the zero value (y-axis) represents the spring high tide.

Appendix P. List of mangrove species from Proserpine, Australia and Turneffe, Belize.

Table P.1. List of mangrove species from Proserpine, Australia used by Saenger (2002) to illustrate Grime's model, and list of mangrove species from Turneffe, Belize which were superimposed on Saenger's triangular ordination.

<u>Australian Species</u>		<u>Belize Species</u>	
<u>Abbreviated name</u>	<u>Full name</u>	<u>Abbreviated name</u>	<u>Full name</u>
<i>C. iripa</i>	<i>Cynometra iripa</i>	<i>R. mangle</i>	<i>Rhizophora mangle</i>
<i>B. parviflora</i>	<i>Bruguiera parviflora</i>	<i>L. racemosa</i>	<i>Laguncularia racemosa</i>
<i>B. gymnorrhiza</i>	<i>Bruguiera gymnorrhiza</i>	<i>A. germinans</i>	<i>Avicennia germinans</i>
<i>H. littoralis</i>	<i>Heritiera littoralis</i>	<i>C. erectus</i>	<i>Conocarpus erectus</i>
<i>B. exaristata</i>	<i>Bruguiera exaristata</i>		
<i>C. tagal</i>	<i>Ceriops tagal</i> var. <i>australis</i>		
<i>A. marina</i>	<i>Avicennia marina</i>		
<i>R. stylosa</i>	<i>Rhizophora stylosa</i>		
<i>A. corniculatum</i>	<i>Aegiceras corniculatum</i>		
<i>A. ilicifolius</i>	<i>Acanthus ilicifolius</i>		
<i>O. octodonta</i>	<i>Osbornia octodonta</i>		
<i>X. granutum</i>	<i>Xylocarpus granutum</i>		
<i>X. australasicus</i>	<i>Xylocarpus australasicus</i>		
<i>L. racemosa</i>	<i>Lumnitzera racemosa</i>		
<i>E. agallocha</i>	<i>Excoecaria agallocha</i>		