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May 2003

# The L-31E Surface Water Rediversion Project Final Report: Implementation, Results, and Recommendations

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# The L-31E Surface Water Rediversion Pilot Project Final Report: Implementation, Results, and Recommendations *(*http://www.fiu.edu/~serp1/projects/l31e/2003fr.exe*)*

*May 1, 2003* 



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# **Executive Summary**

Throughout the southern Biscayne Bay watershed, existing coastal wetland communities have been cut off from sheet flow for decades. With the expectation that reconnection of these wetlands to upstream water sources would alter existing hydrologic conditions and recreate a more natural sheet flow to Biscayne National Park, a demonstration project on freshwater rediversion was undertaken. The objectives of the project were to document the effects of freshwater diversion on: (a) swamp and nearshore water chemistry and hydrology; (b) soil development processes; (c) macrophyte and benthic algal community composition, structure, and production; (d) abundance of epiphytic and epibenthic invertebrates; (e) zonation, production, and phenology of primary producers in the nearshore environment, and (f) exchanges of nutrients and particulates between nearshore and mangrove ecosystems.

The study area is comprised of the coastal mangrove ecosystem bounded by the Mowry, L-31E, and Military Canals on the south, west, and north, respectively, as well as adjacent portions of Biscayne Bay. For this study, a BACI (Before-After Control-Impact) research and monitoring design was chosen. In this design, the interaction of Site with Time was examined, substituting temporal replication for the spatial replication. Among five hydrologically-independent blocks divided by East-West oriented drainage ditches or canals, Blocks 1 and 4 were chosen as Treatment and Control Blocks, respectively. Both blocks were then divided into sub-blocks representing the coastal Fringe and interior Dwarf forests. Within each of the four sub-blocks, hydrologic monitoring and biotic monitoring were performed at one or four locations, respectively. The periodic freshwater delivery from the L-31E Canal into the Treatment sub-blocks started on 28 Aug 1997.

#### *Biogeochemistry and Nutrient Dynamics*

Water quality in Delivery Canal, Dwarf and Fringe mangrove forests, and adjacent Biscayne Bay was monitored between June 1995 and October 2001. Surface waters were analyzed for specific conductivity, NH<sub>3</sub>-N,  $NO<sub>3</sub> + NO<sub>2</sub>-N$ , NO<sub>2</sub>-N, soluble reactive phosphorus, total phosphorus, total nitrogen, total organic carbon, copper, lead, zinc, iron, alkaline phosphatase and chlorophyll-A, and pore waters were analyzed for all parameters except the last two. Delivery Canal and adjacent Biscayne Bay waters had low levels of DOC, TP, TN, and NH3-N. Nutrients in pore water were higher than in surface water, and Fringe forests had 5-7 times greater pore water phosphorus than the Dwarf forests.

Changes in surface and pore water quality from pre- to post-treatment period occurred in both Control and Treatment blocks simultaneously, suggesting that the changes were not simply the result of freshwater delivery from the canal. In the Treatment Dwarf, freshwater delivery neither changed  $\delta^{13}$ C nor relieved P-limitation as evidenced by leaf N:P ratios. The heavy signal of  $\delta^{15}N$  (+5.4) in Treatment Dwarf leaves compared to Control Dwarf leaves may be the result of source effects, i.e., fresh water delivered from the canal, or tidal water, which reaches the Treatment Dwarf basin more readily via the well-developed creek system. Tidal influence on water quality was noticeable in both the Control and Treatment Fringe forests, where pore water salinity increased while TN and TP significantly decreased between pre- and post-treatment periods. In the poorly drained Treatment Fringe, a decrease in pore water TN and TP was associated with an increase in physiological stress, as evidenced by a significant change in  $\delta^{13}$ C. However, this effect was not accompanied by a significant change in phosphorus content or N:P ratio in leaves. We hypothesize that in the Fringe forests, the steady decrease in pore water nitrogen and phosphorus during the course of the study was due to the fact that sites were recovering from an earlier disturbance, one that might have caused a temporary increase in pore water nutrients.

In Biscayne Bay water, a strong pattern of increasing salinity and decreasing nitrogen concentration was observed during the course of the study, indicating that the volume of nitrogen-rich freshwater reaching the Bay, presumably through the Mowry and Military Canals, may have decreased in recent years.

When present in detectable amounts, concentrations of copper, lead and zinc were lowest in Canal and Bay waters, and higher in swamp surface waters than pore waters. In contrast, iron concentrations were higher in swamp pore waters than surface waters. Red mangrove leaves in the Dwarf forests had significantly lower concentrations of foliar iron and zinc than Fringe forest leaves. In the Treatment Dwarf, mean foliar concentration of copper doubled during the post-treatment period compared to the pre-treatment period. Since copper in canal water was, except on

one occasion, below detection level throughout the study period, it was uncertain whether an increase in foliar copper concentration in the Treatment Dwarf sub-block was the effect of freshwater delivery treatment.

#### *Vegetation*

The vegetation in the L-31E study area has changed considerably from the landscape present in 1940. Tall mangrove forest has widened, and dwarf mangrove forest has replaced mixed graminoid marsh. In contrast, the vegetation west of the L31E canal includes more freshwater elements than a half century ago. The mangrove forests in the study area are currently recovering from at least three recent natural disturbances; Hurricane Andrew (August 1992), and two freezes (Jan 1996 and 2000). Hurricane Andrew caused 95% tree mortality in the Fringe forests and extensive defoliation and canopy damage in the Transition forest, but had minimal effects in Dwarf mangroves. Freeze damage was most severe along the sides of the dwarf mangrove basin and was almost nil in the center of the basin. After one decade of recovery, the Fringe Forest had reached its pre-hurricane basal area, and species composition was not substantially changed. The Transition forest was a denser and more diverse community in 2002 than a decade earlier. The coverage and stature of the Dwarf forest did not completely recover to its pre-freeze conditions during the five years between the two freeze events, and species composition was different.

Mangrove species in Fringe and Dwarf forests differed in hurricane and freeze induced mortality and regeneration. *Laguncularia racemosa* sustained the most immediate damage from the hurricane, but exhibited the greatest capacity to resprout from the stem base. *Rhizophora mangle* was less freeze-sensitive than *L. racemosa,* but had very limited ability to sprout. *Avicennia germinans* was the most frost-hardy of the three species, and was a moderate sprouter. Initial plant size was also an important determinant of subsequent growth and mortality in the mangrove forests. During post-hurricane recovery, mortality of large *L. racemosa* in the Control Fringe forest was very low, but large *R. mangle* experienced higher mortality due to inter-specific competition among large stems. This finding suggested that the more productive Control Fringe forest reached the *competitive exclusion* stage of development more quickly than the less productive Treatment Fringe site.

In mangrove forests, leaf production and survival were monitored on a number of branches of selected red mangrove trees for 4-6 years. Red mangrove leaf cohorts in all L-31E forests exhibited a Type I survivorship curve. Temporal variation in leaf survival was similar in both forest types, and had no simple linear or quadratic trend, suggesting that leaf longevity in *R. mangle* is a relatively conservative characteristic. In contrast, significant spatial and temporal variation occurred in leaf production, which we defined in units of leaves per meristem per year. Rates of meristem production and mortality were significantly higher in the Fringe than in the Dwarf forests, and in freezeimpacted portion of Control Dwarf than in portions of the Control and Treatment Dwarf forests not affected by freeze. In the Fringe forests, branch meristem turnover was rapid, and production exceeded mortality in most periods. Branch mortality in those forests was positively correlated with biomass production and shading due to canopy closure throughout the recovery period. Branch production in the Dwarf populations was highly irregular and branch mortality consistently low.

Total aboveground production in the Fringe and Dwarf forests averaged 28.6 Mg/ha/yr and 7 Mg/ha/yr, respectively between 1996 and 2000. Based on our pre-hurricane biomass estimate (168 Mg/ha), and on the rapid rate of biomass accumulation following Hurricane Andrew (~13 Mg/ha/yr over the last 7 years), it seems likely that within the span of two decades, given no other major disturbance, a forest approaching 200 Mg/ha may develop again along the shore of Biscayne Bay. Mean aboveground biomass and annual production estimates did not differ between Control and Treatment Fringe sites, though the total biomass was higher in the former. In 1995, mean aboveground biomass in the two Dwarf forests did not differ significantly. However, by the following year the mean aboveground biomass in the Treatment Dwarf was four times greater than in the Control Dwarf. This gap narrowed in the next five years, and final biomass was only two times greater in Treatment Dwarf than in Control Dwarf mangroves. The increase in biomass in the Treatment Dwarf was not due to the hydrologic treatment, because: 1) the percent increase in biomass during the pre-treatment period and the treatment period were the same, and 2) rates of biomass production in the freeze un-impacted plots did not differ between the Treatment Dwarf and Control Dwarf forests.

The L-31E Dwarf forest sub-blocks include scattered islands of taller trees, commonly referred to as "mangrove tree islands". The species composition of mangrove tree islands is broadly similar to that of the swamps that surround them, though *L. racemosa, A. germinans,* and *Conocarpus erecta* are often more important in the tree

islands than in adjacent communities. At the stand level, initial biomass, stem density, basal area, and rate of biomass increase were all approximately two times greater in the Control than in the Treatment sub-block tree island. Mean tree diameter growth in the tree islands did not differ significantly between species and sites. However, a significant positive relationship between initial size and subsequent growth was observed in the Control Dwarf but not in the Treatment Dwarf tree island. Annual increases in biomass in Dwarf forest tree islands were smaller than those observed in the Fringe forest plots, due in part, perhaps, to the different developmental stages occupied by the two forest communities.

Mangrove species, which have developed a range of mechanisms to maintain osmotic balance under saline conditions, differ in their efficiency to deal with osmotic stress. With the view that changes in salinity regime due to freshwater delivery would also affect the competitive balance between mangrove species, several techniques were used to examine the water relations of two major species, *R. mangle* and *L. racemosa.* The moisture stress in mangrove species varied between years, but was not significantly different between species and sites. However, transpiration rates for *L. racemosa* exceeded those of *R. mangle*, and, within each species, transpiration was higher in the Fringe than in the Dwarf forest. The general trend of negative correlation between plant water potential and salinity was not evident in the present study. Since plant moisture stress is dependent on environmental factors that are highly seasonal, the implications of this study are limited, inasmuch as stress was estimated only twice, during the same season. Nevertheless, the results suggest that episodes of salt stress are probably infrequent in the study area, and that background moisture stress is not responsible for the previously described differences in Fringe and Dwarf forest productivity.

In general, the delivery of fresh water into the Dwarf Mangrove forest treatment was either not sufficient or not properly timed to alter the competitive balance among plant species within the resident Dwarf mangrove community, at least in the short run. However, effects of the freshwater rediversion treatment was observed in terms of the change in species composition in the westernmost portion of the Treatment Dwarf block where *Cladium jamaicense* and *Eleocharis cellulosa*, two freshwater species, appeared during the post treatment period. Therefore, it is possible that freshwater delivery applied over a longer time frame may eventually provide for the further establishment of *C. jamaicense*, *E. cellulosa*, and other freshwater graminoid species.

# *Hydrology*

Topographic contrast between Dwarf and Fringe forests creates disparities in the periodicities and volumes of tidal influx to these forests. Fringe forests were frequently inundated by high tides, whereas water levels in the Dwarf basins exhibited seasonal and diurnal associations with water levels in canals and precipitation. During the fall, when mean basin stages rise to near or above the soil surface and mean tide levels are above average for the year, Dwarf forests experience multiple monthly inundation events caused by brief dry-downs, followed by reinundation by tide. In other seasons, when water recedes below the basin surface, tidal oscillation frequently becomes non-discernible in the Dwarf mangrove basins, probably due to the large and spatially variable water holding capacity of the soils in these forests.

Water levels were generally higher and flooding was more frequent in the Treatment Dwarf than in the Control Dwarf. Observed differences in hydrology between these two sub-blocks suggested that (1) the hydrologic connection between tidal waters and seemingly similar interior mangrove basins can vary widely, (2) seepage from adjacent canals is an important water source in current mangrove forests, and (3) water delivery that is restricted to high canal stages is likely to play only a minor role in the hydrologic budget of these basins. Freshwater delivery from the canal also has a small but noticeable effect on surface water salinity, which showed a strong seasonal pattern in both blocks. Specific conductivity significantly increased in the Control block, but decreased sharply in Treatment Dwarf during the wet season, indicating a treatment effect at that time of year. However, the zone of influence was relatively narrow and prominent within a few meters of the canal, and may reflect not only discharge from the L31E canal, but also canal seepage affecting the areas closest to the fresh water source.

#### *Soils*

Soils in L-31E study area are marls with some organic matter in the Dwarf mangrove forest, and an organicrich fibrous peat in the fringe mangroves. In the dwarf mangroves, soil cores contained mollusks adapted to fresh water and marine conditions in the lower and upper portions, respectively, suggesting a change from fresh waterdominated to marine-influenced vegetation. In the Fringe forests, the peat layer was very thick, probably due to higher productivity in this zone, and a longer duration of mangrove soil accretion. Soil accretion rates apparently decreased from the coast towards the L-31E levee, resulting in the development of a topographic basin where the invading mangroves maintained themselves in the dwarf habitat. During the course of development, a productivity gradient was established in the dwarf basin, in which the central portion has the most microtopographic variation and the lowest elevation, macrophyte cover, and leaf area index.

In the dwarf basin, soil cores of the mangrove tree islands were distinctly different from cores in the surrounding Dwarf forest, with the former typically exhibiting a thicker peat interval. In the dwarf mangroves, replacement of freshwater vegetation by mangroves was associated with a change in soils from marl to peat formation, a pattern referred to as 'marine transgression'. Marine transgression that occurred during the Holocene period due to sea level rise and in the recent years due to elimination of freshwater sheet flow was marked in the soils by the change in salinity index as presented by fossil mollusks. In the coastal mangroves, the variable thickness of the organic intervals in the soil profiles were indicative of alternating periods of higher and lower productivity throughout the Holocene, which might correspond to fluctuations in sea level or climatic factors, especially rainfall.

### *Invertebrates*

Invertebrate diversity in the sampled vegetation plot was low. Major species were *Cerithidea beattyi* Bequaert, *Batillaria minima* Gmelin, *Melampus coffeus* Linne, *Littorina angulifera* Lamarck, *Cyrenoidea floridana*, *Brachidontes exustus* Linne, and *Ucasp.* Among-site differences and seasonal variation in abundance were common. The variability was associated with hydroperiod, vegetative and periphyton cover, availability of water borne food, and surface water salinity.

#### *Periphyton*

Periphyton was sampled bimonthly for two years from May 2000 through May 2002. Development and composition of the periphyton mat community on the natural substratum were measured in cores of benthic material, and biomass production was measured by incubating periphyton accumulated on the rust-proof fine wire-mesh screens. Periphyton mat biomass and its production were highest in the more open sites, as shading from the mangrove canopy slows down the periphyton growth. However, seasonal variation in the periphyton mat biomass was not significant, perhaps as a result of difficulty in separating the periphyton from marl and benthic detritus. Concentrations of nutrients in the periphyton mat varied among sites as well as within an individual location, though the seasonal changes in nutrients were not statistically significant. Total phosphorus decreased from west to east towards the coast, and the high N:P ratios observed in the periphyton mat confirmed the importance of phosphorus limitation in the system.

The distribution of 358 diatom taxa that were recorded in the study area was significantly correlated with water conductivity and N:P ratio. Assignment of diatom taxa to salinity preference categories (brackish, marine, freshwater) indicated that the number of freshwater taxa was highest near the L-31E canal and decreases toward the coast. The increase in freshwater taxa in the Treatment block indicates an ecological effect of increased freshwater flows, suggesting that freshwater diatom taxa will perform well as early indicators of changes in water delivery.

# *Benthic Community*

Three macroalgae/seagrass zones were identified in the stretch of Biscayne Bay nearshore waters between Mowry and Military Canal, extending from the shoreline to 800 m offshore. *Halodule wrightii* was dominant near the coast (until approximately 200 m), *Penicillus capitatus* was dominant between 200-600 m, and *Thalassia testudinum* was dominant with increasing distance from shore (600-800 m). Neither Mowry Canal output nor freshwater delivery in our treatment had a noticeable effect on the biomass and productivity of the nearshore benthic communities. Instead, groundwater had the greatest effect on benthic communities. Groundwater flow is presumably evenly distributed in the inshore area, masking any north-south trend during the period sampled. The expected summer increase in biomass and productivity was only apparent in the *T. testudinum* community. The *H. wrightii* and *P. capitatus* communities did not show this summer increase in either biomass or productivity. This

was probably due to the increase of filamentous algal cover in the nearshore environments, which smothers the seagrass and inhibits its growth.

In summary, topographic variations and natural disturbances (hurricanes and freezes) are important in maintaining habitat variability in the L-31E study area. Temporal changes in hydrology, surface and pore water nutrients, vegetation structure and production, periphyton production, benthic communities and soil development processes were effected by various factors mainly associated with tidal fluxes, canal water delivery and natural disturbances. Except the limited effects on only water salinity, periphyton productivity and diatom populations within a narrow zone near L-31E levee, experimental freshwater delivery had no effects on hydrology and nutrient loads in the basin water to an extent that would translate into a significant change in vegetation structure and production. It may be because the volume of freshwater was either not sufficient or the period of the treatment was not adequate. Therefore, year round freshwater discharges in greater volume may eventually restore hydrology and bring significant changes in the habitat quality in the mangroves and adjacent bay waters.

# **Section A: Project Objectives, Research Design, and Treatment History**

# **A-1.** *Project objectives.*

The Biscayne Bay SWIM Plan (Alleman *et al*. 1995) recommended restoring wetland habitats and mitigating the effects of canal point discharges of freshwater into Biscayne Bay. To that end the South Florida Water Management District, in collaboration with the National Park Service and Florida International University, initiated a demonstration project in 1993 to redistribute freshwater from the South Dade canal system to mangrove wetlands fringing the southwestern portion of Biscayne Bay. The ultimate objective of the project was to provide guidance that would allow managers to recreate a more natural sheet flow to Biscayne National Park, thereby reducing the effects of sudden releases that now occur through existing coastal structures. A secondary objective was to restore, to the degree feasible, the original coastal ecosystems that prevailed prior to construction of the canal system. Monitoring activities associated with the demonstration project were carried out by a team from FIU's Southeast Environmental Research Center (SERC). A report summarizing the results of the project through the fall of 1998 was submitted to the Water Management District in 1999 (Ross *et al*. 1999). The current document brings the 1999 report up to date through January 2002, and also incorporates material from three other recent reports (Meeder *et a*l. 1999, Ross *et al*. 2000a, and Ross *et al*. 2001). In order to incorporate the most pertinent information under a single cover, several sections of the earlier documents describing work concluded prior to 1999 are reproduced here in full, while others are presented in abridged form. Descriptions of research topics that were ongoing through 1999-2001 draw on the earlier documents, but are updated and reinterpreted on the basis of the most recent data.

Throughout the southern Biscayne Bay watershed, existing coastal wetland communities have been cut off from sheet flow for decades. Reconnection of these wetlands to upstream water sources will alter existing hydrologic conditions, augment nutrient loads and perhaps increase exposure to other pollutants. While mangrove species are capable of persistence through a wide range of hydrologic and water quality regimes, the effects of freshwater rediversion on many aspects of ecosystem function are unknown. Before embarking on an extensive application of this hydrologic restoration procedure, the demonstration project was undertaken to narrow some of the major information gaps by documenting – in an experimental field setting – the effects of freshwater diversion on: (a) swamp and nearshore water chemistry and hydrology; (b) soil development and microbiological processes; (c) macrophyte and benthic algal community composition, structure, and production; (d) epiphytic and epibenthic invertebrates; (e) zonation, production, and phenology of primary producers in the nearshore environment, and (f) exchanges of nutrients and particulates between nearshore and mangrove ecosystems. Studies were undertaken to ensure that these responses could be viewed in a historical context, and within the context of the current South Dade landscape as a whole. Finally, the complicating influence of periodic natural disturbance on treatment response became apparent at several points during the study; where possible, these influences were incorporated within the monitoring program on an ad hoc basis.

The area chosen for the project – referred to in this document as the L-31E study area – is the coastal mangrove ecosystem bounded by the Mowry, L-31E, and Military Canals on the south, west, and north, respectively, as well as adjacent portions of Biscayne Bay (**Figure A-1-1**). Before establishing the monitoring design, FIU (a) reviewed all ground and surface water quality data available from the general area (described in **Section B-1**), (b) developed maps representing current and historical vegetation of the study area and adjacent lands, based on existing aerial photos (**Section C-1**), (c) sampled and described wetland soils, emphasizing a coastal gradient that prevailed throughout the area (**Section E**), and (d) determined the suitability of alternative study units by completing detailed topographic surveys (**Section A-2**).

# **A-2.** *Monitoring design and plot establishment*.

Upon completion of the preliminary data-gathering activities outlined above, it was decided that a BACI (Before-After Control-Impact) research and monitoring design (Underwood 1992) was the best choice for the demonstration project. The BACI design is intended to examine the interaction of Site with Time, substituting temporal replication for the spatial replication possible in other research settings. The BACI design may include multiple Control and Impact sites, but the logistics of the demonstration project dictated that monitoring focus on ecosystem structure and function in a single Control and a single Treatment block. The constraints on replication in this case were (a) the absence of publicly-owned mangrove basins in southern Dade County that were sufficiently similar in physiography, size, and hydrologic condition, and (b) the high cost of implementing such a field experiment on an operational scale. The advantage of the design is that many dimensions of the ecosystem can be examined simultaneously on the same experimental unit, thereby providing a more integrated perspective.

East-West oriented drainage ditches or canals divide the study area into five hydrologically-independent blocks of about 25 hectares each **(Figure A-1-1**). The first and fourth blocks from the south were similar in ownership (public, Biscayne National Park) and drainage pattern (well-drained by tidal creeks). The two blocks were also physiographically similar, in that both included an interior basin and a dissected coastal area, with a distinct natural levee along the Biscayne Bay shoreline (**Figure A-2-1** and **A-2-2**). The blocks differed slightly in elevation (lower by *ca* 10 cm in Block 1) and current basin size (larger in Block 1). However, the relative sizes of the major creeks draining the two areas suggest that the pre-development basin that included Block 4 was larger than that of Block 1. Because of their overall similarity, Blocks 1 and 4 were chosen as Treatment and Control Blocks, respectively, for the demonstration project.

Most of the coastal wetlands bordering southern Biscayne Bay exhibit a distinct zonation in mangrove vegetation. The coastward areas support tall forests that may exceed 20 meters in height at maturity, while the interior basins produce a low scrub vegetation with largest stems less than 1.5 meters tall. In the L-31E site these two structural forms are represented in most places by bands of at least 100 meters width. In general, a transitional forest of intermediate height separates these two contrasting mangrove forest types. On the assumption that variation in vegetation structure was indicative of fundamental differences in underlying ecosystem processes, we decided to subdivide the Treatment and Control Blocks into sub-blocks representing the coastal (Fringe forest) and interior (Dwarf forest) zones.

Within each of the four sub-blocks – i.e., Treatment Dwarf (TD), Treatment Fringe (TF), Control Dwarf (CD), and Control Fringe (CF) – a single location was set aside for hydrologic monitoring, and boardwalks were constructed to provide access while minimizing impact on the soft peat or marl sediments. Two wells were established at each site: a 4" diameter, PVC-lined well for water level monitoring, and a 2" well for collection of pore water. Biotic monitoring activities were carried out at four locations in each sub-block, except in the Control Dwarf, where only three plots were established.

## **A-3.** *The rediversion treatment.*

The pilot project was designed to test the feasibility of redistributing fresh water from canals to adjacent coastal wetlands that, if successful, could be applied more extensively throughout the southern Biscayne Bay watershed. At that broader scale, the hydrologic purposes of the treatment would be to restore a more natural temporal and spatial distribution of fresh water to Biscayne Bay, to decrease inorganic nutrient loads to the Bay from urban and agricultural sources while increasing the export of detritus and organically-bound nutrient forms, and to reestablish an estuarine zone with more natural salinity levels and seasonality. The delivery system used to accomplish these large purposes must be flexible and easily controlled, must deliver enough water to significantly reduce canal discharge, and must prevent saltwater intrusion. The mechanics of delivery in the pilot project were therefore also designed to meet these criteria.

The Mowry Canal, with a mean annual discharge of approximately 91,000-acre ft., is the ultimate source of freshwater available for redistribution to the Treatment Dwarf basin (**Figure A-1-1**). However, the availability of water varies seasonally from a mean May discharge of less than 3,000 to a mean July discharge of more than 12,000 acre-feet. A three-foot diameter culvert connects the Mowry Canal to the L-31E (Delivery) Canal approximately 60 m west of Water Control Structure S-20F. During periods of rapidly falling or rising water level in the Mowry Canal, the culvert impedes free flow into or out of the L-31E Canal. The delivery system from the L-31E Canal into the Treatment area consists of two three-foot diameter tubular culverts which deliver water into spreader canals at the eastern foot of the L-31E levee. The two culverts were located on either side of a modest topographic ridge that divides the Treatment block. The much smaller northern segment of the Treatment Dwarf basin drains into a boundary drainage ditch or small tidal creek to the north. The southern segment – the site of all monitoring activities in the Treatment block – drains through a single tidal creek to Biscayne Bay. Each culvert has an end flap

gate on the downstream side to minimize salt-water intrusion. In addition, each culvert delivers into its own spreader canal. The two spreader canals are separated by 10 m of undisturbed marsh at the topographic ridge and are approximately 2 m wide and 40 cm deep.

Design criteria were based on an average head difference between the marsh surface at the foot of the levee and the Mowry Canal of 0.8 ft (Alleman *et al*. 1995). Based upon this head difference and a design conveyance of two 36" diameter culverts, a discharge of 29 feet per second per culvert was expected about 80% of the time, or approximately 33,500 acre-feet annually. Several factors arose that caused actual discharges to be considerably less than predicted discharges. First, the tubular culverts were fitted with a weir structure with an adjustable crest. The weir structure permitted flow only through a maximum of about 33 % of the cross sectional area of the circular tube. In addition, it was necessary to set the weir crest at least two inches above consistent high water stage on the downstream side in order to maintain the minimum nap necessary for the use of published discharge tables. Another problem in the initial projections was in the assumptions underlying the estimation of average head difference. The Mowry Canal stage is managed by season unless untimely rainfall events require additional emergency release. Between May 15 and Oct 15 the target stage is  $2'1''$  and between Oct 16 and May 14 the target stage is 1' 5". During the rainy season when water in the Mowry Canal rises above 2'1" the S-20F gates open and water is discharged into Biscayne Bay until the stage drops to 1'7". The weir crest height was initially set at 1'7". After two days of operation the crest was lowered 3 cm to increase discharge. Even at this lower level, pre-release calculations of potential discharge proved to be substantial overestimates of the actual discharge, for the reasons stated above.

Construction of the culverts was initiated in November 1996 but was not completed for measurable release until 28 Aug 1997. During this period there was some minor leakage, especially during culvert emplacement. A continuous water level recorder was placed on the upstream side of the culvert and surveyed to the weir crest, allowing the calculation of both head and height of water above the weir crest. Stage was recorded every 15 min. The recorder data was used to determine the length of time the delivery canal stage remained at a given height. The stage-time data was applied to determine discharge into the treatment site, using discharge tables for vertically restricted rectangular notch weirs (Leupold and Stevens 1991).

# **Section B: Biogeochemistry and Nutrient Dynamics**

## **B-1.** *Historical water and sediment quality*.

Twenty-one water and sediment quality studies with direct relevance to the L-31E demonstration project were reviewed and submitted to the SFWMD as a special report by the Principal Investigators (Meeder and Ross 1994). Their findings are summarized below.

1. Southern Biscayne Bay water quality is good, especially when compared to source canal water quality. Sample station arrays from point sources along the western shore eastward into the open Bay reveal that concentrations of pollutants currently decrease rapidly seaward to levels below minimum detection for many deleterious chemicals. Rapid mixing of canal waters with Bay waters, and short Biscayne Bay water renewal time appear to prevent pollutant concentration buildup.

Pollutant levels in Biscayne Bay sediments are higher in some cases than in surface water, but in general they also decrease rapidly offshore. This indicates that pollutants passing through the Bay system do so quickly enough to prevent accumulation in the soils.

2. Each canal system has its "signature" water quality problem. Canal discharge contains different levels of specific pollutants depending on the major land use activities in the respective drainage basins. For example, household and yard chemicals and septic tank pollutants are most abundant in canals that drain predominantly residential areas. Other canals, such as the Princeton Canal, drain agricultural areas primarily, while yet others drain basins with industrial and hydrocarbon pollutants. The L-31E study area lies between the Military and Mowry Canals. In contrast to the Mowry Canal, the Military Canal has higher levels of many pollutants. However, the Mowry Canal is generally nitrate-rich due to agricultural runoff.

3. High levels of certain pollutants are found as chronic problems in some canal systems, while others occur episodically. With a few exceptions, levels are usually below Permissible Exposure Levels (when Permissible Exposure Levels have been determined). Occasional or seasonal high levels might occur due to concentration processes during the dry season or in association with rainfall runoff events. Fresh source material at area landfills may also cause high variability in levels at one or more stations. Trace metals in particular may vary considerably within the same area (e.g. one study near the South Dade Landfill reported mercury levels above EPA guidelines, while a second reported no detectable mercury at all).

4. Analysis of water or sediment quality determined during different seasons, with different methodologies, at different sites, and with different research objectives in mind is problematical. It is perhaps most useful in such cases to emphasize the range of values rather than the mean or median values from each report.

#### **B-2.** *Water quality monitoring*

Water quality monitoring was initiated in June 1995 and continued through October 2001. Eleven water sources were sampled. These included surface and pore water at single locations in each sub-block, and surface water at sampling stations in the Delivery Canal and adjacent to each block in Biscayne Bay. Initially, expected sampling variation was assessed from samples collected daily from the Delivery Canal during two weeks in June 1995. Sampling was monthly from July 1995 through October 2000, and then quarterly through October 2001. Surface waters were analyzed in the SERC labs for specific conductivity,  $NH_3-N$ ,  $NO_3 + NO_2-N$ ,  $NO_2-N$ , soluble reactive phosphorus, total phosphorus, total nitrogen, total organic carbon, alkaline phosphatase and chlorophyll-A, and pore waters were analyzed at FIU for the first 8 parameters. Trace metals (copper, iron, lead, and zinc) were analyzed monthly through July 1996; thereafter, sampling was quarterly through July 2000. Trace metal analyses were performed by Ecology and Environment, Inc. (Lancaster, NY). For the most part, the results reported below are based on samples collected over the entire study period (*ca* 75 months). Samples whose concentrations for a given parameter were below detection limits were assigned a value equal to one-half the limit. Occasional missing values were associated with the absence of surface water or difficulty in extracting pore water during dry periods.

Statistics for fourteen surface water parameters measured daily at a single location in the Delivery Canal over the initial two-week period are listed in **Table B-2-1**. Coefficients of variation for N+N, NO2, SRP, Fe, and Zn exceeded 50%, while other measured variables were relatively constant from day to day. This daily variation should be kept in mind when considering the monthly patterns discussed below.

**Table B-2-1**: Means, standard deviations, and coefficients of variation (%) for fourteen water quality parameters, based on daily collections from the Delivery Canal during the period June 15-29, 1995. Units of measurement are µM, except for specific conductivity (mS/cm), alkaline phosphatase (µM per hour), trace metals and chlorophyll *a* (µg/l), and dissolved organic carbon (ppm).

<b>Water Quality Parameter</b>	Mean	<b>Standard Deviation</b>	<b>Coefficient of Variation</b>
Specific conductivity	0.67	0.15	22.4
Alkaline phosphatase	0.24	0.08	33.3
$NO2 + NO3$	21.38	24.07	112.6
NO <sub>2</sub>	0.81	0.51	63.0
NH <sub>3</sub>	5.85	1.22	20.8
<b>SRP</b>	0.15	0.13	86.7
Total nitrogen	51.94	20.01	38.5
Total phosphorus	0.95	0.28	29.5
Chlorophyll a	1.45	0.69	47.6
Dissolved organic carbon	12.77	2.85	22.3
Cu	10.64	3.40	32.0
Fe	88.36	48.96	55.4
Pb	2.71	0.79	29.2
Zn	5.82	4.35	74.7

**Table B-2-2:** Percent of surveys in which concentrations of trace metals exceeded detection limits (Cu, 20 µg/L; Pb, 5 µg/L; Zn, 10 µg/L; Fe, 50 µg/L), June 1995 - July 2000.



Measurable levels of iron were present in most water samples, but more often than not, concentrations of copper, lead, and zinc were below detection limits (**Table B-2-2**). Copper was rarely detected in swamp surface or pore water samples, and never in Bay surface water. The frequency of measurable levels of lead, zinc, and iron were generally in the order: swamp pore waters > swamp surface waters > Canal or Bay surface waters.

When present in detectable amounts, concentrations of metals were lowest in Canal and Bay waters, and higher in swamp surface waters than pore waters. However, the concentrations of iron were higher in swamp pore waters than surface waters, as illustrated in **Figure B-2-1**. Iron is an essential micronutrient, but its primary ecological significance may lie in its impact on the availability of phosphorus (e.g., Chambers and Odum 1990). In anaerobic conditions the ferrous ion forms soluble compounds with phosphorus, but in aerobic conditions the ferric ion has a strong capacity to bind P in insoluble forms.

Like many environmental data sets, our nutrient variables were highly correlated with one another. To eliminate such collinearity and reduce the dimensionality of the data, we extracted orthogonal composite variables by applying principal component analysis (PCA) to various data subsets. **Table B-2-3** lists factor loadings derived from a PCA analysis of monthly means of eight variables at seven surface water and four pore water collection sites.



**Table B-2-3**: Variable loadings for first two factors extracted by principal component analysis of water quality data from eleven sites, July 1995 – October 2001. Factor 1 explained 34.5% and Factor 2 explained 23.3% of the total variation in the eight measured variables.

The first two PCA factors together explained about 58% of the total variation in the data set, while eigenvalues of subsequent factors were very low. Ammonia, SRP, total nitrogen, total phosphorus, and DOC shared strong negative loadings on Factor 1 and the oxidized nitrogen forms loaded positively on Factor 2. High scores on Factor 1 and Factor 2 both were therefore indicative of relatively fresh, organic-poor water with nitrogen predominantly in the oxidized forms.

Site scores for Factors 1 and 2 through the pretreatment period (August 1997) are illustrated in **Figure B-2-2**. Most sampling stations exhibited distinctive water quality characteristics. The results from multivariate analysis of variance (MANOVA) also revealed significant among-sites differences (p <0.001) in water quality. In general, the characteristics of surface waters in parallel sampling stations in the Treatment and Control blocks overlapped considerably. Biscayne Bay and Delivery Canal waters were also similar in having relatively low levels of phosphorus, DOC, total nitrogen, and NH3-N (high scores on both Factor 1 and Factor 2). In contrast, pore waters in the Control Dwarf and Fringe sub-blocks were low in nitrate and nitrite, but contained high levels of nutrient forms characteristic of reducing environments (high scores on both factors). Swamp surface waters, as well as pore water

from the Treatment Dwarf and Fringe sites, were intermediate (low scores on Factor 1, high scores on Factor 2), i.e., they were relatively poor in all measured nutrient forms.

Because of their associations with commonly proposed controls on productivity in mangrove ecosystems, specific conductivity and concentrations of total nitrogen and phosphorus in ambient waters are of special relevance to the L-31E experimental re-diversion. Means and standard deviations for these parameters in pore waters of the study area are listed below (**Table B-2-4**).

**Table B-2-4:** Mean values of three water quality parameters in swamp pore water at four sites in the L-31E study area. Based on samples collected monthly between July 1995 and August 1997. Standard deviations are in parentheses.



Pore water specific conductivity did not differ among sites (p <0.851), but differences in both total phosphorus ( $p<0.001$ ) and total nitrogen ( $p=0.001$ ) were observed. Concentrations of nitrogen were lowest in the Treatment Dwarf and highest in the Control Dwarf site, with intermediate concentrations in the two coastal soils (**Table B-2-4**). In contrast, total-P was uniformly higher in coastal Fringe sites than interior sites.

The distinct positioning of Delivery Canal and Bay waters in relation to swamp surface and pore waters in **Figure B-2-2** was considered a useful marker of temporal trends associated with the experimental delivery. It was expected that periodic inundation of the swamp in the treatment would force sample position to shift within the ordination diagram toward the signature of the Delivery Canal. Deviations from this prediction might be interpreted as signs of (a) limited treatment duration, (b) *in situ* biological or chemical transformations within the mangrove ecosystem itself, or (c) rapid exchange of water with the adjacent marine system.

Pre- and post-treatment data from paired Control and Treatment sub-blocks and from the Delivery Canal were ordinated separately with PCA. There was a modest indication that surface water quality in the Treatment Dwarf sub-block was affected by fresh water delivery through October 2001 (**Figure B-2-3A**). In contrast, the Treatment Fringe sub-block showed no such trend (**Figure B-2-3B**). Repeated measures ANOVA indicated that six of 8 major surface water quality parameters did not change from pre to post-treatment period in the TD sub-block, whereas mean TN and TOC were significantly lower during the post-treatment period (**Figure B-2-4A & B)**. However, the changes in mean TN and TOC were primarily attributable to a short period of exceedingly high values in the summer of 1996. Moreover, while both TN and TOC showed monthly variation, only the latter exhibited consistent seasonality, with high dry season concentrations (**Figure B-2-4B**). With these patterns in mind, we wished to test whether the observed changes in the Treatment Dwarf sub-block were due to fresh water delivery, or alternatively to other factors acting on a broader scale and resulting in simultaneous change in the Control sub-blocks as well. Working with the pre- and post-treatment periods separately, and further dividing the data into two seasons in each year (wet season, May to October; dry season, November to April), we calculated differences between Treatment and Control means for individual water quality parameters. Model 1 ANOVA was then applied, with Period (pre and post) and Season as fixed effects. A significant difference between periods could now be interpreted definitively as an effect of the freshwater delivery treatment to the Treatment Dwarf sub-block. These analyses revealed no significant effects of Period on any of the eight water quality parameters tested, including TN and TOC. In light of

the earlier results, the analysis suggests that changes in surface water quality occurred in both blocks simultaneously, and could not be simply attributed to the freshwater delivery from the Canal.

Our expectation was that changes in pore water quality would be more reflective of the fresh water delivery treatment, because the residence time of pore water in the swamp is probably orders of magnitude higher. An ordination of both pre- and post-treatment pore water data from paired Control and Treatment sub-blocks revealed that pore water quality in both Dwarf and Fringe sub-blocks changed during the post-treatment period (**Figure B-2- 5**). Nitrogen oxides, SRP and TOC in the pore water of the Treatment Dwarf sub-block were lower during the posttreatment period than the pre-treatment period **(Figure B-2-6)**. However, results of the multivariate analysis of variance (MANOVA) showed that simultaneous changes occurred in these pore water quality parameters in the Control Dwarf sub-block as well. Changes in pore water nutrients were more distinct in Fringe than Dwarf forests. For example, concentrations of all major components, such as  $NO_x$ , SRP,  $NH_3-N$ , TN and TP in the pore water significantly decreased between pre- and post-treatment periods in the both Fringe sub-blocks (**Figure B-2-7A-F**). For instance, the mean phosphorus content of Fringe pore water decreased by 3- to 4-fold in the post-treatment period. Unlike the other water quality parameters, specific conductivity of the pore water increased after the beginning of the treatment period (**Figure B-2-7F)**. However, a closer examination of the data suggests that the decreasing trend in the concentrations of SRP, NH<sub>3</sub>-N, TN and TP had clearly begun prior to treatment in August 1997 (**Figure B-2-8**). The steady decrease in pore water nitrogen and phosphorus over the course of the study has several possible explanations. One is that the sites are recovering from an earlier disturbance that caused a temporary increase in pore water nutrients. We are not aware of any disturbances other than Hurricane Andrew in 1992 that might have had such an impact. Hurricane Andrew's severe effects on vegetation structure were concentrated in the Fringe forests (**Section C-2**). Ross *et al.* (1994) previously observed elevated concentrations of dissolved nitrogen and SRP in ground water in portions of the Florida Keys immediately outside Hurricane Andrew's primary zone of influence, but such peaks did not persist for more than few months. Therefore, it is not certain that the high concentrations of pore water nitrogen and phosphorus in the beginning of the present study i.e. 3 years after the hurricane, were related in any substantial degree to Hurricane Andrew, and consequently that the steady decrease in TN and TP in the pore water thereafter represented a phase in the recovery process.

A comparison between Control and Treatment sub-blocks revealed that temporal changes in pore water quality in Control and corresponding Treatment sub-blocks were not identical. For instance, in the Control Dwarf and Control Fringe sub-blocks, the increase in average specific conductivity of the pore water during the posttreatment period was significantly higher than the increase in the corresponding Treatment sub-blocks (**Figure B-2- 7F**). In the Control Dwarf site, specific conductivity increased from pre- to post-treatment period uniformly in both wet and dry seasons, whereas in the Treatment Dwarf, a significant increase was observed in the wet season only (**Figure B-2-9A**). Also, an observed decrease in SRP concentration in pore water over the sampling period was much more pronounced in the Control Dwarf sub-block than in the Treatment Dwarf sub-block, and in the wet season than in dry season (**Figure B-2-9B**). In the analysis of differences between Control and Treatment means (C-T) for SRP, this resulted in significant Period and Season effects (p = 0.048). Likewise, TN and TP pore water decreased more sharply in the Control Fringe than in the Treatment Fringe sub-block (**Figure B-2-7**), and this resulted again in significant Period effects on C-T differences in pore water nitrogen ( $p = 0.025$ ) and phosphorus (p  $= 0.030$ ). There was no effect of Season in this analysis ( $p > 0.05$ ), as pore water TN and TP decreased uniformly during wet and dry seasons (**Figure B-2-10**). A more than 3-fold decrease in pore water phosphorus and about 50% decrease in nitrogen concentrations from pre- to post-treatment period in the Fringe but not in the Dwarf mangroves suggest a strong influence of tidal factors, but not freshwater delivery, because the Dwarf mangrove ecosystem was the one which was more directly affected by the freshwater delivery from the L-31E Canal.

To compare the quality of surface and pore water within each sub-block, we performed paired T-tests on data for all measured water quality parameters. Since surface water was not always present at the time of sampling, the data analysis included only months in which both surface and pore water were sampled. Means for most water quality parameters were higher in pore water than in surface water within a particular sub-block, with the following exceptions: (1) the mean concentrations of  $NO<sub>x</sub>$  and TP were not significantly different in surface and pore water in the Control Dwarf sub-block, and (2) the mean concentration of  $NO<sub>x</sub>$  was higher in surface water than in pore water in the Treatment Dwarf and both Fringe sub-blocks. As described earlier for Control – Treatment differences, twoway ANOVA was performed on Surface - Pore water quality differences, in order to test whether differences in these two media were the same throughout the pre- and post-treatment periods, and in dry and wet seasons. ANOVA results revealed that the differences in specific conductivity and the mean concentrations of all major nutrients in the

surface and pore water in the Control Dwarf sub-block remained relatively constant during the pre- and posttreatment periods ( $p > 0.05$ ), but varied between wet and dry seasons. Under wet season conditions in the Control Dwarf sub-block, concentrations of pore water  $NH_3-N$  and TP were significantly lower during the post-treatment period, while in the dry season the post-treatment period was characterized by relatively high concentrations of these nutrients (**Figure B-2-11B & F**). In the Treatment Dwarf sub-block, differences in phosphorus concentrations between surface and pore water varied with Period ( $p = 0.028$ ). Mean TP in surface water decreased in the wet season but increased in the dry season during the post-treatment period, while mean TP in pore water decreased in both seasons during that period (**Figure B-2-12F**). Throughout the study period, the mean concentrations of NH3-N, SRP, TN and TP were higher in the pore water than in the surface water in the both Control and Treatment Fringe sub-blocks. However the contrast between surface and pore water concentrations differed between Periods in the Control Fringe sub-block (**Figure B-2-13**), while remaining relatively stable in the Treatment Fringe sub-block (**Figure B-2-14**). In the Control Fringe, the mean concentrations of NH3-N, SRP, TN and TP in pore water in both seasons were significantly lower during the post-treatment period than the pre-treatment period, while surface waters were relatively insensitive to Period (**Figure B-2-13**).

Pore water quality in the coastal Fringe forests was strongly influenced by tidal events, but not by freshwater delivery. This conclusion is supported by a steady increase in pore water salinity throughout the study period in the both Fringe sub-blocks (**Figure B-2-15**). Pore water TN and TP were negatively correlated with salinity (**Figure B-2-16**), suggesting a water source with relatively high salinity and low TN and TP. During the post-Treatment period, our data show a strong pattern of increasing salinity and decreasing nitrogen concentration in Biscayne Bay water (**Figure B-2-17A & B**), implying that the volume of nitrogen-rich freshwater reaching the Bay, presumably through the Mowry and Military Canals, may have decreased in recent years. Unlike total nitrogen, TP concentration in Bay water and Delivery Canal water were virtually identical, and remained relatively constant throughout the study period (**Figure B-2-17C**). This suggests that the observed decrease in Fringe pore water phosphorus is related to factors other than source; a detailed study on the biogeochemistry of phosphorus in the pore water in these ecosystems is needed.

#### **B-3.** *Chemical composition of mangrove leaves***.**

#### **i.** *Nutrients.*

Sampling for leaf tissue analysis began in March 1996 and continued at about three-month intervals thereafter. Every sampling period, ten mature leaves were collected from five individual *R. mangle* stems in each of the four sub-blocks. Samples collected through October 2001 were analyzed for carbon, nitrogen, phosphorus,  $\delta^{15}N$ , and  $\delta^{13}$ C. During the pre-treatment period, selected samples were analyzed for  $\delta^{15}$ N on a few occasions. However, the analysis for  $\delta^{15}N$  became regular beginning in January 1998. To address the question of whether the mangrove ecosystem is nitrogen or phosphorus limited, molar N:P ratios were calculated. Concentrations of trace elements, i.e., copper, iron, lead and zinc were determined in the samples collected through July 2000. Inasmuch as red mangrove leaves are initiated a minimum of 3-6 months prior to reaching maturity, no measurable effect of the August 1997 water delivery on the composition of mature leaves was considered likely before January 1998. Therefore, unlike the water data for which all samples collected after August 1997 were considered as posttreatment samples, leaf samples collected through October 1997 were treated as pre-treatment, and the samples collected after that time were considered as post-treatment samples.

For the pre-treatment period, data analysis focused on site variation in all measured elements. Repeated measures analysis of variance was inappropriate in this situation because individual trees were not re-sampled time after time. Instead, our analysis was a two-step process. First, we tested the effect of sampling period by applying a one-way analysis of variance and post-hoc comparisons (Duncan's multiple range test) for each parameter. If the effect of sampling period was significant in the initial analysis, we analyzed the data using two-way ANOVA, with site and month two factors. In this analysis, we replaced sampling period with month in order to address the issue of seasonality more effectively. If no significant temporal effect was observed, we tested the effect of site without regard to month, applying one-way ANOVA to data sets consisting of 35 observations per site (7 sampling periods x 5 replicates per period). If site variation was statistically significant in the second analysis, we tested an orthogonal contrast for Zone (Dwarf v. Fringe sites), and a second contrast for Block (Treatment v. Control sites).

Temporal effects on almost all leaf components were significant in all sites except the effects on Lead in the Control Dwarf, and on Phosphorus and Zinc in the Control Fringe. However, some elements, such as Copper, Lead and Zinc did not exhibit regular seasonality over the short period of record. On the other hand, the temporal peaks and valleys in carbon, nitrogen, phosphorus and iron content (**Figure B-3-1**) showed more continuity of pattern from one sampling period to the next. Mean leaf iron content from the March 1996 sample (42-67 mg/kg) was more than three times as high as any other sample, while subsequent periods varied little among themselves. The March 1996 results may have been related to a freeze, which affected several sites two months earlier (see **Section C-2**); because this sampling period represented a serious outlier in the data set, it was eliminated from further analysis of site differences.

As illustrated in **Table B-3-1**, significant among-site variation was found for all leaf components tested  $(p<0.05)$  except lead (overall mean =  $0.42$  mg/kg). Nitrogen and copper content varied between Control and Treatment blocks of both Dwarf and Fringe zones, but not between zones. In both Dwarf and Fringe, nitrogen was higher in the Control (mean =  $1.45\%$  &  $1.50\%$ , respectively) than the Treatment blocks (mean =  $1.28\%$  &  $1.35\%$ , respectively), while copper concentration was higher in the latter (**Table B-3-1**). Unlike N and Cu, other components such as C, P, Fe and Zn did not differ between blocks ( $p$ >0.05), but their mean concentrations in the Fringe exceeded the concentrations in the Dwarf zone. Mean molar N:P ratio was significantly higher in the Control Dwarf sub-block (mean N:P = 42.2) than in the Control Fringe (mean N:P = 31.3), but it did not differ between Treatment Dwarf and Treatment Fringe sub-blocks (mean N:P = 35.3 and 35.4, respectively).

Changes in leaf nutrient concentrations between the pre- and post-treatment periods were more distinct in the Fringe than in Dwarf zone. However, a change in mean carbon content in the leaves was significant in both the Control and Treatment Dwarf, but only in the Treatment sub-block of the Fringe forests. In both the Control and Treatment Dwarf, mean carbon content in the leaves increased from pre to post-treatment (**Figure B-3-2A**). Increase in carbon in these sub-blocks occurred primarily in the months of July and January, while decreasing in April.

A change in leaf nitrogen and phosphorus between pre- and post-treatment periods in the both Dwarf forest plots was not significant ( $p > 0.05$ ), though their concentrations all showed a generally decreasing trend through time (**Figure B-3-3**). On the other hand, mean leaf nitrogen increased significantly from pre- to post-treatment period in the Treatment Fringe (mean N = 1.35%, 1.47%, respectively) but not in the Control Fringe (**Figure B-3- 2B**). In contrast, phosphorus content decreased in the Control Fringe but barely changed in the Treatment Fringe (**Figure B-3-2C**).

<b>SITE</b>	<b>ELEMENT</b>							
	Carbon	Nitrogen	Phosphorus	Copper	Iron	Lead	Zinc	
Control Dwarf	45.27	1.45	0.077	3.02	20.52	0.351	5.09	
<b>Treatment Dwarf</b>	45.67	1.28	0.084	5.90	21.95	0.318	5.11	
Control Fringe	46.67	1.50	0.106	4.26	25.94	0.360	5.94	
<b>Treatment Fringe</b>	46.54	1.36	0.092	5.42	27.86	0.305	6.14	
Site effects	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	ns	0.039	
Seasonality	< 0.001	< 0.001	0.046	ns	< 0.001	ns	ns	
Dwarf vs Fringe	< 0.001	ns	< 0.001	ns	< 0.001	$\overline{a}$	0.005	
<b>Block contrast</b> in Dwarf zone	ns	0.002	ns	< 0.0001	ns	$\overline{\phantom{0}}$	ns	
Block contrast in Fringe zone	ns	0.006	ns	0.015	ns	$\overline{\phantom{0}}$	ns	

**Table B-3-1**: Mean composition of several elements in red mangrove leaves, March 1996 - October 1997. Concentrations are in % for N and P, and in mg/kg for the four trace metals.

The N:P ratios in plant tissues have been considered, in some cases, to be good indicators of the availability of nitrogen and/or phosphorus available in the environment. More precisely, the ratios are often used to ascertain that a system is either nitrogen or phosphorus limited (Fourqurean *et al.*, 1992a; Doering *et al.* 1995; Verhoeven *et al.* 1996). Mean molar N:P ratios higher than 16 in the both Dwarf and Fringe forests (**Figure B-3-2D**) strongly suggest that both of these ecosystems are phosphorus-limited. N:P ratios in all four of these mangrove forests were much higher than the values found in other wetlands (Bedford *et al.* 1999). Inter-site variation in the mean N:P ratio was significant (p < 0.001), as dwarf mangroves had higher N:P ratios than the tall mangroves at the fringe (**Figure B-3-2D**). Among the dwarf sites, the Control Dwarf had the higher mean N:P ratio than the Treatment Dwarf. A significant increase in mean N:P ratio was observed from pre to post-treatment period in the Treatment sub-block of the dwarf forest, and in the Control sub-block of the fringe forest. The change in leaf N:P ratios are apparently sitespecific and unrelated to the fresh-water delivery treatment, because no changes in nitrogen or phosphorus content in the water column or in pore waters within the Treatment Dwarf sub-block due to freshwater delivery were observed.

A significant increase in N:P ratio in one of the Fringe sub-blocks (**Figure B-3-2D**) may be interpreted as an increase in phosphorus deficiency in the system, because it was paralleled by a decrease in pore water phosphorus concentration over the course of the study beginning in July 1995 (**Figure B-2-8**). However, a sharp decrease in total phosphorus in pore water in both Control and Treatment Fringe sub-blocks was not immediately translated into a change in N:P ratio in the leaves. For example, a significant decrease in pore water phosphorus concentration in the Treatment Fringe sub-block was accompanied by a simultaneous decrease in pore water nitrogen concentration causing mean N:P ratio to remain relatively constant from pre to post-treatment period (**Figure B-3-2D**). Our results indicated that pore water nutrients reflect the relative availability of nitrogen and phosphorus for red mangroves. Though the surface water is believed to be the major water source for mangroves (Lin and Sternberg 1994), other research has shown that groundwater can be an important source of water in mangrove ecosystems (Ovalle *et al.* 1990; Wolanski 1992). Water sources used by various mangrove forest types vary seasonally, with elevation playing an important role in the shift in water source (Lin and Sternberg 1992). Moreover, the relative use of water and nutrients from various sources by mangroves may depend on site-specific characteristics, such as proximity to the ocean, relative position of saline and freshwater tables, frequency of tides, depth of the tidal water, proximity to the canals, and amount of seepage water from the canal entering mangrove ecosystems, etc. A detailed isotopic study on the various water sources for mangroves in these sites is needed.

Micronutrients, such as iron, copper and boron have been considered important in mangrove growth (Sternberg, L. D. S. L, *personal communications*). In the present study, inter-site variation in foliar concentrations of copper, iron and zinc was significant ( $p < 0.001$ ;  $p = 0.002$  &  $p < 0.001$ , respectively). Trends for copper were mixed; concentrations were lower in one of Dwarf sites – Control Dwarf- but were higher in the Treatment Dwarf than in either Fringe forest site (**Figure B-3-4A**). However, individuals in the Dwarf sites had significantly lower concentrations of foliar iron and zinc compared to individuals in the Fringe forests (**Figure B-3-4 B & C**). Lower concentrations of iron and copper in dwarf than tall mangroves have also been reported in other studies (Sternberg L. D. S. L. *personal communications)*. Changes in copper concentrations from pre- to post treatment period were significant in all sites except the Control Dwarf ( $p = 0.18$ ), but the changes in iron concentrations were significant only in the both Control and Treatment Dwarf sub-blocks ( $p = 0.007$  and 0.004, respectively). In the Treatment Dwarf, mean concentration of foliar copper almost doubled during the post-treatment period (Mean = 9.3 mg/kg) compared to the pre-treatment period (Mean = 5.9 mg/kg). In contrast, foliar copper concentration decreased in the Treatment Fringe from 5.4 mg/kg in pre- to 4.3 mg/kg in the post-treatment period. Since, copper in canal water was below detection level throughout the study period except on one occasion (**Table B-2-2**), it was uncertain whether an increase in foliar copper concentration in the Treatment Dwarf sub-block was the effect of freshwater delivery treatment. Iron concentration increased in both Dwarf sub-blocks, indicating again that the source of iron was probably different from the canal water.

# **ii.** *δ15 N study of nitrogen use by R. mangle*.

In order to gain further insight into nitrogen cycling processes within L-31E mangrove ecosystems, we surveyed variation in leaf *δ<sup>15</sup>*N within the study area. This research is discussed in more detail in the paper (Fry *et al.* 2000). In the fall of 1994, *R. mangle* leaves were collected along a transect extending from Biscayne Bay to the L-31E levee. Mature leaves were collected from the crowns of 5-10 individual trees at each location and prepared for %N and *δ<sup>15</sup>*N analysis. Leaf midribs were removed, dried samples were ground and combusted to nitrogen gas in a

Carlo-Erba elemental analyzer, and *δ<sup>15</sup>*N was determined by continuous flow stable isotope mass spectrometry in the FIU-SERC labs. The results are summarized in **Figure B-3-5.** Leaf %N was highest within 100 meters of Biscayne Bay, peaking at 2% about 50 meters from shore. N content subsequently decreased inland as far as the L-31E levee, where it was less than 1.2%. Leaf  $\delta^{15}N$  was about +7 units immediately adjacent to the Bay, increasing to +11 units at *ca* 50 meters, then decreasing below 0 units before the levee.  $\delta^{15}$ N of plants growing on the banks of the Mowry and L-31E Canals was nearly +13 units. Such a heavy isotopic signal is typical of canal waters that receive high loading from agricultural fertilizers.

The pattern of *δ<sup>15</sup>*N in the L-31E swamp fits a model in which the isotope character of source water and the extent of isotopic fractionation occurring during nitrogen uptake jointly affect leaf  $\delta^{15}N$ . Mangroves near the Biscayne Bay shoreline are bathed in isotopically heavy Bay waters that are strongly affected by Mowry Canal outflow. Moving inland, this source effect may change, with tidal water representing a smaller portion of the total water budget, and direct precipitation and temporary storage in the interior basins becoming more important. Secondly, isotopic discrimination may change, with strongest fractionation (i.e., lightest isotopic signal) in the interior Dwarf forest. Data available on leaf *δ<sup>15</sup>*N for the post-treatment period also revealed that fractionation was stronger in the Dwarf forests than in the Fringe forests (**Figure B-3-6**). Mangrove leaves in the Control Dwarf had the lightest isotopic signal ( $\delta^{15}N = +1.4$ ), and the Treatment Fringe forest had the heaviest isotopic signal ( $\delta^{15}N =$ +9.0). The heavy signal in Treatment Dwarf leaves ( $\delta^{15}N = +5.4$ ) compared to Control Dwarf leaves may be the result of source effects, i.e., fresh water delivered from the canal, or tidal water, which reaches the Treatment Dwarf basin more readily via the well-developed creek system. Among-site variation in fractionation may also play a role. According to current models of plant isotopic fractionation, greatest discrimination against the heavy isotope occurs where plant growth is slow and nitrogen is largely in the ammonium form (Goericke *et al.* 1994). This model was not borne out in the present case, at least with respect to surface water: The % of TN in the ammonium form did not significantly differ between Treatment Dwarf and Control Dwarf (6.9% and 6.3%, respectively). However, pore water in the Control Dwarf sub-block, where the leaves were isotopically light, was characterized by 43.2% of total nitrogen in the ammonium form, while pore water in TD was 13% of total. The relatively high proportion of ammonium in CD pore water seems to support our earlier supposition that this medium represents the primary nutrient pool accessed by the red mangroves. Certainly, more research is needed to determine whether the source effect or the fractionation effect is primarily responsible for the remarkably clear gradient in leaf  $\delta^{15}N$  illustrated in **Figure B-3-5.**

# **iii.** *δ13 Carbon content of red mangrove leaves***.**

The carbon isotope composition of plants has been shown to reflect the ratio of internal to external carbon dioxide concentration in the leaf (Farquhar *et al.* 1982a). In most ecological settings, this ratio is controlled by the rate of carbon dioxide uptake through stomata (Farquhar *et al.* 1982b). Since stomatal conductance is itself controlled by the gradient in moisture potential between leaf and atmosphere, intra-specific variation in carbon isotope composition most often reflects variation in moisture stress (e.g., Guy *et al.* 1980; Ross *et al.* 1994).

As described in **Section B-3-i**, we collected *R. mangle* leaf samples for determination of carbon isotope composition at quarterly intervals beginning in January 1996. Leaves were ground and combusted with cupric oxide. The resulting CO2 was cryogenically purified and subjected to mass spectrometry analysis in the laboratory of Dr. Leo Sternberg at the University of Miami through 1998, and in the FIU isotope lab during the last half of the project. One set of samples was analyzed at both U of Miami and FIU, and the results from the two labs were in close agreement. Carbon isotope composition was expressed as  $\delta^{13}C$ .

$$
\delta^{13}C = 1000 \text{ x (R}_{sample} - R_{standard})/R_{standard}
$$

where  $R_{sample}$  and  $R_{standard}$  were the  ${}^{13}C/{}^{12}C$  ratio of the sample and the PDB standard, respectively. Low (large negative) values of  $\delta^{13}$ C were expected to reflect low moisture stress during carbon fixation, and high values to indicate high stress. Statistical analysis of site effects was performed as described in **Section B-3**.

*R. mangle* leaf  $\delta^{13}$ C did not differ among sampling periods, but site effects were found to be highly significant  $(p<0.001)$  in the subsequent one-way analysis of variance (**Figure B-3-7A**). Mean  $\delta^{13}$ C values over the pretreatment period were: Control Fringe, -28.51; Treatment Fringe, -27.69; Control Dwarf, -26.12; and Treatment

Dwarf, -25.83. Orthogonal contrasts yielded highly significant differences between forest types and between blocks, indicating lower stress in the Fringe forest relative to the Dwarf, and in the Control block relative to the Treatment. In light of the negative evidence regarding differences in moisture stress (**Section C-8**) among sub-blocks, we hypothesized that the consistent differences in  $\delta^{13}$ C reflect the effects of nutrient limitation – specifically phosphorus limitation – on stomatal conductance and photosynthetic rate. We are not aware of other studies supporting a direct connection between nutrient limitation of any sort and carbon isotope composition. Since the presence of the nutrient effect hypothesized above does not preclude the well-established effect of moisture stress on leaf  $\delta^{13}C$ , diversion of fresh water into the Treatment block was expected to reduce the relative concentration of heavy isotopes in fixed carbon slightly. However, we expected that even if our hypothesis were true, diversion of water low in phosphorus would not entirely eliminate the site effects.

No significant change in  $\delta^{13}C$  from the pre- to post-treatment period due to freshwater delivery was observed in the Treatment Dwarf (**Figure B-3-7B**), but this was not unexpected because delivery neither decreased salinity/conductivity in surface or pore water (**Figures B-2-7F** and **B-2-15A**), nor relieved P-limitation (as evidenced by leaf N:P ratios; **Figure B-3-2D**). In contrast, mean  $\delta^{13}$ C value increased from –27.69 in pre to -26.99 in post treatment period in the Treatment Fringe sub-block, and the change in  $\delta^{13}$ C was highly significant (Two-way ANOVA;  $p = 0.0016$ ), showing an increase in physiological stress in the coastal forests during the post-treatment period. However, this effect was not accompanied by a significant change in phosphorus content or N:P ratio in leaves in that sub-block (**Figure B-3-8A**).

In summary, in the Dwarf mangroves, the hypothesis that freshwater delivery would reduce the concentration of heavy isotopes in fixed carbon was not supported. In the Treatment Fringe mangroves, the observed increase in plant stress appeared to be associated with a decrease in pore water TN and TP, and an increase in conductivity, but evidence of increasing nutrient limitation in the leaves was absent.

#### **B-4.** *Sediment alkaline phosphatase activity as an index of available phosphorus*.

Data presented above demonstrated a strong spatial association between apparent ecosystem productivity, as reflected in existing stand structure (described in detail in **Section C**), and phosphorus content in (a) pore water (**Section B-2**), and (b) mangrove leaf tissue (**Section B-3**). The hypothesis that growth may be limited by phosphorus availability in mangrove ecosystems has been discussed by others (e.g., Feller 1995). We examined the hypothesis further through studies of soil phosphatase activity over a two-year period, at sites distributed throughout the L-31E study area.

Inducible enzyme systems are good candidates for environmental monitoring, since they respond rapidly to changes in the environment. Phosphatases (acid and alkaline) are inducible enzymes in plants, algae, and microfauna, which are produced in response to an organism's need for phosphate. They may be induced and released (or retained in the extracellular space) as a single enzyme response, or may be produced and released in association with other systemic responses such as induced senescence in plants (Morita *et al.* 1996). Phosphatases have been found in microfauna as well as algae and marine macrophytes (Lapointe and O'Connell 1989; Hernandez *et al.*, 1992, 1993, 1994). Both microorganisms and plants have the capacity to release phosphatase to the external environment. However, Spier and Ross (1978) argue that microorganisms supply most of the soil enzyme activity because of larger biomass, high metabolic rate, and short lifetimes, all of which facilitate the release of relatively large amounts of enzyme. However, associated plants, animals and bacteria may also benefit from this extracellular release.

Characterization of available P in natural ecosystems has been a topic of intense study. Estimates of phosphorus availability to plants and microfauna have used serial extraction procedures coupled to measures of tissue and sediment phosphorus (Powell, 1989; Short *et al.*, 1990; Fourqurean *et al.*, 1992a; Ruttenberg, 1992; Delgado *et al.*, 1993; Jensen and Thamdrup, 1993; Jensen *et al.*, 1995). Soluble reactive phosphorus (SRP) has been used as one measure of available phosphorus for bacteria and plants in aquatic ecosystems (Ruttenberg, 1992; Delgado and Vidal, 1993), and is defined methodologically as that phosphorus released from acid-labile inorganic and organic compounds during an acidification extraction procedure. These determinations may require photooxidation, acidic digestion, or both. The soluble non-reactive phosphorus pool and the total dissolved phosphorus pool is subsequently derived by difference (Ridal and Moore, 1990), and available phosphorus is some component

of these pools. SRP therefore, may be used as an estimate of minimum available phosphorus. The sequential extraction methods may indicate potential for removal by microbes and plants. Actual C:N:P ratios found in plants and sediments have been found, in some cases, to be integrative correlates for amounts of phosphate available in the environment (Powell, 1989; Short *et al.*, 1990; Fourqurean *et al.*, 1992b). All of the above methods require lengthy laboratory procedures, and, while supplying historical integrative information on nutrient input, are not good detectors of environmental changes on a shorter time frame.

Alkaline phosphatase (APASE) has been shown to play a role in phosphorus regeneration in aquatic systems (Gage and Gorham, 1985; Jansson *et al.*, 1988; Chrost 1993; Hernandez *et al.*, 1993). Because alkaline phosphatase activity is a more direct index of phosphate limitation and phosphate availability than the indirect methods described above, we initiated a study of APASE in the L-31E study area, in collaboration with Dr. Myrna Jacobson of the Georgia Institute of Technology. This study is described in detail in Jacobson *et al.* (unpublished manuscript). We determined APASE activity at nine sites – six in the Treatment block and three in the Control block – between January 1996 and July 1998. Swamp sampling locations in each block were arrayed from 50 meters east of the L-31E levee to *ca* 30 meters from the Biscayne Bay shoreline. APASE analyses were performed on five replicate 5-cm soil cores collected from each site on ten dates during the period. Total sediment phosphorus was also determined for cores collected in March 1996 in the Treatment Dwarf sub-block.

Mangrove biomass generally increased with distance east of the L-31E levee (**Figure B-4-1A**). In conjunction with this trend, APASE and sediment phosphorus data provide further circumstantial support for the hypothesis of phosphorus limitation on ecosystem production. The spatial distribution of APASE and sediment phosphorus in the Treatment Dwarf sub-block presented nearly a mirror image of one another during the March 1996 sampling period: sediment phosphorus increased and APASE activity decreased with distance from the L-31E levee (**Figures B-4-1B & C**). Results from other L-31E sites are also consistent with the hypothesis of P-limitation: low APASE in the Treatment Fringe sub-block (**Figure B-4-2**), and similar decrease in APASE from Dwarf to Fringe forest sites in the Control block (**Figure B-4-3**).

APASE activity throughout the study area exhibited very strong temporal patterns that were largely consistent among sites (**Figure B-4-2** and **B-4-3**). However, neither the peaks observed in May - July of 1996 and November - January 1998, nor the very strong trough of February 1997, are indicative of regular seasonal patterns or the diversion treatment itself. These temporal patterns are expressed most strongly in the Dwarf forest sites furthest from the coast (**Figure B-4-2** and **Figure B-4-3**). At present, we cannot explain these patterns, beyond suggesting that they are a response to some factor or factors (probably hydrologic and/or climatic) that affect all portions of the study area to some degree.

Our APASE monitoring did not extend far enough into the post-diversion period to indicate what effect the treatment will ultimately have on phosphorus availability. Given the low phosphorus concentration (and N:P ratio) of water in the Delivery Canal (**Table B-2-1**), one might predict that phosphorus deficit – and hence APASE activity – will increase in the Treatment Dwarf sub-block as the effects of the diversion reverberate more thoroughly through the mangrove ecosystem.

# **Section C: Vegetation**

The discussion of L-31E vegetation studies from 1992 through the present is divided into four general subject areas: historical and current vegetation of the study area and adjacent areas, plant community responses to natural disturbance, annual variation in plant community structure and population dynamics, and mangrove water relations.

### **C-1.** *Historical and current vegetation of the study area.*

[Written in 1995, the perspective of Current Vegetation in this section is that of the immediate post-hurricane period].

**Historical vegetation.** Historical photo-interpretation was based on aerial photo CJF 6-29 (Soil Conservation Service, July, 1940), in conjunction with recent groundtruthing, and our current understanding of ecological relationships in the coastal zone. These sources suggest that prior to the construction of the L-31E levee and canal, an east-west coastal gradient from intertidal to supratidal to non-tidal freshwater wetlands encompassed the non-agricultural portions of the study area and immediately surrounding lands (**Figure C-1-1**).

The intertidal portion of the gradient consisted of taller and shorter variants of mangrove forest, appearing black and gray, respectively, on the photo. In 1940, the tallest mangrove trees occupied a very narrow  $\leq 200$  meters) fringe along the Biscayne Bay shoreline. The **Fringe Mangrove Forest** also encroached inland along tidal drainages that, with several exceptions, were confined to a coastal zone considerably less than a kilometer in width. In most portions of the study area, a dense, shorter-statured mangrove forest bound the tall coastal fringe toward the interior. This **Transitional Mangrove Forest** zone was absent immediately north and south of the current Military Canal, an area dissected by a number of short tidal creeks. In contrast, low mangrove forest appears to have constituted a broad band along several major tidal creeks reaching well into supratidal zones.

Throughout the study area, a light-colored vegetation zone is evident on the 1940 aerial photo immediately interior to the low mangrove forest, and in broad areas between tidal creeks. Working with the same photo series south and west of Turkey Point, Egler (1952) described a zone (Belt IV) appearing as a distinct white band immediately interior to the mangrove belt (Belts V-VII). Egler's sample plots of 1946 indicated that the vegetation of Belt IV was a sparse, relatively even mixture of sawgrass (*Cladium jamaicense*), spikerush (*Eleocharis cellulosa*), and red mangrove (*Rhizophora mangle).* In this context, the white appearance of Egler's Belt IV is probably indicative of reflectance from the white marl substrate, or from a continuous periphyton mat able to form in the wet, open conditions of this graminoid-dominated ecosystem. We suggest that prior to construction of the L-31E levee and canal, a similar **Mixed Graminoid with Red Mangrove** assemblage was also present immediately landward of the mangrove forest zones between Turkey Point and Black Point. However, because of the narrowness of the mangrove belt in this section, the graminoid assemblage may have included a stronger representation of species more typical of supratidal wetlands, e.g., *Distichlis spicata, Juncus roemerianus,* and *Spartina spartinae,*  than that described by Egler*.* The relative abundance of these three coastal species in comparison to *C. jamaicense* and *E. cellulosa,* which are found in both fresh and brackish marshes, is unknown. *D. spicata* and *J. romoerianus* are currently very minor components in the scrub mangrove zone east of L-31E (*D. spicata,* Blocks 1 and 5; *J. romoerianus*, Block 5 in **Figure C-1-2**).

In much of the coastal zone between Convoy and Fender Points, the 1940 aerial photo indicates a band of large-crowned, open-spaced trees paralleling the shoreline at about 0.5 miles distance, i.e., at about the current position of the L-31E Canal and immediately to its west. During our field surveys of several portions of this band, we found many spreading buttowoods (*Conocarpus erecta)* – both alive and dead – whose size suggest that they were well-established by 1940. In South Florida, extensive **Buttonwood Woodlands** occur over a wide range of salinities, from near seawater strength along the coast to essentially zero in interior sloughs and depressions. Understories in such woodlands vary accordingly, from (A) red mangroves, salt-tolerant grasses, and/or succulent herbs, to (B) sawgrass and other species usually associated with fresh water conditions. At this distance from shore, we consider Alternative B, a sawgrass-dominated understory, to be the more likely scenario.

By 1940, a system of east-west canals had already been established in the study area, directly impacting all portions of the coastal vegetation complex through drainage and diversion of flow from natural tidal creeks. Areas interiorward from the zone of **Buttonwood Woodlands** had been further modified by drainage (a dense system of relatively deep mosquito ditches oriented north-and-south, connecting the larger canals), as well as clearing and tillage for agriculture. These lands fall into two generally recognizable classes: **Drained Fresh Water Marsh**, and **Agricultural Lands.** The latter category may be further divided into **actively farmed** fields, and fields apparently **reverting** to a wild state at the time of the photo. To the best of our knowledge, agriculture in the area was predominantly truck crops, e.g., potatoes, tomatoes, etc. Based on the 1940 photo, the coastward limit of intensive agriculture in the study area was approximately 500 meters west of the current L-31E canal.

**Current vegetation.** The current vegetation mosaic in the L-31E study area (**Figure C-1-2**) is considerably changed from the landscape present in 1940. Within this landscape, intertidal mangrove communities still occupy the coastal positions, but have increased in extent. The narrow fringe of **Fringe Mangrove Forest** (8-20+ meters high at full development) has widened to a band of 400 meters or more in places, especially in the northern end of the study area. Overall, red mangrove (*Rhizophora mangle)* is the dominant species, though extensive areas of white mangrove (*Laguncularia racemosa)* occur, and large black mangroves (*Avicennia germinans)* are scattered throughout. Of course, this community is currently in an early stage of recovery from Hurricane Andrew. Because of the severity of hurricane damage in this zone, recovery has been primarily via recruitment of new seedlings, which in places already form barely penetrable thickets 3-8 meters in height. Immediately west of the **Fringe Mangrove Forests** lies a dense medium stature (2-6 meters in height) forest (**Transitional Mangrove Forest**). In general, white mangroves dominate this forest's canopy. Red and black mangroves along with buttonwood are typically less abundant components of the forest canopy, and there is little or no herbaceous understory. It is not yet clear to us whether this forest represents an intermediate stage in the long-term development of more open tall mangrove forest. Hurricane impacts in this community were much less than in the taller coastal forests, and resprouting of broken stems has played a more important role in forest recovery. Although the species composition of this assemblage suggests an intertidal position, a wide band of compositionally and structurally typical **Transitional Mangrove Forest** occurs north of Military Canal and west of the L-31E Canal, outside the influence of daily tides. Finally, **Dwarf Mangrove Forest**, a structural variant of the modern intertidal landscape that was not identified on the earlier photo, has become well-established throughout the area previously occupied by **Mixed Graminoid Marsh with Red Mangrove**. **Dwarf Mangrove Forest** currently occupies the shallow basins immediately east of the L-31E levee. The dwarf canopy (0.5-2 meters height) is virtually pure red mangrove. White and black mangrove are scattered emergents along the periphery of these basinal communities and in small islands of larger trees which pepper the area, but in the center of the basins they occur primarily as seedlings in subordinate positions amongst the prop roots of the larger red mangroves. Occasional *D. spicata* and *J. roemerianus* clumps are apparently rare relicts of the historical saltmarsh. A photograph from 1965, immediately prior to levee construction but well after drainage of the area, suggests that the beginnings of the transition from open marsh to mangrove scrub predate the L-31E itself, though the levee undoubtedly hastened the process by intercepting freshwater sheetflow entirely.

In direct contrast to the situation described above, the L-31E canal and levee has served as intended to intercept saltwater that had historically reached lands to the west during storms and other high tide events. On this basis, one would predict an increase in the relative abundance of plant species typical of fresh water swamps since 1966. In fact, the prominence of sawgrass or cattails in most of the plant communities west of the L-31E levee (i.e., **Sawgrass marsh, Cattail marsh, Mixed Broadleaf swamp,** and **Austrailian Pine swamp)** suggests the fresh water nature of these ecosystems. In the last-mentioned community, tall stands of sawgrass occur beneath an open canopy of *Casuarina spp.,* occasional buttonwood stems, and little else. These communities are largely confined to unplowed lands previously occupied by **Buttonwood Woodland**. **Mixed Broadleaf swamp** is also a relatively open forest with sawgrass in mixture with buttonwood, wax myrtle, and the mangroves, especially *L. racemosa*. Open **Sawgrass** and **Cattail** (*Typha spp.)* **Marsh** are relatively restricted in area; drainage and the invasion of exotic trees have both contributed to the apparent increase in the overall coverage of woody vegetation. **Brazilian pepper**  *(Schinus terebinthifolius)* **forests** are monocultures that occupy abandoned agricultural lands in the western portions of the study area. Despite the preponderance of these three invasive exotics west of the L-31E, their absence in undisturbed mangrove forests east of the levee is significant. However, **Disturbed lands** throughout the area, especially the levees to the omnipresent mosquito ditches, are almost without exception exotic-dominated. Exotic removal that does not return the land to its original contour and hydrologic regime will ultimately be a fruitless exercise.

#### **C-2.** *Plant community responses to natural disturbance*.

The mangrove forests of the L-31E study area are currently recovering from at least four recent natural disturbances. Though no corner of the area escaped all four events, the impacts of individual disturbances on vegetation structure were distributed very unevenly. The most dramatic effects, of course, were associated with Hurricane Andrew (August 1992), but as the discussion that follows will show, damage from this Category 5 storm was centered on the tall forests nearest the coast. Conversely, the effects of cold temperature events in January of 1996, 2001, and 2003 were restricted to the low dwarf forests of the interior basins. A thorough reading of the historical record indicates that South Florida mangrove ecosystems rarely recover fully from one disturbance before the next one arrives (e.g., Neumann *et al.*, 1981; Olmsted *et al.*, 1993), so that the occurrence of three significant events in a single decade ought not be considered exceptional. The information we gathered about the disturbances at the L-31E study area is valuable in the general insights it provides regarding the influence of site productivity on mangrove community response to disturbance. More importantly for our current purposes, a proper appreciation of these impacts is critical in accurately evaluating the effects of our hydrologic treatment. The hurricane occurred prior to the initiation of the project, and its effects were distributed approximately equally in Control and Treatment Fringe forests. The freezes occurred one, five, and eight years after initial plot establishment, and their effects were most significant in the Control Dwarf sub-block.

#### **i.** *Hurricane Andrew.*

As it moved west from the Atlantic Ocean onto the South Florida mainland in the early morning hours of August 24, 1992, Hurricane Andrew was an extremely compact, fast-moving storm whose center passed a few miles north of the study area. The Category 5 storm produced sustained winds estimated at ca 155 mph (Powell and Houston 1996), but precipitation was generally  $\leq 3$ ". Damage caused by storm surge was restricted to local portions of the coast. Ten months later, beginning in June 1993, we established two East-West transects, extending from the L-31E levee to Biscayne Bay in Blocks 2 and 4, and distributed sampling stations at 20-meter intervals along them. A distance-based point-centered-quarter (PCQ) method was employed to describe the structure and composition of the forest (Cottam and Curtis 1956). In four quadrants at each station, we located the closest living stem of *R. mangle, L. racemosa, A. germinans,* and *Conocarpus erectus* in three size classes – Category I, < 60 cm height; Category II, 60 - 250 cm height; and Category III,  $>$  250 cm height – as well as the nearest hurricane-killed stem  $>$  5 cm DBH, to a maximum distance of 5 meters. For live stems, we recorded the height, DBH (or basal diameter), crown diameter, and distance from the plot center. For hurricane-killed trees, we recorded the distance from tree base to plot center, DBH, and an estimated pre-hurricane height based on the length of the uprooted or broken stem. The survey of live stems was repeated at the same locations in portions of the Fringe forest in February 1996, and along the entire length of the two transects in January-February 2002. PCQ data were summarized as follows: for each point, we calculated the density of each species in each size class. If a species/size class was not present within five meters of the point in any of the four quadrants, we assigned it a density of 0. If it was present in 1-3 quadrants, we assigned it a distance of 10 meters in the quadrants in which it was absent. We also calculated point estimates of crown area (CA) and basal area (BA; Category III stems only) by multiplying the density estimate for each category by the average CA and BA for sampled stems. Similarly, we estimated the diameter distribution of Category III stems from the proportions of sampled stems, using ≥ 2.5 cm diameter classes. PCQ data were generally evaluated by zone across both transects. Twenty-six points were sampled in the **Dwarf Mangrove Forest** zone, which we defined as that portion of the transect whose current canopy height was < 2.5 meters. 17 points were sampled in the **Transitional Mangrove Forest** (< 6 meters tall), and 25 in the taller **Fringe Mangrove Forest**. Data from the permanent census plots in Block 4 (**Section C-3**) were additional sources of information used to analyze forest development following Hurricane Andrew.

Estimates of maximum canopy height prior to the hurricane and one, four, and ten years afterward are presented for both levee-to-bay transects in **Figure C-2-1**. In 1992, vegetation zonation in Block 2 consisted of a relatively broad (360 meters) Dwarf Forest, a narrow (60 meters) Transitional Forest, and a Fringe Forest zone about 200 meters in width and ranging up to 19 meters in height. Hurricane Andrew removed the upper forest canopy between meter 440 and the coast, but direct effects on the low forests of the interior were not observed. By 2002, the Fringe Forest in Block 2 had recovered to about half its pre-hurricane stature, while tree heights in the Transition and outermost portions of the Dwarf Forest were slightly greater than before the storm. In Block 4, where the height gradient was more gradual and structural zonation less well-defined prior to the hurricane, temporal patterns were

much the same as in Block 2. Within about 300 meters of the coast, a clear pattern of hurricane destruction and gradual recovery is evident, but direct storm effects are not readily discernible further inland, where local variations in canopy development appear to be unrelated to the hurricane.

The PCQ surveys provide further detail regarding spatial patterns in stand development during the decade following Hurricane Andrew. Changes in the Dwarf, Transitional, and Fringe mangrove forest zones are described separately below.

**Dwarf Forest**. Observations of direct hurricane effects in the Dwarf Forest one week after the storm revealed very minor structural damage. Wrack deposits were locally significant, but mortality and even defoliation were minimal, probably because the low  $(1 \text{ m})$  tree canopy that prevailed in most of the zone was submerged during the period of highest winds. **Figure C-2-2** illustrates changes in dwarf mangrove forest structure over the next decade in the extensive portion of Block 2 that was not impacted by the freeze events of 1996 or 2001 (see *Freeze*, below). In general, canopy development was significant in this community over the period, but change in species composition was relatively minor. In 1993, *R. mangle* was the overwhelming dominant in a dwarf "forest" in which more than 80% of the ca  $5x10^5$  stems/ha were less than 60 cm in height. Over the next ten years, the density and crown cover of both *R. mangle* and *L. racemosa* in size class I decreased. However, the reduction in small stems was balanced by an increase in the abundance of both species in size class II, which represented the upper canopy of the Dwarf Forest. On an absolute basis, ingrowth to Category II was greatest in *R. mangle*, leaving the species even more dominant than it had been at the beginning of the period. The status of *A. germinans*, a minor understory component absent from upper layers of the forest in 1993, was constant through 2002. Given the minimal direct impacts of Hurricane Andrew in this zone, the structural changes in the Dwarf Forest during the study interval may represent recovery from previous disturbance events, or may be a response to more general long-term changes in the condition of coastal wetlands in the area.

**Transitional Forest**. Structural and compositional changes in the Transitional Forest are summarized in **Figures C-2-3** and **C-2-4**. Estimates of tree species density, basal area, and diameter distribution in 1992 were calculated from independent samples of live and dead trees in both blocks in 1993. The Transitional Forest experienced extensive defoliation and canopy damage during Hurricane Andrew, but tree mortality rates calculated on a density or basal area basis were less than 20% (**Figure C-2-4**). The lower strata of this forest were *Rhizophora*dominated throughout the study period, with *L. racemosa* and *A. germinans* important understory associates. However, only the last of these three species increased in abundance after the hurricane (**Figure C-2-3**). In direct contrast to the lower canopy strata, the Transitional Forest tree stratum was largely composed of *L. racemosa* in 1992. In terms of basal area, *L. racemosa* remained the most abundant tree species through 2002, primarily because its population included a scattered cohort of relatively large, multi-trunked individuals (DBH classes 5-10 and 10- 15cm in **Figure C-2-4**). Many of these trees were damaged during the hurricane, but resprouted aggressively to occupy broad portions of the forest canopy. At the same time, a strong wave of ingrowth and/or recruitment into the tree stratum by *R. mangle, A. germinans*, and *C. erecta* – the latter not encountered in 1993 – caused the Transitional Forest to be a denser and more diverse community in 2002 than it was a decade earlier (**Figures C-2-3** and **C-2-4**).

**Fringe Forest.** The high winds associated with the hurricane's leading edge broke, uprooted, and brought the tall trees of the Fringe Forest crashing down into towering piles oriented toward the SSE. The response of the mangrove community to this disorganizing event are illustrated in **Figures C-2-4** through **C-2-5**, which are based on the 17 points sampled in 1993, 1996, and 2002. Prior to the hurricane, the forest canopy comprised about  $4 \times 10^3$ stems/ha  $> 2.5$  m in height, with a basal area of nearly 30 m<sup>2</sup>/ha (**Figure C-2-4**). On a density basis, *R. mangle* was the most abundant tree, but *L. racemosa* was by far the leading species in terms of basal area. *A. germinans* was also occasionally present in the canopy. Seedling densities were very low (**Figure C-2-5**), as they so often are in mature, undisturbed mangrove forests (Janzen 1985). When the passage of Hurricane Andrew resulted in tree mortality of nearly 95%, the site was left virtually barren of vegetation, and the forest floor entirely exposed. Periodic observations indicated that, except in isolated microsites along some drainages, this open condition prevailed for the next two years. As time went on, seedling recruitment became more widespread. By the time of the 1996 survey a healthy crop of *L. racemosa* and *R. mangle* seedlings had become established, and a discontinuous tree canopy was in place. As canopy development continued over the next few years, however, seedling populations (especially *L. racemosa*) declined precipitously (**Figure C-2-5**). By 2002, the Fringe Forest had reached its pre-hurricane basal area, distributed among a dense population of small stems (**Figure C-2-4)**. Stand composition was not substantially

different than in 1992: *R. mangle* was the most numerous species, but *L. racemosa* maintained the highest basal area (**Figure C-2-5**).

# **ii.** *Freeze.*

During the frigid (by South Florida standards!) night of January 9, 1996, temperatures of 30°F were recorded within the study area (Oberbauer unpublished data), causing locally severe impacts in the mangrove community. On January 5, 2001, a milder cold front (minimum temperature 37.4°F at Homestead Air Reserve Base, ~2 miles west of the study area) elicited similar ecological consequences. A third freeze occurred in Jan 2003. However, because this freeze occurred during the preparation of this document and months after the field portion of the L-31E Pilot Project research had been concluded, its effects are not described here. We used three sampling procedures to evaluate the immediate effects of the 1996 and 2001 freeze events and their aftermath:

- 1. 3-4 weeks after the events, we documented direct impacts via observations of leaf damage along three transects in the Control Block. The transects were approximately 60 meters apart, extending east from the L-31E levee to a point beyond which no further freeze damage was observed. At 10-meter intervals along each transect, we estimated the proportion of browned/fallen v. green leaves within 20-cm height strata from the bottom to the top of the plant canopy. Estimation of damage was facilitated by viewing each canopy stratum against the background of a rectangular ( $20 \times 30$  cm) white board, held at  $\sim 50$  cm distance from the eyes of the observer. A damage profile was created for each point by averaging separate observations facing north and south in each height stratum.
- 2. We examined variability among species at 100 points distributed among five areas of extensive freeze damage between the Mowry and Military Canals. We established sampling stations at 10-meter intervals along N-S-oriented transects, and located the nearest live or freeze-killed *R. mangle, L. racemosa*, and *A. germinans* stem taller than 80 cm, to a maximum distance of 5 meters. We then recorded the total prefreeze height and the height of the highest surviving leaf on each sample tree. The survey was conducted between February 15 and March 15, 1996, 1-2 months after the 1996 freeze. Species effects on mortality across all sample points were tested using a G-test of independence outlined in Sokal and Rohlf (1997), followed by unplanned comparisons among individual species. We used one-way ANOVA to test for among-species differences in the damage sustained by surviving individuals. The index of damage was percent height loss, with an arcsine transformation applied to normalize the data. To ensure independence between the mortality and damage analyses, the latter was restricted to the subset of 16 points in which the sampled individual of all three species survived the freeze.
- 3. Census Plots CDI and CDE, established in 1995 in the Control Block (see **Section C-3**), were impacted by the 1996 and 2001 freezes, while a third Control plot (CDW) was outside the damage zones of both freezes. Annual monitoring of mortality, seedling recruitment, and growth over the period 1995-2002 therefore provided a detailed comparison of community dynamics in adjacent impacted and unimpacted areas.

**Damage – spatial variation and species responses.** Damage patterns in the Control Dwarf sub-block after the 1996 freeze (**Figure C-2-6A**) were reflective of patterns observed in several other mangrove basins situated immediately west of the Fringe forest. Freeze damage was not observed east of the point where forest canopies began to exceed two meters in height. Within the damage zone, impacts usually decreased downward from the top of the plant canopy, with the level beneath which leaf damage was minimal varying from about 20 cm to more than 1 meter above the soil surface. Overall, damage was most severe where average canopy height was 1-2 meters, i.e., along the sides of the dwarf mangrove basin. In the center of the basin, where initial canopy height was lowest, damage was nil or restricted to crowns emerging above the general canopy level of *ca* 80 cm. This pattern could be extended to the study area as a whole; in general, the largest basins sustained the least freeze damage.

The spatial distribution of leaf damage in the CD sub-block following the January 2001 cold temperature event (**Figure C-2-6B**) resembled the 1996 pattern, in that freeze damage was once again most severe in the upper portions of the canopy. However, damage was spatially more uniform within the basin in 2001, and – despite the likelihood that temperatures were slightly higher – generally penetrated further into the canopy than following the earlier freeze. This result suggests the importance of canopy vegetation in buffering the understory from

temperature extremes. In this instance, the pre-1996 coverage and stature of the Dwarf forest canopy had not completely recovered during the five years between events (note the lower maximum heights in **Figure C-2-6B**), allowing the cold air impacts to reach nearly to the ground surface throughout most of the basin.

Survival from the 1996 freeze varied among sites and among the three mangrove species **(Table C-2-1)**. Local variation in freeze damage was considerable, even among areas that were visibly affected. For instance, all stems > 80 cm were killed in the surveyed portion of Block 3, while minimal damage was observed in the extensive basin south of it (Block 2). Mortality percentages varied significantly among species (G= 39.09,  $X^2_{\text{crit.001}[2]}$ =13.82), with *L. racemosa* experiencing 76% mortality across the five impacted sites, and *R. mangle* and *A. germinans* experiencing 46% and 30%, respectively. Individual unplanned comparisons indicated that mortality in *L. racemosa* was significantly higher than in either *R. mangle* or *A. germinans* ( $p$ <0.001), but the latter species did not differ ( $p$ >.05). Similarly, the extent of crown dieback in surviving individuals also varied among species ( $F<sub>2.45</sub>=5.37$ , p=.008). In plots in which all three species survived, dieback was 18% in *L. racemosa*, but only 7% in both *A. germinans* and *R. mangle.*

	<b>SPECIES</b>					
	<b>Transect</b>	A. germinans	R. mangle	L. racemosa		
	l-A	86	95	4.		
Percent survival	1-B	30	45			
		100	100	70		
			$\theta$			
	$\overline{4}$	100	30			

**Table C-2-1:** Mortality of three mangrove species following the freeze of January 1996. Transect numbers correspond to basins illustrated in **Figure A-1-1**.

The growth responses of *R. mangle* and *L. racemosa* may be assessed from trends in the mean annual height of individuals that were tagged in 1995 and survived both 1996 and 2001 freeze events. Three size classes of survivors are distinguished, and populations within and outside the damage zone in Block 4 are plotted separately in **Figures C-2-7A** & **B**, respectively. Outside the freeze boundaries, in Plot CDW, growth of Category 1 (< 40 cm initial height) individuals of both species was minimal (**Figure C-2-7B**). In the same plot, *R. mangle* stems in both Category 2 (40- 80 cm) and Category 3 (> 80 cm) grew slowly (*ca* 2 cm per year), while Category 2 *L. racemosa* grew at a rate of almost 5 cm per year. Inside the damaged area, Category 1 stems of both species grew very rapidly (7-10 cm per year) in the first two years after the 1996 freeze (**Figure C-2-7A**). Subsequently, height growth of small *L. racemosa* stems virtually stopped, but *R. mangle* in this size class continued to grow rapidly throughout the monitoring period, nearly reaching the Dwarf forest canopy by 2001. The rapid growth of seedlings in Plot CDI was clearly a response to mortality and damage among large individuals in this plot. Mortality of large *R. mangle* stems in this plot was 100%, and surviving Category 2 and Category 3 *L. racemosa* individuals suffered substantial dieback during the 1996 freeze. However, these damaged individuals recovered to equal or exceed their pre-freeze height by 1998 (**Figure C-2-7A**), only to die back again following the 2001 freeze. This pattern leads us to suspect that many of the *L. racemosa* individuals that appeared dead in our transect surveys 1-2 months after the 1996 freeze (i.e., **Table C-2-1, Transect 4**) may have subsequently resprouted by the next census, about 10 months later; in turn, a number of *R. mangle* stems may have died. Clearly, the direct effects of a freeze may not become apparent for months or years thereafter, and unraveling species or community response patterns sometimes requires a combination of long term monitoring and opportunistic surveys.

The establishment and subsequent survival of *R. mangle* and *L. racemosa* seedlings in the Control Dwarf subblock between 1995 and 2001 are presented in **Figure C-2-8A-D)**. The densities of "seedlings" established in 1995 are probably somewhat inflated, since these were mixed-age cohorts < 30 cm tall when tagged during the initial census. In the freeze-affected plots, *L. racemosa* seedling establishment exceeded that of *R. mangle* in every year (**Figure C-2-8A** & **B**). In this zone, establishment of both species was relatively high in 1995 and 1996, the year after the freeze, but declined nearly to zero in 1997. *L. racemosa* establishment recovered in subsequent years, but

recruitment of *R. mangle* remained low through the end of the study period. As in the plots impacted by freeze, establishment of *L. racemosa* seedlings in 1995 and 1996 in the plot not affected by the freeze was very high, far exceeding that of *R. mangle* (**Figure C-2-8C** & **D**). In 1997 there was no recruitment of either species, and in subsequent years establishment continued to be slow, i.e., recovery comparable to that observed for *L. racemosa* in the freeze-affected plots was not observed. Thus, neither the peak in establishment in Year 1 following the 1996 freeze nor the Year 2 recruitment failure can be attributed to site-specific conditions inside the freeze zone, since the same pattern was observed outside its boundaries. However, the recruitment of white mangroves in the freezeaffected areas after Year 2 may be construed as a positive response to the relatively open canopy conditions that prevailed in that zone.

For both species, mortality among seedlings of the 1995 mixed-age cohort was clearly elevated in 1996 as a result of the freeze, although cumulative survival through 2001 was not substantially affected (compare **Figures C-2-8A** & **C** with **Figures C-2-8B** & **D**). In contrast, mortality rates within the 1996 *L. racemosa* and *R. mangle* seedling cohorts were lower in the freeze-impacted area than outside, both after one year and through the remainder of the study. Mortality of subsequent *L. racemosa* cohorts was uniformly low within the freeze boundaries; with no evidence of elevated seedling mortality following the 2001 freeze. However, inter-site comparisons cannot be made with confidence because of small cohort sizes in the unaffected zone. *R. mangle* seedling cohorts in 1997-2000 were too small to supply meaningful estimates of mortality in either impact zone.

**Table C-2-2** summarizes the dynamics of individuals that entered the seedling pool in the Control Dwarf subblock during the post-freeze period. Total contribution of 1996-2001 seedlings to the current *L. racemosa* population was more than three times higher in the freeze-affected area than outside of it. For *R. mangle*, seedling contribution to the current population was 50% higher inside the boundary of the freeze. Moreover, in the area impacted by the freeze, a much higher percentage of recently established individuals of both species grew beyond the seedling size class prior to the end of the study.



**Table C-2-2**: Fate of *L. racemosa* and *R. mangle* seedlings established after the 1996 freeze event (i.e., during 1996-2001) in impacted and unimpacted portions of the Control Dwarf sub-block. Data are total densities  $\cdot$   $\cdot$   $\cdot$   $\cdot$   $\cdot$   $\cdot$   $\cdot$ sample areas in each zone. "Graduated" seedlings grew beyond 30 cm height.

# **Conclusions – disturbance and mangrove community development**

Our observations compare and contrast the responses of the Fringe forest to Hurricane Andrew and the Dwarf forest to the 1996 freeze event. The direct effects of the two disturbances were similar in being concentrated on the upper canopy strata of the impacted forests. In both disturbances, the concentration of mortality among dominant individuals (1) released previously suppressed "advance regeneration", and (2) stimulated the establishment and development of new stems of seedling origin. Recovery from the two disturbances differed in the relative importance of Responses (1) and (2) above. New seedling regeneration was clearly the primary source of stems for the developing Fringe forest canopy following the hurricane, because advance regeneration was nearly absent in the pre-hurricane forest. In turn, the rapidly developing Fringe forest canopy effectively inhibited further seedling regeneration within a few years. In the pre-freeze Dwarf forest, a dense, mixed-species cohort of advance regeneration was the first to take advantage of the resources made available when most stems in the canopy were freeze-killed. In part because of a subsequent freeze event in 2001, recovery of the low Dwarf forest canopy was relatively slow. Consequently, recruitment and growth of mangrove seedlings on this site were not noticeably inhibited throughout the 5+ years that our study continued, and some of these new recruits are likely to find a place in the Dwarf mangrove canopy by the time crown closure is achieved.

The species dynamics of mangrove forests may be affected by hurricanes and freezes as markedly as the structural attributes discussed above. As above, species responses comprise both resistance to the immediate disturbance and responsiveness during the subsequent stages of recovery. Our studies did not address the relative sensitivity of individuals of the three major mangrove species to wind damage, but did shed considerable light on the capacity of *R. mangle, L. racemosa,* and *A. germinans* to tolerate freezing temperatures. *L. racemosa* appeared to sustain the most immediate damage, but exhibited the greatest capacity to resprout from the stem base. *R. mangle* was initially less freeze-sensitive than *L. racemosa*. However, because its dormant buds do not retain viability for more than a year or so (Tomlinson 1986), the species has very limited sprouting ability. *A. germinans* is the most frost-hardy of the three species, and is a dependable sprouter. Seedling recruitment and performance after both disturbance types also appeared to differ among species. *A. germinans* seedlings were never abundant in any of our plots, though they were persistent once established. *L. racemosa* seedling recruitment was generally high in the first few years after disturbance, but establishment declined rapidly after crown closure. In comparison, *R. mangle* was less prolific, but possibly more tolerant of shading. An important element not addressed directly in this study was the proximity and size of potential seed sources, which are affected by the structure of the pre-disturbance community and the direct impacts of the disturbance on it. Temporal changes in species composition in the mangrove forest are explored further in **Section C-3**.

The uneven distribution of hurricane and freeze impacts in the landscape is perhaps as significant ecologically as the finer-scale effects described above. Hurricane Andrew toppled large trees near the coast, while passing over the gnarled Dwarf forest stems without visible effect (possibly because they were covered by water during the period of highest winds). Conversely, the two freeze events weighed heavily on the Dwarf forest, but did not penetrate the tall mangroves. These sorts of interactions are somewhat predictable, are created by a combination of natural processes and human alterations to the landscape, and should be factored into our considerations of the role of disturbance in mangrove ecosystems. They also represent an unavoidable complication in interpreting vegetation responses to the L-31E rediversion experiment.

#### **C-3.** *Population dynamics of mangrove individuals.*

In this section we first describe broad vegetation changes that took place in the study area over the period 1995-2001, then consider several population processes in more detail. Changes in overall stand structure and composition within Dwarf and Fringe forests are described in **Section C-3-1** & **Appendix A**. Subsequent analyses reduce community dynamics to three components: (a) establishment of seedlings, (b) growth of established individuals, and (c) mortality of seedlings and older age classes. Variation in these processes ought to reflect responses to the biotic and abiotic conditions experienced in different portions of the study area over the past six years. We explored several sources of variation. One source was the disturbance impacts already described in **Section C-2**. Another likely source of variation, of course, was the *raison d'etre* for the project, i.e., the delivery of fresh water into the Treatment Block. Because diverted waters were delivered directly into and retained longest in the basins of the Dwarf Forest, we assess the population consequences of the hydrologic treatment in **Section C-3-2** by comparing establishment, growth, and mortality in Treatment plots TDWW and TDW with Control plot CDW. Finally, in the Fringe Forest, where the hydrologic treatment was unlikely to have had much effect, two factors that may have influenced development during the early stages of post-hurricane recovery were: (1) the initial rate of colonization, and (2) flooding regime. With these variables in mind, we compare establishment, growth, and mortality in census plots of the Treatment Fringe and Control Fringe sub-blocks in **Section C-3-3**.

**Sampling methods.** During April-July 1995, a total of 15 rectangular plots were set up and censused in the Treatment and Control blocks. Four plots were established in the Treatment Fringe, Control Fringe and Treatment Dwarf forests, and three were established in the Control Dwarf forest. The plots were rectangular in shape, with widths of 0.5 meters and lengths varying from 3 to 10 meters (in order to establish an initial monitoring population of at least 100 individuals, if possible). Over the course of the study, the number of individuals per plot varied from as few as 35 stems to nearly 200. During the initial census and subsequent surveys, each newly encountered, lignified individual that had produced a minimum of two sets of leaves was labeled with an aluminum tag and added to the database.

After establishment, the plots were resampled during November/December of each successive year through 2001. The following information was recorded annually for each tagged individual: viability (live/dead), crown

center and stem base coordinates within plot  $(\pm 5 \text{ cm})$ , height at crown base, total height, crown length and width, basal diameter, diameter at breast height (DBH: stems >200 cm), and reproductive output (numbers of fruits or flowers). Also, the seasonality of seed germination was examined via winter and summer germinant counts in 1996 and 1997. Winter germinant counts within the plots were continued annually through 2001.

#### **C-3-1.** *Community structure and composition***.**

**Dwarf Forest**. Initial stem densities in the Dwarf forest were roughly  $5x10<sup>5</sup>$  stems per hectare in both the Control and Treatment sub-blocks (**Figure C-3-1A**). However, structure and species composition differed between sub-blocks. The Treatment Dwarf canopy had a lower maximum height than the Control, but most Control Dwarf individuals were within the 1-60 centimeter height range, whereas most Treatment Dwarf stems were 40-79 centimeters in height. *L. racemosa* abundance in the upper height strata was greatest in the Control Dwarf forest, but *R. mangle* was the dominant species in the upper canopy of both blocks. *L. racemosa* exhibited the highest understory densities, and *A. germinans* was restricted to the lower height classes.

By 2001, the Dwarf mangrove forests had changed in both Control and Treatment blocks. *Conocarpus erecta*, a species undetected in the initial census, was observed in both blocks during the 2001 census (**Figures C-3-1A & B**). Other changes were block-specific. Total stem density increased in the Control Dwarf plots over the 6-year period, with increases in *L. racemosa* stems more than compensating for decreases in *R. mangle* (**Figures C-3-1A & B**). There was also a reduction in upper canopy height in the Control Dwarf plots, exemplified by a marked decrease in the number of individuals exceeding 80 centimeters in height. In the Treatment sub-plots, changes in size structure were more significant than any compositional changes (**Figures C-3-1A & B**). During this period, *R. mangle* appeared in the upper height classes, i.e., canopy heights in 2001 approached 200 centimeters in the eastern reaches of the sub-block. Total stem density increased since 1995, with *L. racemosa* becoming more abundant in the two smallest size classes.

**Fringe Forest**. The Fringe mangrove sites were much more open than the Dwarf sites in 1995, with a density of approximately  $1x10^5$  stems per hectare (**Figure C-3-2A**). All individuals except the largest stems in these forests had become established after the hurricane. The largest storm survivors were 3-4 meters tall in the Control Fringe forest, and slightly shorter in the Treatment Fringe forest. As in the Dwarf forest, *R. mangle* dominated the upper canopy levels, but *L. racemosa* and *A. germinans* co-dominated with *R. mangle* in the lower strata.

By 2001, both Fringe forests had increased greatly in stature, with heights approaching 10 meters in the Control plots (**Figure C-3-2B**). In both blocks, the upper canopy was comprised primarily of *R. mangle*, but also contained a small number of *L. racemosa* and *A. germinans* individuals. In the Control forest, the initially dense *L. racemosa* understory had given way to an lower stratum comprised mostly of *R. mangle* stems < 60 cm in height. Over the same period, density in the intermediate layers of the Control forest decreased markedly. At high densities, survivorship of smaller stems typically decreases in response to crowding caused by the rapid growth of dominant individuals. This self-thinning process contributes to an increase in the average size of individuals, and often results in predictable yields regardless of plant density (Kira *et al*., 1953).

# **C-3-2.** *Population responses to freshwater delivery in the Dwarf forest.*

The culverts through which fresh water passes from the L-31E Canal into the mangrove swamp were completed to begin the diversion treatment in late August 1997. After that time, releases of freshwater into the Treatment Block occurred when the Mowry Canal was at a high water level- primarily from May-October (see **Section B**). *R. mangle* is believed to be the most flood tolerant of the mangrove species present at the L-31E study site (Koch 1997). We predicted that, with the consequent increase in duration of flooding in the Dwarf mangrove basins, *R. mangle* would become more abundant and dominant. In the next few paragraphs we examine the effects of the addition of freshwater on establishment, growth, and mortality of *R. mangle* and *L. racemosa*. The abundance of *A. germinans* individuals was at all times too low to justify inclusion in these considerations.

**Seedling establishment and survival.** The establishment of mangrove seedlings involves (1) germination while on the tree (*R. mangle*) or upon release (*L. racemosa, A. germinans*), (2) rooting and emergence of the cotyledons and first leaves, and (3) survival through the first year or so on the forest floor. Our sampling design distinguished two stages within this process: the *germinant stage*, when seedlings were unlignified and/or had not yet produced at least two sets of true leaves, and the *seedling stage*, when the individual had passed through the germinant stage of development. In the Dwarf and Fringe Forest alike, we characterized spatial and temporal variation in establishment by calculating a cumulative establishment rate, i.e., the density of seedlings recruited into the population each year.

The cumulative annual establishment and subsequent survival of seedlings of *R. mangle* and *L. racemosa* in two Dwarf forest plots subject to freshwater diversion (TDW and TDWW) and a plot of similar structure and composition in the Control block (CDW) are outlined in **Figure C-3-3**. Patterns in the Control block have been discussed earlier (**Section C-2**); low establishment of *L. racemosa* in 1996-2000 may have been attributable to a decline in seed production following the 1996 freeze. In the Treatment block, establishment of both species was reasonably consistent throughout the study period, exhibiting substantial annual variation but providing no evidence of response to the enhanced wet season water levels that began in 1997. Survival curves were generally steeper (mortality was higher) for *L. racemosa* than *R. mangle*, but no temporal trend was evident for either species. Thus, neither seedling establishment nor survival of either species appeared to be influenced by the hydrologic treatment.

**Growth Rates.** As above, the effects of the hydrologic treatment on stem growth were examined by comparing both species in Treatment v. Control sub-blocks (plots TDWW/TDW v. CDW, respectively). To control for size-related growth differences, stems were divided into three height classes: < 40cm, 40-100cm, and > 100cm. Total height increase from 1995 to 2001 was the measure of growth. To avoid violating ANOVA assumptions, the data were square root transformed when distributions were non-normal. Since the individuals sampled in 1995 were from a natural population, densities of individuals from each species and size class were not always adequate for statistical comparisons. The range of the initial size and growth rate comparisons is therefore limited but still informative.

Height growth was very slow in portions of the Dwarf forest that were unaffected by the 1996 freeze, with annual means in the 1-2 cm/yr range for most categories (**Figure C-3-4**). The single exception was Height Class 2 *L. racemosa* individuals in the Control block, which grew at an average rate of nearly 5 cm/year. No indication of a hydrologic treatment effect was evident in inter-block comparisons within species:size categories (*L. racemosa*, Class 1: F1,26=0.005, p=0.942; *R. mangle*, Class 1: F1,34=2.861, p=0.100; *R. mangle*, Class 2: F1,162=0.0549, p=0.815).

Having found no effect of the freshwater delivery on growth rate, we evaluated the effect of size class within species. As suggested above, *L. racemosa* individuals in Height Class 2 in the Control Dwarf forest grew significantly faster than their Class 1 neighbors (F<sub>1,24</sub>=14.186, p=0.001) (**Figure C-3-4**). In contrast, height growth of *R. mangle* was unaffected by size (Control and Treatment data combined:  $F_{0.05,196}$ =6.010, p=0.091). These results indicate that *L. racemosa* growth is more sensitive to canopy position than *R. mangle*, and therefore support the view that the former is dependent on disturbance and gap formation, while the latter is better suited to sustain itself in the Dwarf Forest understory, where light is somewhat reduced.

**Mortality**. We evaluated the effect of freshwater delivery on this aspect of Dwarf mangrove population dynamics by visual examination of mortality curves of several categories of individuals tagged during the initial (1995) census. The following height classes were employed:  $\leq$  30 cm, 31-60 cm, and 61-100 cm. We were especially interested in changes that became evident in 1998 and beyond, because fresh water delivery began a few months prior to the 1997 census.

Cumulative annual survival patterns of *R. mangle* and *L. racemosa* in the Treatment and Control Dwarf subblocks are illustrated in **Figure C-3-5**. Where more than one size class was present, survival through 2001 was always highest among the largest stems. Survival among the smallest size class ranged from 20-65%, while survival of individuals > 30 cm in height was 80% or higher. Survival did not appear to differ between species or sites. Most pertinently, **Figure C-3-5** provides no evidence of treatment-related changes, i.e., inflections between the 1995-97 and 1998-2001 intervals of the delivery basin survival curves.

**Conclusion**. Judging from the absence of treatment-related effects on establishment, growth, or survival indicated above, one can only conclude that the delivery of fresh water into the Dwarf Mangrove forest treatment was either not sufficient or not properly timed to alter the competitive balance within the resident Dwarf mangrove community, at least in the short run. As described in **Section D**, the delivery treatment was concentrated in the wet season, when water levels are usually high and salinities low even in untreated basins. However, the absence of treatment effects on mangrove populations does not preclude effects on associated plant species. Temporal changes in the flora of the Dwarf Mangrove Forest are explored in **Section C-6**.

#### **Section C-3-3.** *Population processes in the Fringe Forest, 1995-2001.*

In this section, we describe the population demography of *R. mangle* and *L. racemosa* in four plots apiece in the Treatment and Control Fringe forests. Because the diversion of water from the L-31E canal was not enough to have substantially affected the Treatment Fringe plot, we interpret variation in population dynamics between the two forests as the result of differences in site history and intrinsic site characteristics. Mortality of canopy individuals during Hurricane Andrew in 1992 was almost 100% in both stands (see **Section C-2**), and our observations began in 1995, early in the development process following this disturbance. Nevertheless, even at this early stage the two areas differed clearly in site occupancy, with mean crown volumes of 21.7 and 9.3  $\text{m}^3/\text{m}^2$  ground surface in the Control and Treatment sites, respectively. The relatively rapid early development in the Control site may have resulted from chance factors or from historical contingency, e.g., the density of seedlings established before the hurricane and surviving it, or the survival of scattered seed-producing adult trees.

The Treatment and Control Fringe sites are distinct from one another in several respects, e.g., hydrology, soil characteristics, water quality, microclimate. From the point of view of plant populations, the most significant of these is probably the hydrologic regime of the two sites. Elevations of the census plots in the Fringe forest were surveyed using an automatic level during the summer of 1995, and a water level recorder has been maintained in the mouth of the tidal creek entering the Treatment Block since 1996. The average elevation in the four Treatment Fringe plots was 17.4 cm above sea level, while the Control Fringe plots averaged 41.6 cm above sea level. With an average difference in surface elevation of roughly 25 cm, the frequency of inundation and volume of tidal influx are significantly greater in the Treatment than the Control forest (see **Section D**). Thus, though both are classified within the Coastal Fringe forest type, the Treatment and Control stands described below represent poorly-drained and well-drained variants.

**Seedling establishment and survival.** Establishment of *L. racemosa* seedlings in Treatment and Control Fringe sub-blocks peaked in 1996 at  $\sim$ 7 and  $\sim$ 9 seedlings per m<sup>2</sup> per year, respectively (**Figure C-3-6**). Establishment of this species declined sharply in subsequent years to a rate of less than 1 seedling per  $m<sup>2</sup>$  per year in 2000. In contrast, *R. mangle* establishment remained relatively steady (Treatment Fringe) or increased (Control Fringe) over the period 1996-2000 (**Figure C-3-6**).

Despite the large crops of *L. racemosa* seedlings established during the early years of the study, few individuals survived through 2000 (**Figure C-3-6**). Many of the *L. racemosa* seedling cohorts experienced more than 50% mortality in the first year after establishment, with elevated mortality rates being most characteristic in the Control Fringe sub-block. Survival of *R. mangle* seedlings was much higher, such that the majority of seedlings produced during the course of the study were still alive in 2000.

The seedling establishment and survival patterns illustrated in **Figure C-3-6** probably reflect temporal variation in seed production and canopy development during the study period. Following Hurricane Andrew, large *L. racemosa* individuals that had been severely damaged by the storm soon resprouted and reassembled their crowns. These multi-trunked trees were copious seed producers, and the open conditions that still characterized the Fringe forest 4-5 years after the hurricane were conducive to seedling establishment. However, most of the seedlings became suppressed and died as the Fringe forest canopy closed in Years 5-9 (see **Section C-5**). Our own observations suggest that the mast year experienced by *L. racemosa* in 1996 has not been repeated, perhaps because of increasing crown competition. In contrast, *R. mangle* propagule production may have increased as small individuals released by Hurricane Andrew or established immediately thereafter grew to reproductive size. The mortality rates in **Figure C-3-6** suggest that *R. mangle* is somewhat more shade-tolerant than *L. racemosa*, and less sensitive to low light conditions.

**Growth Rates.** Annual height growth of individual stems over the six-year period following plot establishment was used as an indicator of stand development, and of the growth potential of sites, species, and size classes in the Fringe Forest. Mixed-aged *R. mangle* and *L. racemosa* "cohorts", which consisted of individuals
present inside the plots in 1995, are grouped into three initial height classes in **Figure C-3-7**: Class 1, < 40 cm; Class 2, 40-100 cm; and Class  $3, > 1$  meter tall. The graph provides visual evidence of the importance of initial size as a determinant of subsequent growth in the early stages of recovery following Hurricane Andrew. Statistical analyses bear out the message of **Figure C-3-7**. For instance, considering only the best-represented population, i.e., *R. mangle* in the Treatment Fringe forest, the effect of size class on annual growth was highly significant  $(F<sub>1,130</sub>=11.999, p<0.001)$ . In general, Class 2 and 3 stems of both species grew much more rapidly than Class 1 individuals when they co-occurred in the same stand, and Class 3 *R. mangle* individuals grew faster than conspecific Class 2 neighbors. The extent to which this size effect was due to suppression of smaller individuals by larger ones is unknown, but is probably considerable.

Our data also suggest that site productivity was higher in the Control Fringe than in the Treatment Fringe forest, based on the relative growth rates of the largest *R. mangle* individuals in **Figure C-3-7**. Extension growth averaged 62 cm/yr in the former and 29 cm/yr in the latter, and the difference between populations was highly significant ( $F_{1,114}$ =53.75, p<.001). The superior growth in the Control Fringe forest may have resulted from its better drainage conditions, alluded to above. Finally, mean height growth of the two mangrove species were similar when only the two smallest initial size classes were considered, but *R. mangle* growth was faster than that of white mangrove within the largest size class. We expect that such a comparison is specific to Fringe forest sites only, and would not hold for more interior sites where *L. racemosa* is more dominant in the forest canopy.

**Mortality**. Size-specific mortality curves for Fringe forest populations tagged in 1995 are presented in **Figure C-3-8**. With several minor exceptions, mortality of both species increased with decreasing initial size at both sites. The few exceptions (relatively low mortality of *R. mangle* in 30-60 cm size class in the Control Fringe forest, relatively high mortality of *L. racemosa* in 30-60 cm class in the Treatment Fringe forest) involved groups with low sample sizes. In the Treatment Fringe forest, cumulative (1995-2001) mortality of large individuals (i.e.,  $> 60$  cm initial height) of both species was < 10% over the six-year period. In the Control Fringe forest, mortality of initially large *L. racemosa* was likewise very low, but large *R. mangle* experienced relatively high mortality (62% for 1-2 m individuals,  $35\%$  for individuals  $> 2$  meters tall). We interpret the accelerated mortality in *R. mangle* as a reflection of interspecific competition among large stems struggling to form the future forest canopy. By this view, the Control Fringe forest reached the *competitive exclusion* stage of development (Oliver and Larson, 1990) more quickly than the less productive Treatment Fringe site.

## **Section C-4:** *Demography of R. mangle branch and leaf populations.*

One path to understanding woody plant populations is to employ a hierarchical approach that integrates the dynamics of individuals, branches, and leaves (White, 1979). In **Section C-3** we described the dynamics of Dwarf and Fringe forest populations of the major mangrove species, based on monitoring of individuals. From a management point of view, **Section C-3's** most important result was the insensitivity of mangrove populations to fresh water delivery, at least at the level of the individual plant. However, the dynamics of leaf and bud populations of individual trees might reflect a finer-scale response than do plant populations *per se* to changes in the external environment. For this reason, we incorporated into the general program of vegetation monitoring a study of the dynamics of leaves and meristems on selected *R. mangle* individuals. Red mangrove was chosen because it was an important component of the species assemblage in all portions of the study area. In this section, we explore whether *R. mangle*'s bud and leaf populations exhibited the same lack of response to the hydrologic treatment as we observed at the higher level of population organization.

**Section C-3** also illustrated the spatial and temporal variability in the effect of individual plant size on the growth and survivorship of mangrove individuals. Population processes were strongly size-related in the Fringe forest; large individuals exhibited fast growth and low mortality rates, and small individuals grew more slowly and died earlier. In the Dwarf forest, significant effects of size on growth and mortality were also observed, though trends were not as consistent across species and size classes. In both forests, the chance occurrence of disturbance (Hurricane Andrew in the case of the Fringe forest, a January 1996 freeze in the Dwarf mangrove community) released understory stems from the repressive effects of the canopy. In this section, we describe seasonal and among-site variation in the demography of branches and leaves of *R. mangle* individuals that were in a dominant or co-dominant canopy position at the beginning of the study. We also examine variation associated with branch age, which is often related to canopy position when the forest is developing rapidly. We expected that production and

mortality in bud and leaf populations would be very sensitive to site productivity, the stage of stand development following disturbance, and position within the crowns of individual trees.

**Sampling methods**. The study of branch and leaf demography was initiated in December 1995. In the Dwarf forest, leaf production and survival were monitored on all branches of sixteen dominant or co-dominant *R. mangle* individuals (two or three in each of the permanent plots). In the Fringe forest, the fate of leaf cohorts was tracked on five branches representing different strata within the canopy of eight large *R. mangle* stems (one tree per plot in both blocks). During the first survey, a loop of thin, colored wire was tied between the distal and second-to-distal leaf pair on all shoot tips, and all leaves including the distal ones were counted on each shoot. At subsequent surveys, conducted at approximately 4-month intervals, leaves of previously circumscribed cohorts were counted, and new leaves were demarcated as before. The position of insertion of each branch was measured at the initial survey, and its length monitored through all subsequent periods. New branches were incorporated in the sampling design as they formed. On Dwarf forest trees, the demography of leaves on all new branches was monitored. In the Fringe forest, where branch production was more prolific, one new branch per sampling period was randomly selected for monitoring. By counting and grouping all branches according to their period of initiation, it was possible to scale up observations from representative branches to the tree as a whole. Sampling continued through August 2000 in the Fringe Forest (14 surveys) and February 2002 in the Dwarf forest (18 surveys).

**The demography of branching**. In conjunction with extension growth, branching is the primary mechanism by which the crowns of trees and shrubs expand in space. The production of new *R. mangle* branch meristems and the mortality of existing ones in six sites – the east and west portions of Control and Treatment Dwarf sub-blocks, and the Fringe forest sites in each block – are summarized in **Figure C-4-1.** With the removal of two trees that died during the course of the study, the graphs illustrate mean meristem production and mortality rates experienced by 2- 5 individuals per site during each sampling period. The histograms from Fringe and Dwarf forest sites differ clearly. In the former, meristem turnover was rapid, and production exceeded mortality in most periods. Based on the trees we sampled, meristem number consequently increased in the Control and Treatment Fringe forest by 50 and 150%, respectively, between 1996 and 2000. Conversely, branch production in the Dwarf populations was highly irregular and branch mortality consistently low. As a result, some of these unproductive forests exhibited a small net loss of meristems, while others gained slightly. The most dynamic of the populations was in the Control Dwarf East. Monitoring of branches and leaves in these plots was not initiated until December 1996, about one year after a freeze event had eliminated the low forest canopy, leaving the site to be occupied by a mixed-age cohort of understory stems that survived the freeze (see **Section 2**). The small, nearly unbranched *R. mangle* survivors ramified rapidly over the next five years, only to undergo extensive (though incomplete) meristem mortality following a less severe freeze in January 2001. At the conclusion of observations, sample trees from this area averaged 5.8 meristems per individual, which was more than 50% higher than initial meristem density, but still much less than the 9-12 meristems per sample individual in other portions of the Dwarf forest.

Our analytical strategy was to test first for site differences, using repeated measures ANOVA, and then search for evidence of seasonality within relatively homogeneous site groupings. The results of the initial repeated measures analysis are summarized in **Table C-4-1**. Unit rates of meristem production and mortality were both significantly higher in the Fringe than the Dwarf forest; in these data, production also varied with Time, the withinsubject factor, and the interaction of Time and Site was statistically significant. Within the Dwarf Forest, there was no evidence of a treatment effect (TD-west v. CD-west comparison in **Table C-4-1**). However, because of the freeze event described earlier, production was higher in the eastern portion of the Control Dwarf forest than in the non-impacted western half. Finally, in the comparison of Control and Treatment Fringe trees, neither production nor mortality differed between sites. However, both Time and the Time-Site interaction had significant effects on the former variable, primarily due to enhanced production during the early stages of the sampling program, especially in the Treatment Fringe sub-block (**Figure C-4-2**).

				Between-Subjects		Within-Subjects				
				Effects				Effects		
									Time x Forest	
Production				Forest		Time		Interaction		
Site 1	Mean 1	Site 2	Mean 2	p-value	power	p-value	power	p-value	power	
TD	0.071	Both F	0.3841	0.001	0.973	0.001	0.959	0.002	0.952	
<b>CF</b>	0.3076	ТF	0.4606	0.338	0.143	< 0.001	0.998	0.014	0.881	
TD West	0.1531	CD West	0.1035	0.375	0.122	0.317	0.305	0.743	0.133	
CD West	0.2125	CD East	0.4159	0.028	0.757	0.118	0.524	0.694	0.226	
		Mortality								
TD	0.071	Both F	0.2604	0.003	0.909	0.173	0.533	0.41	0.352	
<b>CF</b>	0.3586	TF	0.1621	0.062	0.483	0.309	0.306	0.513	0.203	
<b>TD</b> West	0.0773	CD West	0.1306	0.391	0.123	0.189	0.659	0.581	0.403	
CD West	0.1014	CD East	0.3059	0.37	0.118	0.398	0.32	0.207	0.459	

**Table C-4-1**: Group means and analysis of variance for R. mangle meristem production and mortality (units: meristems/meristem/year).

Based on the between-site comparisons outlined above, we decided to test for seasonal effects on meristem production and mortality in one relatively homogeneous data set that included seven Fringe Forest trees and encompassed twelve sampling occasions between December 1996 and August 2000. Since each year of the monitoring program included a sequence of late wet season, dry season, and early wet season sampling periods, we analyzed the data as a randomized complete block design, with individual Trees as blocks, and Year and Season as fixed treatment effects. The ANOVA results are presented in **Table C-4-2.** Meristem production exhibited significant ( $p$ <0.05) annual variation. Seasonal variation in production was only significant at the more relaxed *p*<0.10 standard, at least in part because statistical power was low, but the Year x Season interaction was highly significant. As illustrated in **Figure C-4-2,** the interaction effect was due largely to a substantial depression in dry season branch production during the first two years of the monitoring program, followed by a weakening in seasonality during the last two years. Like production, meristem mortality varied with Year, but the effect of Season and the Year x Season interaction were non-significant **(Table C-4-2)**. Mortality of meristems was highest in Year 3 of the monitoring program.

			Within-Subjects Effects			
	Year		Season		Year x Season	
	p-value	power	p-value	power	p-value	power
Production	0.005	0.901	0.087	0.449	0.012	0.843
Mortality	0.016	0.416	0.611	0.097	0.249	0.298

**Table C-4-2**: Repeated measures analysis of variance of meristem production and mortality of seven Fringe forest trees.

The survival function of meristems with time is examined further by tracking the cumulative proportional survival of branch axes of 8 Fringe forest trees during the first 13 sampling periods after meristem initiation **(Figure C-4-3)**. Data through the first period are therefore based on mean survival from 13 branch cohorts, survival through the second period are composited from 12 branch cohorts, etc. Because of variation around the mean sampling interval of four months, the graphs in **Figure C-4-3** only approximate each tree's average meristem survival curve with time. In the Fringe Forest, the monitoring period (June 1996 through August 2000) comprised Years 5-8 after the near-total destruction of the forest canopy by Hurricane Andrew. Branch mortality in all eight trees was low during the first four periods (*ca* 16 months) after initiation. In most of these trees, mortality subsequently

accelerated for 4-6 periods (1-2 years) before leveling off. The steepening of the branch mortality function in Years 2 and 3 was more clearly expressed in the eastern (coastal) portion of the forest than in the west, and more distinct in the Control than the Treatment sub-block (**Figure C-4-3**). Thus, the portions of the Fringe forest where branch mortality was highest were those in which canopy closure was achieved most rapidly after the hurricane (**Section C-2**), and in which biomass increase was fastest throughout the recovery period (see **Section C-5**). Jones (1985) successfully demonstrated (in an experimental setting) the sensitivity of branch modules to competition from neighboring trees, as well as to higher branches on the same tree. Our data for *R. mangle* extend these observations by illustrating the effects that site productivity and disturbance history can have on branch population dynamics in a naturally developing mangrove forest, through their influence on the competitive environment around and within individual tree crowns.

**The demography of leaf populations**. In designing the L-31E monitoring network, we placed considerable emphasis on tracking the rate of production and senescence, i.e., the demography of leaves of *R. mangle*, the overwhelmingly dominant plant species in the pre-treatment mangrove swamp. It was our expectation that leaf populations would be sensitive to fundamental ecosystem change on an intermediate time scale: responses would not be as immediate as for physiological processes like gas exchange, nor would they lag as much as, for example, the relative cover of resident plant species. We reasoned that, even for the halophytic *R. mangle*, fresh water delivery might relieve plants of the physiological costs of maintaining osmotic balance in a saline environment, and mitigate nutrient stress by increasing the loading of phosphorus to their roots. The result might be an increase in leaf life spans and/or an increase in the production of new leaves. We also expected to see that these same patterns might emerge in comparisons of the leaf demography of naturally productive and unproductive sites, i.e., the Fringe and Dwarf forests.

Red mangrove leaf cohorts throughout the L-31E forests typically exhibited a Type I survivorship curve (Deevey, 1947): a low initial mortality probability, followed by an increasing risk of death as the leaves age (**Figure C-4-4**). Often, a few old leaves remained attached long after most others in the cohort have dropped, but the functional capacity of these survivors is unknown. One may calculate a mean leaf life span by integrating under such survivorship curves, or a cohort's "half-life" may be determined algebraically; these measures are closely correlated but not identical. Visual assessment of cohort mean leaf longevities reveal no clear differences in longevity among sub-blocks (**Figure C-4-5**). In order to evaluate these data more quantitatively, we used repeated measures ANOVA to assess the evidence that the survivorship of red mangrove leaves was affected by the hydrologic treatment (**Table C-4-3**), or by inherent differences in site productivity (**Table C-4-4**). Neither analysis indicated significant differences in leaf survival associated with the main site factor. It is important to note that with only a few individuals monitored within each site, these analyses had relatively low power. Tests for the effects of the repeated measures factor were more powerful, however, and in the comparison of Dwarf and Fringe individuals in the Treatment block, variation among cohorts was highly significant (**Table C-4-4**). This temporal variation was similar in both forest types (non-significant Sub-block x Cohort interaction), and had no simple linear or quadratic trend (only higher-order contrasts were significant). In general, these data suggest that leaf longevity in *R. mangle* is a relatively conservative characteristic.



**Table C-4-3:** Repeated measures ANOVA of effects of hydrologic treatment on the mean leaf longevity of leaves of several *R. mangle* individuals in the western portions of the mangrove swamp.



**Table C-4-4:** Repeated measures ANOVA of effects of site productivity on the mean leaf longevity of leaves of *R. mangle* individuals in the Treatment block.

In contrast to the rather invariant mortality patterns demonstrated above, we observed highly significant spatial and temporal variation in leaf production of *R. mangle*. To avoid confounding the production of leaves and new branches, we expressed leaf production in units of leaves per meristem per year. On this basis, the rates of leaf production maintained by trees in the Fringe sub-blocks ranged from  $\sim$ 1.3 to 4 times higher than those attained in the Dwarf units. Moreover, sub-blocks within the same forest type exhibited remarkably similar temporal patterns in leaf production, but these patterns differed markedly from one forest type to the other (**Figure C-4-6**). This variation is explored further in **Figure C-4-7**, which presents mean production rates achieved during sampling periods representing the dry, early wet, and late wet seasons of four years (late wet season 1997 through early wet season 2000). Highest leaf production rates were attained in the late wet season in all sites, but the period of lowest production varied among sites; the dry season and early wet season were the periods of lowest leaf production in the Fringe and Dwarf forests, respectively.

Summaries of statistical analyses of the leaf production data are presented in **Tables C-4-5** and **C-4-6**. In the repeated measures ANOVA of Dwarf and Fringe forest populations in the Treatment block, the effect of Site (between-subject effect) was highly significant, as were all within-site factors and interactions (**Table C-4-5**). The statistical results support the strong Season x Site interaction illustrated in **Figure C-4-7**. In the second analysis, in which the responses of the two Dwarf populations were compared, the between-subjects effect of Site was nonsignificant, but several within-subject effects, including Season, were again highly significant (**Table C-4-6**). The high power associated with many of the tests was a very surprising aspect of these analyses. Because sample sizes were relatively low, these high values are clearly attributable to extremely low population variance during each sampling period. Considered together, these data suggest that leaf production in *R. mangle* is under strong environmental control, with factors such as light, hydrology, and/or nutrient availability of great potential importance.

					murviquais in the Treatment Dwarf and Fringe.										
			Between						Within-Subject Effects						
			Subjects Season x Site Year $(4)$ Year x Site Season $(3)$ Effects (Site)							Year x Season		Year x Season x Site			
Site	N	value	power	value	power	value	power	value	power	value	power	value	power	p- value	power
TD	Q														
		0.000	000	0.008	0.851	0.017	0.783	0.000	1.000	0.000	1.000	0.000	.000	0.000	1.000
TF	Δ														

**Table C-4-5:** Repeated measures ANOVA of effects of site productivity on per unit leaves per meristem per year of *R. mangle* individuals in the Treatment Dwarf and Fringe.

					muividuais in the Treatment Dwarf and Control Dwarf.										
			Between						Within-Subject Effects						
	Subjects Effects (Site)				Year $(4)$	Year x Site		Season $(3)$		Season x Site		Year x Season		Year x Season x Site	
Site	N	p- value	power	$p-$ value	power	value	power	value	power	value	power	value	power	p- value	power
TD	4														
		0.539	0.082	0.007	0.904	0.854	0.086	0.000	-000	0.495	0.139	0.002	0.970	0.926	0.117
CD															

**Table C-4-6:** Repeated measures ANOVA of effects of site productivity on per unit leaves per meristem per year of *R. mangle* individuals in the Treatment Dwarf and Control Dwarf.

Given the temporal patterns described above for the unit production and senescence of leaves and branches, it is instructive to examine how the total number of leaves maintained by individual *R. mangle* differed over the course of the study. **Figure C-4-8** tracks the total leaf populations of each of the 23 demography trees from January 1996 to January 2002. One should bear in mind that a range of within-stand factors, including microsite variables and the behavior of neighboring individuals, contribute to the responses of individual trees. Nevertheless, in the Treatment Dwarf sub-block, all nine trees maintained relatively invariant leaf populations throughout the period. The same was true of the two trees in the portion of the Control Dwarf sub-block that were not affected by the 1996 freeze (CDW-14 and -48), but three of the four trees in the freeze-affected sections (plots CDI and CDE) experienced an expansion in leaf number. In the Fringe forest, where the period of record was one of intense competition among trees and a rapidly closing canopy, the leaf population of one tree expanded tremendously (TFS-40), while others experienced modest increases (TFE-27, TFI-4, CFS-13), little change (CFI-16, CFW-16, TFW-2), or precipitous decrease (CFE-33). Many of these trees displayed a seasonal decrease in leaf number during the winter months, a time of year when leaf and branch production appear to be low, while senescence continues unabated.

## **C-5.** *Aboveground biomass and production in Fringe and Dwarf forests.*

## **Methods:**

**Biomass***.* The two transects used to describe hurricane-related vegetation changes (**Section C-2**) were also used to estimate Fringe forest biomass prior to 1995. Densities of live *R. mangle, L. racemosa,* and *A. germinans* in three height classes (0-60 cm, 60-250 cm, and >250 cm), as well as hurricane-killed trees (>5 cm DBH) of each species, were determined. Mean stem and crown diameter for each species-size category at each point were calculated. Aboveground biomass for these mean individuals were estimated from regression equations and multiplied by density to provide point estimates of biomass per unit area. Similarly, a mean DBH of dead stems was calculated for each species at each point. Pre-hurricane biomass of these large stems was estimated from diameterbased regression equations for *R. mangle, A. germinans,* and *L. racemosa* in French Guiana (Fromard *et al.*1998). Live aboveground biomass in 1993 was calculated as the mean of twelve point estimates, and pre-hurricane (1992) tree biomass from the mean of point estimates based on dead stems plus living stems > 2.5 meters height.

In April-August 1995, 15 permanent plots were established at the study site (**Figure A-1-1**). Seven plots were in the Dwarf forest (four in the Treatment block, three in the Control block), and eight were in the Fringe forest type (four in each block). Construction of a network of boardwalks allowed us to approach and work in the rectangular plots without severely disturbing the soil surface. Plots were 0.5 meter wide, and ranged from 3 to 10 meters in length, with smaller plots in areas of higher stem density. Each mangrove individual rooted within the plots was tagged and given a grid coordinate, and the following measurements were recorded: total height (TOTHT), height to base of crown (CRWNHT), crown length and width (CRWNL and CRWNW), stem diameter at 30 cm  $(D_{30})$ , and 140 cm ( $D_{140}$ ) (for stems taller than 40 and 150 cm, respectively). The product (CRWNHT • CRWNL • CRWNW) provided an index of crown volume (CRWNV). These measurements have been repeated annually since 1995 and were generally completed between November and December of each year. However, some plots were sampled as early as September (1996), or as late as the first week of January (1997).

Post-hurricane biomass regressions for *R. mangle, L. racemosa,* and *A. germinans* were provided by Ross *et al.* (2001). Regressions were based on relationships between the structural measures listed above and biomass components (trunk, branch, proproot, leaf, and total aboveground biomass) of individuals harvested from adjacent areas that resembled the study plots in vegetation structure. The regression data set included 53 *R. mangle*, 44 *L. racemosa*, and 21 *A. germinans* stems. These individuals encompassed a range of sizes from 40 cm to 6.5 meters in height. 5-14 individuals < 40 cm height of each species were also sampled and weighed. All possible regression models of the form

ln (biomass component) =  $b_0 + b_a *$ ln (independent variable a) + ...  $b_z *$ ln (ind. var z)

were examined, where the independent variables were  $(D_{30})$ , TOTHT, CRWNV, and  $[(D_{30})^2$ <sup>\*</sup>TOTHT]. A single model form was chosen for each species-tissue combination, based on variance explained and the distribution of residuals. Two-parameter models were selected over more heavily-parameterized ones when the latter did not substantially improve model performance.

For trees in the permanent plots, biomass of stems taller than 40 cm was estimated by applying the regression models to annual structural measurements. According to Baskerville (1972), if  $\hat{\mu}$  is the estimate of Ln(Y), and  $\hat{\sigma}^2$ is the sample variance of the logarithmic equation, then the estimated value of Y in arithmetic units is:

$$
\hat{Y}=e^{(\hat{\mu}+\hat{\sigma}^2/2)}
$$

Individuals 40 cm or less in height were assigned stem, branch, proproot, and leaf biomass equal to the mean of the sample of small stems of each species. Biomass components were calculated on an area basis for each plot.

Freeze events in January 1996 and, to a lesser extent, in January 2001 caused extensive mortality and dieback in two out of the three Control Dwarf plots (see **Section C-2**). As a result, we eliminated these two freeze-affected plots from all analyses designed to assess the effects, if any, of the hydrologic treatment on the biomass and productivity of the Dwarf mangrove forest. Furthermore, we did not estimate biomass in the Dwarf mangrove forest prior to 1995 because the point-quarter method used to estimate Fringe forest biomass is ineffective at estimating density in extremely dense vegetation like the Dwarf communities in our study area (Cottam and Curtis 1956).

**Production**. Structural measures in each of the fifteen permanent plots were used to estimate aboveground production. In forest communities, aboveground production consists of the growth of woody tissues and leaf production. We calculated annual wood production as the yearly increase in total biomass minus the yearly increase in leaf biomass. Biomass for each census date were calculated as described earlier, and a linear interpolation between successive census dates was used to estimate biomass and production on the  $1<sup>st</sup>$  of July in the years 1996-2000.

In combination with data from the annual structural censuses, leaf demographic observations (see **Section C-4**) were employed to estimate the annual production of mangrove leaves. The method was based on the balance between leaf production, senescence, and standing crop:

*Leaf Standing Crop*  $Y_r(x+1) =$  *Leaf Standing Crop*  $Y_r(x)$  + *Leaf Prod'n*  $Y_r(x+1)$  - *Leaf Mortality*  $Y_r(x+1)$ and therefore,

Equation 1: *Leaf Prod'n*  $Y_{Y}(x+1) = \Delta$  *Standing Crop*  $Y_{Y}(x,\mathbf{x}+1) + \text{Leaf Mortality } Y_{Y}(x+1)$ 

A major assumption of this method is that the production and mortality rates underlying the first and third terms in Equation 1 were similar whether expressed on a density or biomass basis. In solving Equation 1 for biomass, *∆ Standing Crop*  $Y_r(x,x+1)$  was calculated by applying our biomass regression equations to structural data from censuses of successive years in each plot. *Leaf Mortality Yr (x+1)* was calculated as follows:

- 1. Mean leaf turnover rate (in leaf generations per leaf per year) was calculated for all leaf cohorts initiated after March 1996, and were based on the total number of red mangrove leaves tagged and surviving to each subsequent sampling period within each plot (see **Section C-4** for a discussion of leaf turnover rates). Leaves were assumed to have been initiated or to have died at the midpoint of the interval prior to observation. Mean cohort longevity (in days) was calculated by integrating the area under the survivorship curve, assuming a linear decrease in leaf density between periods. Turnover rate therefore equaled 365 divided by the mean longevity (Dai and Wiegert 1996). Annual turnover rate on a density basis,  $T_{dens}$ , was calculated by weighting the turnover rate of each cohort by its relative contribution to the total leaf population during the year beginning July 1, 1996.
- 2. We calculated *Biom*  $Y_{Y(x+1)}$ , the annual mean standing crop of leaves, as the average crop estimate for each plot during a 365-day period beginning and ending on July 1 and June 30, of each subsequent year, respectively.
- 3. Equating *Tdens* with *Tbiom* (turnover rate on a biomass basis), we calculated leaf mortality as: Equation 2: *Leaf Mortality*  $Y_{Y}(x+1) = T_{biom-Yr} (x+1) * Biom_{Yr} (x+1)$ ; and solved for *Leaf Prod'n*  $Y_{Y}(x+1)$  in Equation 1.

# **Results:**

**Biomass**. The regression equations used to calculate leaf and total biomass between 1995 and 2001 are listed in **Appendix B**. Although separate allometric equations were developed for stem, branch and proproot biomass, we calculated wood biomass as the difference between total biomass and leaf biomass rather than the sum of stem, branch, and proproot biomass, because of the relative weakness of the equations for branches and proproots.

Mortality from Hurricane Andrew in the Fringe forest reduced mean aboveground biomass from nearly 170 Mg/ha (1 Mg = 1000 Kg) to about 15 Mg/ha (**Figure C-5-1**). Recruitment of new seedlings was patchy during the next few years, but by the winter of 1995 most of the site had been reoccupied by a dense stand of mangrove saplings whose total biomass was estimated at about 17 Mg/ha. Subsequent stand development was rapid. By the winter of 1997-98, 5 years after Hurricane Andrew, mean aboveground biomass had increased to 56 Mg/ha and has since nearly doubled to about 108 Mg/ha (**Figure C-5-1**).

As a rule, mean aboveground biomass in the Control Fringe forest was 1.7 times greater than in the Treatment Fringe in any given year (**Table C-5-1**). However, yearly mean aboveground biomass estimates in the Control and Treatment Fringe sites were not significantly different at *p* < 0.05. Likewise, yearly estimates of leaf and woody biomass between the Control Fringe and the Treatment Fringe did not differ at *p* < 0.05, though leaf and woody biomass estimates averaged 1.3 and 1.7 times greater, respectively, in the former (**Table C-5-1**). The allocation of biomass to leaves and woody tissues followed the same pattern in both Fringe sites. In general, the ratio of wood:leaf biomass increased from 5:1 to about 11:1 and 8:1 in the Control and Treatment Fringe, respectively, between 1995 and 2001. This result is in line with other studies of post-disturbance succession, which have documented that leaves become a smaller proportion of total biomass as recovery proceeds (e.g., Sprugel 1985).



**Table C-5-1:** Mean leaf, wood, and total biomass estimates in the Control Fringe, Treatment Fringe, Control Fringe, and Treatment Dwarf forests plots of Biscayne National Park, 1995-2001.

Our initial (1995) estimate of mean aboveground biomass for the Dwarf forest was 16.9 Mg/ha (**Table C-5-2**). However, the winter freeze of 1996 dramatically altered the structure of the Control Dwarf vegetation by decreasing mean aboveground biomass approximately 30%, to 12 Mg/ha (**Table C-5-1, Figure C-5-2)**, and shifting the forest toward an earlier stage of development (see **Section C-2**). By 2001, however, mean aboveground biomass had increased to 20.5 Mg/ha (**Table C-5-2**).



**Table C-5-2:** Mean leaf, wood, and total aboveground biomass estimates in the Fringe and Dwarf mangrove forests of Biscayne National Park, 1992–2001.

a-based on a point-quarter sampling design (see Section C-2).

Estimates of mean aboveground biomass in 1995 in the two Dwarf forests were not significant different at *p* < 0.05 (**Table C-5-1, Figure C-5-1**). However by 1996 this was no longer the case (**Table C-5-2, Figure C-5-1**). As a result of the 1996 freeze, mean aboveground biomass in the Treatment Dwarf forest was four times greater than in the Control Dwarf (**Table C-5-1**). By 2000, however, mean aboveground biomass in the Treatment Dwarf forest was only two times greater than in the Control Dwarf. In 1995 the wood:leaf biomass ratio for the Control and Treatment Dwarf forest were approximately 6:1 and 7:1, respectively. However, following the freeze of 1996, the Control Dwarf wood:leaf biomass ratio decreased to 3:1, and is presently about 4:1. In the Treatment Dwarf, the wood:leaf ratio decreased to about 4.7:1 in 1996 but has averaged around 5:1 since then.

The decrease in the wood:leaf biomass ratio in the Control Dwarf was unquestionably caused by the freeze of 1996 (see **Section C-2**). However, the decrease in the Treatment Dwarf's wood:leaf ratio after 1995 cannot be attributed to the freeze because there was no evidence of damage or tree mortality in the Treatment Dwarf after that event (see **Section C-2**). So, if the freeze was not responsible for the decrease in the wood:leaf biomass ratio, what was? The disturbance history of this site suggests the following two possibilities: a prior freeze or Hurricane Andrew (1992). The hypothesis that this site was recovering from a prior freeze does not seem realistic because the last known freeze to affect the South Florida coastline was in December of 1989 (Olmsted *et al.* 1993) and thus plenty of time would have passed to allow this forest to recover. On the other hand, the Hurricane Andrew hypothesis is more possible because Andrew's winds and storm surge would have battered the Dwarf's canopy and caused the loss of many leaves and there by increasing the wood:leaf ratio. Furthermore, in the one Control Dwarf plot not affected by the 1996 freeze (CD-W), the same pattern existed; in 1995, its wood:leaf ratio was 5.5:1, but dropped to 4:1 in 1996, where it has remained.

Estimates of mean aboveground biomass in 1995 for the Dwarf and Fringe forests were not significantly different at *p* < 0.05 (**Table C-5-2, Figure C-5-1**). However by 1996 this was no longer the case (**Table C-5-2, Figure C-5-1**). At present (2001), the mean aboveground biomass in the Fringe forest is 4.1 times greater than in the Dwarf Forest (**Table C-5-2**), and all indications are that this gap in biomass will continue to increase for some time in the absence of a major disturbance (**Figure C-5-1**).

**Production**. Total aboveground production in the Fringe forest averaged 28.6 Mg/ha/yr, with leaf and wood production averaging about 12.3 and 16.4 Mg/ha/yr, respectively, between 1996 and 2000 (**Table C-5-3**). Annual production estimates for the Control and Treatment Fringe forests did not differ significantly at *p* < 0.05, even though the former was on average 1.5 times more productive than the latter (**Table C-5-4**). Likewise, leaf and wood production were 1.2 and 1.8 times higher, respectively, in the Control Fringe than in the Treatment Fringe forest, but, other than wood production in 1998-99, these differences were not significant at  $p < 0.05$ . Expressed as a percentage of the total aboveground production, leaf production was lower and wood production higher in the Control than the Treatment Fringe forest (**Table C-5-4**).

	<b>Mean Biomass (Mg/ha)</b>									
Year		Fringe			Dwarf					
	Leaf	Wood	Total	Leaf	Wood	Total				
96-97	10.3	16.1	26.4	4.3	2.4	0.6				
97-98	12.5	16.4	28.9	4.4	2.9	7.4				
98-99	12.7	16.1	28.8	4.7	4.1	8.7				
99-00	3.5	16.8	30.3	4.8	3.4	8.2				
Mean	12.3	16.4	28.6	4.6	3.2	7.7				

**Table C-5-3:** Mean leaf, wood, and total aboveground biomass production estimates in the Fringe and Dwarf mangrove forests of Biscayne National Park, 1996-2000.

Mean total aboveground production in the Dwarf forest averaged 7.7 Mg/ha/yr, with leaf and woody production averaging about 4.6 and 3.2 Mg/ha/yr, respectively between 1996 and 2000 (**Table C-5-3**). Annual production estimates in the Control Dwarf and Treatment Dwarf were statistically different. In general, the Treatment Dwarf was 1.8 times more productive than the Control Dwarf, with leaf and wood production higher by 1.6 and 2.1 times, respectively. Leaf production represented a slightly higher proportion of total aboveground production in the Control Dwarf than the Treatment Dwarf forest between 1996-2000 (**Table C-5-4**).

	Mean Biomass (Mg/ha/yr)												
Year		Control Fringe			<b>Treatment Fringe</b>			<b>Control Dwarf</b>			<b>Treatment Dwarf</b>		
	Leaf	Wood	Total	Leaf	Wood	Total	Leaf	Wood	Total	Leaf	Wood	Total	
96-97	10.9	19.7	30.6	9.7	12.5	22.2	3.1	1.4	4.5	5.1	3.1	8.2	
97-98	13.7	20.9	34.5	13	119	23.2	3.0	1.9	4.9	5.5	3.7	9.2	
98-99	14.6	21.5	36.0	10.8	10.8	21.6	3.7	2.4	6.1	5.4	5.3	10.7	
$99-00$	5.0	21.7	36.7	2.0	119	23.9	3.8	2.3	6.1	5.5	4.4	9.8	

**Table C-5-4:** Mean leaf, wood, and total biomass production estimates in the Control Fringe, Treatment Fringe, Control Fringe, and Treatment Dwarf forests plots of Biscayne National Park, 1995-2001.

Between 1996 and 2000, mean total aboveground production in the Fringe forest (28.6 Mg/ha/yr) was 3.7 times higher than in the Dwarf forest (7.7 Mg/ha/yr) (**Table: C-5-3**). This difference was accompanied by an equally striking contrast in tissue allocation. Compared to the Dwarf forest, Fringe forest leaf and woody production rates were approximately 3 and 5 times higher, respectively (**Table C-5-3**). However, leaf production constituted only 43% of the aboveground production in the Fringe forest compared to 58% of aboveground production in the Dwarf forest. Speaking anthropomorphically, this contrast in leaf production appears to result from intense interand intra-specific competition for light within the Fringe forest, leading trees to allocate more photosynthate to wood production and height growth in order to keep their canopies exposed to the sun.

# **Discussion:**

The results presented above call attention to the dynamic nature of community structure in hurricane-prone mangrove ecosystems, especially the size and distribution of aboveground biomass components. Successional changes in standing crop biomass are accompanied by changes in measured production, though maximum production is achieved earlier in stand development than is maximum biomass (Daniel *et al.* 1979; Sprugel 1985). In comparing the hurricane-damaged Fringe forest with the relatively unaffected Dwarf forest, it is important to bear in mind this contrast in the temporal functions of biomass and production.

**Biomass and Production.** We are aware of two other studies in which the biomass of a Dwarf mangrove forest similar in height (< 1.5 m) to our Dwarf Forest was estimated. Lugo and Snedaker (1974) harvested leaves, stems, and proproots in three 9-m<sup>2</sup> plots in another location in the Biscayne Bay watershed, and found a total aboveground biomass of 7.9 Mg/ha. Woodroffe (1985) found even lower aboveground biomass (6.8 Mg/ha) in an *Avicennia*-dominated Dwarf forest in New Zealand. Our Dwarf forest mean total biomass of 20.5 Mg/ha (2001) included plot estimates ranging from 9.9 (CD-I) to 40.7 (TD-I) Mg/ha. Plots with higher biomass were generally located closer to the Fringe forest, while low-biomass plots were farthest from the coast and close to the L-31E levee. This gradient of decreasing biomass with distance from the coast within the Dwarf mangrove zone parallels the inter-zonal contrast between Fringe and Dwarf forest, and may be a widespread pattern in the Biscayne Bay watershed, if not more generally. For example, along a transect 15 km south of Convoy Point, in which a continuous band of Dwarf mangrove vegetation < 1.5 meter in height stretched interiorward from the shoreline for several kilometers, total macrophyte cover decreased from about 40% adjacent to the coast to less than 10% within one kilometer (Ross *et al.* 2002).

Among mangrove studies reviewed by Saenger and Snedaker (1983), no research site above 10° north or south latitude exceeded 200 Mg/ha in total aboveground biomass. While mangrove forests of large stature are increasingly rare in Florida, biomass in mature Fringe or Riverine forest in southwest Florida averaged 170-180 Mg/ha, and exceeded 200 Mg/ha in individual plots (Lugo and Snedaker 1975). Based on our pre-hurricane biomass estimate (168 Mg/ha), and on the rapid rate of biomass accumulation following Hurricane Andrew  $\sim$  13 Mg/ha/yr over the last 7 years), it seems likely that within the span of two decades, given no other major disturbance, a forest approaching 200 Mg/ha may develop again along the shore of Biscayne Bay.

Standard methods for estimating leaf production in mangrove or other forest ecosystems often involve litter collection (e.g., Day *et al.*, 1987; Megonigal *et al.*, 1997). However, effective litter sampling methods are difficult to devise in tidal shrublands, where tidal waters sometimes rise well into the crowns of dominant stems. In its utilization of demographic parameters such as mean leaf longevity and turnover rate, our method of estimating leaf production resembled a non-destructive method applied by Dai and Wiegert (1996) in *Spartina alterniflora* marsh. In their study, leaf demography of all stems within nine small  $(0.25 - 1 \text{ m}^2)$  quadrats was monitored at short intervals over a 21-month period, and annual leaf production was calculated as:

# *mean stem density* • *mean leaf number per stem* • *mean leaf turnover* • *mean leaf mass*

In contrast, we calculated leaf turnover rates from a small sample of mangrove individuals, then multiplied this rate by the mean standing crop of leaves in our large  $(1.5 - 5 \text{ m}^2)$  plots, assuming that a density-based turnover rate (leaves • leaf<sup>-1</sup> • year<sup>-1</sup>) was equal to a biomass-based turnover rate (grams • grams<sup>-1</sup> • year<sup>-1</sup>). This assumption should be valid if leaves grow to reach a fixed size range before senescing, and this size distribution does not change substantially within the year. We have made a few observations that suggest these assumptions are roughly true on our sites. Another assumption of our method is that the leaf longevity patterns exhibited by the sampled individuals are representative of the community as a whole. Since our demographic surveys were restricted to *R. mangle,* this assumption is unlikely to be true. However, in light of the dominance of *R. mangle* in these forests (96 and 90% of total biomass in Fringe and Dwarf forest, respectively), application of these data to *L. racemosa* and *A. germinans* shouldn't alter community production estimates substantially.

Our estimates of aboveground biomass production were near the high end of the range of values reported from similar mangrove forests. Our mean Fringe forest production of 28.6 Mg/ha/yr (1996-2000) exceeded the 16.0 Mg/ha/yr and 24.6 Mg/ha/yr found by Day *et al.* (1987) in adjacent Fringe and Riverine forests in Mexico. Similarly, our mean Dwarf forest production of 7.7 Mg/ha/yr, respectively, was slightly higher than the annual

aboveground production over a seven-year period for an *A. germinans* dominated Basin forest (3.2 - 4.8 Mg/ha/yr) (Day *et al.* 1996). Teas (1979) calculated production rates of 32.1 and 3.8 Mg/ha/yr in adjacent Fringe and Dwarf forest sites in South Florida, using an expansion factor of 3 times to estimate NPP from litterfall measurements. However, it is not possible to determine how much of the variation among these studies is attributable to: (1) methodological differences, (2) inter-annual variation associated with climatic or hydrologic conditions, (3) fundamental differences in site potential, and (4) differences in the developmental stage of the mangrove community. With regard to the last source of variation, most models of successional change in forest production following disturbance include an early reorganization period during which stand production increases steadily to a maximum level (Peet, 1981; Sprugel, 1985). Though this recovery period sometimes lasts less than a decade (Marks, 1974), at about 10 years old the Fringe forest may not yet have passed entirely through it. If it has not, the contrast in production between the Fringe and Dwarf sites, demonstrated through identical methods and over the same period, may be expected to increase slightly from its current ratio of 3.7:1

The site differences in biomass allocation and structure discussed above are probably due to the contrast in the developmental stages of the two forests. Because of their rapid turnover rates in comparison to woody tissues, leaves become a smaller proportion of total biomass as stand development proceeds following disturbance (Sprugel, 1985). Fromard *et al.* (1998) emphasized the effect of stand age on mangrove structural characteristics, including biomass partitioning. In their youngest Guianese mangrove stands (ages 3-5 yrs), leaves accounted for 6-10% of total aboveground biomass, but by the time these forests reached structural maturity, this percentage had decreased to less than 3%, despite an absolute increase in leaf biomass. Furthermore, Covington and Aber (1980) showed that leaf biomass tends to reach an asymptote early in stand development, around 10 to 30 years. In our case, the yearly proportional change in leaf biomass has steadily decreased from +0.5 to < 0.0 during the last 6 years (**Figure C-5-3**). This decrease suggests that leaf biomass in the Fringe forest is reaching or has reached the asymptote described by Covington and Aber (1980). Furthermore, the yearly proportional change in woody and total aboveground biomass at both Fringe sites has steadily decreased as well, from +0.5 to about +0.1during the last 6 years (**Figure C-5-3**). This reduction in the proportional change in woody biomass through time is directly related to forest height (King, 1990) — a function of stand age, site productivity, and the morphology of macrophytes. According to King (1990), as the distance between leaves and roots increases, the photosynthate required for leaf and root turnover and stem maintenance becomes so great that little is left over for other processes (e.g., accumulation of new woody tissue). Thus as stand age increases and tree height stabilizes, the yearly mean proportional change in biomass should decrease to a value near zero.

**Hydrologic Treatment***.* Initial visual inspection of the Dwarf forest following Hurricane Andrew suggested that Andrew's winds and storm surge caused little or no damage to this forest. However, total aboveground biomass estimates and the wood:leaf ratio suggest otherwise. (**Table C-5-2**). Close inspection of these data show that the Treatment Dwarf's mean aboveground biomass steadily increased from 15.8 Mg/ha, in 1995, to 26.7 Mg/ha, by 1999 (**Table C-5-2**). Since then (1999-2001), yearly aboveground biomass estimates have averaged 26.2 Mg/ha (**Table C-5-2**). Unfortunately, because of the freeze of 1996, which adversely affected the two easternmost plots in the Control Dwarf (**Figure: C-5-2**), we were unable to determine with certainty if this apparent increase and leveling in total aboveground biomass is a response to some prior disturbance (e.g., Hurricane Andrew) or if it is related to the hydrologic treatment. Certainly the hydrologic treatment would have affected numerous ecosystem components with the potential to affect productivity, including nutrient availability, pore water and surface water salinity, soil aeration, the build up of sulfides, to list but a few.

All indications, however, are that the hydrologic treatment is probably not responsible for the observed increase in mean total aboveground biomass in the Treatment Dwarf nor in an increase in productivity because: 1) the percent increase in biomass during the pre-treatment period (1995-97) and during the treatment period (1997- 2001) were the same, 29.7% vs. 29.3%, respectively; and 2) comparison of total biomass and leaf, woody, and total biomass production between the two westernmost plots in the Treatment Dwarf (TD-W & TD-WW) and the westernmost plot in the Control Dwarf (CDW, the only plot in the sub-block not affected by the freeze) showed no difference in their rates of biomass accumulation and production through time (**Figure: C-5-4** & **C-5-5**).

# **Conclusion:**

The contrast in productivity between mangrove forests occupying the ocean fringes vs. neighboring communities inhabiting interior basins has been observed and discussed by many researchers (e.g., Davis 1940, Lugo and Snedaker 1974; Twilley, 1998). In a sense, these analyses are based on an infrequently tested assumption, i.e., that existing variation in forest structure may be equated to variation in the rate at which biomass is produced. Our results generally confirm the validity of this assumption for the two sites we examined, with biomass and production elevated by 5.3 and 3.7 times, respectively, in the Fringe forest relative to the Dwarf forest in 2001. However, based on the trajectories we expect these variables to follow as stand development proceeds, the production rates of these two ecosystem types may not be nearly as different as their respective standing crops at maturity. Moreover, mature Fringe and Dwarf forests are expected to differ more in woody tissue biomass than in leaf biomass, in line with the strong contrast in how production is allocated in the two forest types.

Five years into the hydrologic treatment all indications are that the treatment has had little or no effect on biomass and production in the Dwarf mangrove forests. However, we believe that the lack of response we have observed in these two critical ecosystem functions does not necessarily reflect the response to all possible water management scenarios that incorporate rediversion of L-31E canal water. In particular, the results of the current treatment do not address the effects on the mangrove ecosystem of diverting water of different quality, or in greater volumes, or over a more extended season.

## **C-6:** *Changes in plant species composition in the mangrove swamp*

In the fall of 1997 seven 3 x 30 meter vegetation plots were established in the Dwarf forest. Each of these plots was associated with a 0.5 meter-wide census plot that had been established in 1995 for detailed monitoring of vegetation dynamics. The new plots were oriented such that the census plot was nested in their northwest corner, and sampling consisted of annual (September) species cover estimates in ten 1 x 1 meter quadrats. Quadrat locations were selected in a stratified random manner in 1997, and the same locations have been resampled each year thereafter. The purpose of the large plots was to augment the coverage of the existing vegetation monitoring program, and ensure that the establishment of new species into the swamp was adequately sampled. In 1998 an eighth large plot, TDWW-20, was established between plot TDWW and the L-31E levee.

Mean species cover percentages in the 3 x 30 meter plots are summarized for the last five years in **Table C-6- 1**. The data shows a contrast between the relatively static composition of the Treatment Dwarf forest and the more dynamic Control Dwarf forest from 1997 onward. The disparity between blocks is the result of the freeze of January 1996, which caused extensive mortality and dieback among the mangroves of the Control forest while leaving most of the Treatment block unaffected. In the 1997 survey, nearly two full growing seasons after the freeze event, cumulative mangrove species cover ranged from 20 to 50% in the Control plots, with white and red mangrove (*Laguncularia racemosa* and *Rhizophora mangle*) sharing dominance evenly among the woody plants. *Philoxeris vermicularis* provided a thick ground cover in places, and *Conocarpus erecta* was uncommon and absent from the sampling plots entirely. Between 1999 and 2001, *C. erecta* seedlings that had become established several years after the freeze emerged through the rapidly closing mangrove canopy, which was once again dominated by *R. mangle*. The early abundance and subsequent decline of *P. vermicularis* was probably related to freeze-related dieback followed by canopy recovery.

From the point of view of the rediversion treatment, however, the most significant feature of **Table C-6-1** is the appearance of sawgrass (*Cladium jamaicense*) and spikerush (*Eleocharis cellulosa*) in the plot TDWW20. Though not abundant, *C. jamaicense* and *E. cellulosa* are two graminoid species typical of freshwater marshes. Another is *Typha domingensis*. Like *Distichlis spicata*, a relatively salt-tolerant grass that was present (though uncommon) in the center of the basin prior to the treatment, *C. jamaicense* appear to become established almost exclusively on the raised surface beneath adult red mangrove shrubs. As the freshwater rediversion treatment continued, the overall cover of freshwater graminoids increased. Therefore, freshwater delivery applied over a longer time frame may eventually provide for the further establishment of *C. jamaicense*, *E. cellulosa*, and other freshwater graminoid species.

							<b>SPECIES</b>					
<b>PLOT</b>	DA	<b>RHIM</b>	<b>LAGRA</b>	<b>AVIGE</b>	PHIV	<b>RHA</b>	<b>PLUOD</b>	<b>DISSP</b>	<b>CONE</b>	<b>SESPOR</b>	<b>CLAJ</b>	<b>ELEC</b>
	TE	AN	$\mathbf C$	$\mathbf R$	ER	<b>BIF</b>	$\mathcal{O}$	I	RE		AM	AR
<b>CDE</b>	9/97	22.6	32	5.5	25.4	1.6	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/98	33.4	21.2	1.0	2.8	0.8	0.2	$\boldsymbol{0}$	0.1	0.1	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/99	46.2	19.8	0.6	0.3	1.2	$\boldsymbol{0}$	$\boldsymbol{0}$	5.4	0.1	0.2	$\boldsymbol{0}$
	9/00	48.7	20.15	1.2	0.45	0.65	$\boldsymbol{0}$	$\boldsymbol{0}$	10.45	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/01	33.05	13.6	0.8	0.35	1.5	$\boldsymbol{0}$	$\boldsymbol{0}$	6.7	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
<b>CDI</b>	9/97	8.3	11.4	0.9	5.8	0.2	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/98	18.7	26.2	1.4	1.8	0.6	0.2	$\boldsymbol{0}$	$\theta$	$\theta$	$\theta$	$\boldsymbol{0}$
	9/99	32.3	27.6	2.0	0.6	$\boldsymbol{0}$	$\boldsymbol{0}$	$\theta$	$\theta$	$\theta$	$\theta$	$\boldsymbol{0}$
	9/00	34.5	16.55	4.1	0.7	0.15	$\boldsymbol{0}$	$\boldsymbol{0}$	0.3	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/01	39.5	12.15	2.15	1.45	0.1	$\boldsymbol{0}$	$\theta$	0.3	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
<b>CDW</b>	9/97	14.4	7.4	0.6	3.3	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$00\,$
	9/98	59.6	10.7	0.4	0.8	0.1	0.1	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/99	62.9	15.8	0.6	0.5	0.1	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	0.1	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/00	43.9	15.35	$\mathbf{1}$	0.65	0.3	$\boldsymbol{0}$	$\boldsymbol{0}$	0.25	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/01	45.4	10.7	0.9	1.2	0.15	0	$\theta$	0.25	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
TDE	9/97	79.6	7.4	1.4	$\boldsymbol{0}$	$\boldsymbol{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/98	83.0	6.2	0.6	$\boldsymbol{0}$	$\boldsymbol{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/99	79.6	17.6	0.4	$\boldsymbol{0}$	$\boldsymbol{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/00	83	9.45	0.1	$\boldsymbol{0}$	$\overline{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/01	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\overline{0}$	$\boldsymbol{0}$	$\theta$	$\theta$	$\theta$	$\theta$	$\boldsymbol{0}$
TDI	9/97	79.6	6.6	0.1	$\boldsymbol{0}$	$\boldsymbol{0}$	0	0.1	$\theta$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/98	89.0	3.8	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	0	0.1	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/99	83.0	5.5	0.1	$\boldsymbol{0}$	$\boldsymbol{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/00	79.65	1.1	0.15	$\boldsymbol{0}$							
	9/01	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$
<b>TDW</b>	9/97	62.9	4.4	$\boldsymbol{0}$	$\boldsymbol{0}$	$\overline{0}$	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/98	76.3	1.3	$\boldsymbol{0}$	$\boldsymbol{0}$	$\overline{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/99	83	5.5	0.1	$\boldsymbol{0}$	$\boldsymbol{0}$	0	$\boldsymbol{0}$	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/00	72.35	2.05	0.05	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$
	9/01	$\boldsymbol{0}$										
<b>TDW</b>	9/97	1.4	1.4	0.1	$\boldsymbol{0}$							
W												
	9/98	0.7	0.7	$\boldsymbol{0}$								
	9/99	$1.8\,$	1.8	$\boldsymbol{0}$								
	9/00	32.45	0.25	$\boldsymbol{0}$								
	9/01	34.1	0.5	$\boldsymbol{0}$	$\boldsymbol{0}$	$\theta$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\theta$	$\theta$	$\boldsymbol{0}$	0
<b>TDW</b> $\rm W\,20$	9/98	35.6	0.5	$\boldsymbol{0}$								
	9/99	34.9	1.8	$\boldsymbol{0}$	0.2	$\boldsymbol{0}$						
	9/00	28.05	0.65	$\boldsymbol{0}$	0.5	0.25						
	9/01	28.05	$0.5\,$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	$\boldsymbol{0}$	0.05	$\boldsymbol{0}$	1.3	0.05

**Table C-6-1:** Mean species cover in eight 3x30 meter plots in the Convoy Point Dwarf forest on five dates (four for TDWW20). Plots CDE, CDI, and CDW are approximately 160, 120, and 60 meters east of the L-31E levee, and Plots TDE, TDI, TDW, TDWW, and TDWW20 are approximately 340, 280, 180, 50, and 20 meters east of the levee, respectively.

## **C-7.** *Radial growth in mangrove tree islands*.

The two L-31E Dwarf forest sub-blocks – like many marshes and swamps throughout South Florida – include scattered islands of taller trees embedded in a matrix of low vegetation, commonly referred to as "tree islands". The species composition of L-31E tree islands is broadly similar to that of the swamps that surround them, though *L. racemosa, A. germinans,* and *C. erecta* are often more important in the tree islands than in adjacent *R. mangle*dominated communities. A monitoring program was developed with the objective of evaluating the effects of the hydrologic treatment on these tree islands, and comparing their growth rates to other communities in the L-31E landscape.

**Methods.** In September 1996 and December 1996 we identified a single tree island in each sub-block that was suitable in size and composition for monitoring radial growth of *R. mangle* and *L. racemosa*. We tagged approximately 25 stems of each species at breast height (1.4 meters above the ground). Selected "dendrometry" trees were >1 cm DBH, and as a group represented the range of sizes present in the stand. Using a vernier caliper, we measured each tree's diameter immediately above the tag to the nearest 0.1 mm, and marked the two vertices of the measured diameter with nail polish for future measurements. Additional stems were added at later periods to supplement the dataset. Tree diameters were remeasured at 4-6 month intervals after initial sampling, through December 2001. Cumulative diameter growth was calculated for each individual, and a mean annual rate of growth was calculated on the basis of the duration of monitoring for each individual.

In April 1999, we established a  $10 \times 10$  m plot within the "dendrometry" tree populations in each tree island. Diameter at breast height was measured for each individual in the plot whose stem diameter exceeded 1 cm. The following procedure was used to estimate net annual biomass accumulation during an average year in these plots:

- 1. Using data from the "dendrometry" trees, we developed and tested species- and site-specific linear regressions in which initial diameter was the predictor and mean annual diameter increment over the period of record as the dependent variable. These growth relationships were used to predict the diameter of each tree in the 10 x 10 m plots one year after establishment  $(D_{2000})$ , based on its initial diameter (D<sub>1999</sub>). If the slope coefficient for the appropriate site-species regression was significant at  $p \le 0.05$ , we used the equation to predict  $D_{2000}$ . If the coefficient was non-significant,  $D_{2000}$  was estimated as  $D_{1999}$ plus the mean annual diameter growth for the group.
- 2. We used species-specific equations published in Ross *et al.* (2001) to estimate aboveground biomass of each tree from its stem diameter at the time of plot establishment, and after one year of growth. Because the equations in Ross *et al.* (2001) were based on diameter 30 cm above the ground (D30), and diameters in the tree island plots were measured at breast height (DBH), it was necessary to first develop regressions that related DBH to D30. Based on data sets from the Fringe Forest census plots (**Section C-3**), we developed equations that explained 78% and 92% of the variation in D30 for *R. mangle* and *L. racemosa*, respectively (*R. mangle*: D30 = 8.20 + 1.08 \* DBH; *L. racemosa*: D30= 3.05 + 1.42 \* DBH; where all measurements are in mm).
- 3. Net annual biomass accumulation was calculated by summing individual tree biomasses at  $D_{1999}$  and  $D<sub>2000</sub>$ , then subtracting the first plot total from the second. Unlike our estimates of biomass change in the census plots (**Section C-5**), this method therefore does not account for mortality or the contribution of the understory. However, these sources usually represent relatively small proportions of the total biomass pool in closed mangrove forests, except following major disturbances.

**Results.** Mean diameter growth (with standard error) for all trees was 0.101 (0.084 SE) cm per year, with individual population means ranging from 0.112 cm/yr for *L. racemosa* in the Treatment Dwarf tree island to 0.086 cm/yr for *R. mangle* in the Treatment Dwarf site (**Figure C-7-1**). A two-way Model I analysis of variance identified no statistically significant effects of species, site, or their interaction on growth during the period (**Table C-7-1**). The most notable feature of these data is the slow growth exhibited by both species in both tree islands. For comparison, it is instructive to consider the subset of census trees (**Section C-3**) in the Fringe forest that had reached 1 cm DBH by 1997. During the 12-month period between the 1997 and 1998 surveys, 101 such *R. mangle* stems

averaged 0.29 cm diameter growth, and 11 *L. racemosa* stems averaged 0.32 cm growth; these growth rates are approximately three times those of stems in the tree islands in the Dwarf forest.

<b>Effect</b>	<b>Sum of Squares</b>	Degrees of Freedom	<b>Mean Square</b>	<b>F</b> -statistic	p-value
<b>Site</b>	0.0044		0.0044	0.46	0.500
<b>Species</b>	0.000039		0.000039	0.004	0.949
Plot*Species	0.0057		0.0057	0.60	0.442
Error	0.840	88	0.00955	$- -$	--

**Table C-7-1:** ANOVA results examining site, species and interaction effects on DBH growth of *L. racemosa* and *R. mangle* in tree islands in the Treatment and Control Dwarf sub-blocks.

To examine biomass change at the stand level, it was necessary to apply the individual tree growth data to the initial size distributions in the 10 x 10 m plots, which are summarized in **Figure C-7-2**. The size distributions of *R. mangle* and *L. racemosa* were similar to one another in each stand, but the two islands differed in forest structure. Total stem density and the number of relatively large (i.e., >3 cm DBH) stems were both higher in the Control Dwarf than the Treatment Dwarf tree island.

Before estimating growth in these two stands, it was necessary to explore the size:growth relationship in detail. The relationships of initial tree size and diameter growth rates were examined by linear regression analyses, which are summarized in **Table C-7-2**.

**Table C-7-2:** Regression coefficients and *p*-values for predicting diameter growth from initial size in Control and Treatment Dwarf sub-block tree islands. The equations take the form: Annual growth in cm =  $\alpha + \beta$  \* (Initial Stem Diameter in cm).

<b>Sub-Block</b>	<b>Species</b>	<b>Regression Coefficient</b>		
		$\alpha$	β	<i>p</i> -value
Control Dwarf	L. racemosa	$-0.025$	0.0267	0.014
	R. mangle	$-0.004$	0.0295	0.011
<b>Treatment Dwarf</b>	L. racemosa	0.139	$-0.0074$	0.335
	R.mangle	0.0413	0.0129	0.110

Both species' growth and diameter were significantly correlated in the Control Dwarf sub-block, but no significant size-growth relationships were identified in the Treatment Dwarf forest. Consequently, we used the corresponding regression formulae to estimate diameter growth in the  $10 \times 10$  m plot in the Control tree island over a one-year period, but based growth estimates for the Treatment sub-block tree island on the mean growth rates in **Figure C-7-1**. After converting the measured Year 0 (1999) DBH and estimated Year 1 (2000) DBH of each tree to basal diameter by regression (see **Methods**), the data were substituted into biomass regressions (Ross *et al.* 2001) to estimate the initial and final biomass in each Dwarf mangrove tree island plot. The following biomass regressions were applied:

*R. mangle*: Ln(Total Weight) = 4.051 + ( 1.481\* Ln(Diam))

*L. racemosa*: Ln(Total Weight) =  $4.489 + (1.021 * \text{Ln}(Diam))$ 

The first term on the right side of the equation incorporated a correction factor ( $\sigma^2/2$ ) that accounts for estimation bias associated with the logarithmic form of the regression (Baskerville 1972).

As described earlier, a comparison of individual tree growth in Control and Treatment tree islands provided no evidence of an effect of the hydrologic treatment. At the stand level, initial biomass, stem density, basal area, and rate of biomass increase were all approximately twice as high in the Control as in the Treatment sub-block tree island (**Table C-7-3**). Because only one island was sampled in each unit, no statistical comparison can be made at this level of organization, and the relative stand growth patterns cannot be attributed to the hydrologic treatment. In fact, it is most likely that rates of production in the two islands are more closely related to underlying geomorphologic variables than to recent changes in hydrologic regime.

In 1999, tree density was less in the tree islands than in the Fringe forest, but the two forest types overlapped in biomass and basal area (**Table C-7-3**). Annual increases in biomass in both tree islands were considerably smaller than those observed in the Control and Treatment Fringe forest plots during 1999-2000, suggesting lower innate productivity in the tree island sites. However, it is also important to bear in mind the developmental stage of the two forest communities. The recently-established Fringe forests were in an exponential growth phase following a major disturbance, while the tree islands were composed almost exclusively of older stems that survived Hurricane Andrew. These trees – some of which may have been in a suppressed position in the mangrove forest canopy prior to the hurricane – may not have the vigor to take advantage of the light and nutrient resources made available through hurricane mortality, or may require several more years to respond to their opportunity.



**Table C-7-3:** Structural measures in mangrove tree islands and Fringe forests, 1999-2000.

## **C-8.** *Mangrove water relations.*

While mangroves as a group are defined by their ability to function in saline conditions, their photosynthetic rates generally peak in fresh or brackish water (Lin and Sternberg 1992). Mangrove species have developed a range of mechanisms that allow the maintenance of osmotic balance under conditions that cause death in non-adapted species. For instance, *R. mangle* is reportedly efficient at excluding salts at the root-soil interface, while *L. racemosa* and *A. germinans* excrete salts through specialized glands and at the leaf surface, respectively (Tomlinson, 1986). One may suppose that the mechanism utilized by *A. germinans* is the most effective, because black mangrove is known to survive at salinities well above those that would be lethal for the other two species (Tomlinson, 1986). However, Ball (1988) points out that all mechanisms for dealing with osmotic stress entail costs in terms of growth or other plant functions. Thus, there is good reason to expect that the changes in salinity regime that the L-31E treatment regime should eventually bring about will also affect the competitive balance between these three species. For these reasons, we used several techniques to examine the water relations of the two dominant mangrove species in our study area, *R. mangle* and *L. racemosa.* 

## *i***.** *Plant moisture stress as measured by the pressure bomb.*

Scholander *et al.* (1965) introduced the use of the pressure bomb as a tool to assess plant moisture stress in woody plants. The instrument measures the pressure necessary to force water out of xylem vessels exposed at the cut end of a severed twig. The units of measurement are positive atmospheres of pressure, and the readings have been shown to effectively index the moisture potential in the water column prior to severing (Waring and Cleary 1967).

Moisture stress may be induced in several ways, including low matric or osmotic potentials in the soil, or some combination of the two. In the L-31E study, we measured plant moisture stress in mid-April of both 1996 and 1997, i.e., at a time of year when moisture stress in the mangroves should be at a maximum because pore water salinities are approaching their annual maximum. Between 5:30 A.M. and 7:30 A. M., we collected single shoot tips from six *R. mangle* and six *L. racemosa* saplings at each site, and obtained pressure bomb readings within five minutes of collection. Measurements were completed prior to full sunrise on the same morning at both Dwarf forest sites, and the Fringe forest samples were completed on another morning within the next few days. Pore water conductivity was measured once during the collection period, though it was not possible to collect a water sample in the Control Dwarf sub-block in 1996, and in the Treatment Fringe sub-block in 1997. Data were analyzed as a mixed model analysis of variance, with Sub-block and Species as fixed effects, and Year as a random effect. The analysis indicated a significant difference in moisture stress between years, and a significant Year x Site interaction, but no Species or Site effects. Direct examination of the data indicated that moisture stress was lower during the 1997 than the 1996 survey at all sites except the Control Fringe (**Figure C-8-1**).

In their paper, Scholander *et al.* (1965) utilized mangrove species to illustrate osmotically induced moisture stress, and showed that plant water potential was negatively correlated with salinity across a wide range of salinities. Across the relatively small conductivity range (36 - 60 mS/cm/s) present during the two sampling periods of our study no such general relationship was evident (**Figure C-8-2**). Considering only the two sites with complete data sets from both years, though, we found that both moisture stress and conductivity were higher during the 1997 survey at Site CF, while both were lower in 1997 at site TS (**Figure C-8-2**).

Our results indicated low levels of moisture stress in both *R. mangle* and *L. racemosa* during the two sampling periods. Measured tensions at the Convoy Point sites ranged from 18 to 23 atmospheres, which is considerably less than the 35-40 atmospheres reported by Scholander *et al.* (1965) for the same species in Baja California, and also less than those sometimes reached by upland tree species during the dry season in the Florida Keys (Ross unpublished data). Of course, plant moisture stress is dependent on environmental factors that are highly seasonal, and our surveys were done only twice, during the same season. However, these limited results do suggest that episodes of salt stress are probably infrequent in the study area, and that background moisture stress is not responsible for the differences in Fringe and Dwarf forest productivity previously described.

#### *ii***.** *Estimation of mangrove community transpiration.*

We used a stem heat balance method (Sakuratani, 1981; Baker and Van Bavel, 1987) to measure the transpiration rate of red and white mangrove individuals on a leaf area basis, and subsequently scaled up these estimates to the ecosystem level through an independent assessment of leaf area index (area of leaf surface per unit ground area). In the stem heat balance method, estimation of sap flow rate is achieved by continuous heating of a stem section over a short vertical distance, partitioning of the components of heat conduction and convective transport via the sap stream, and calculation of sap mass flow rate from the measured rise in sap temperature (Dynamax, Inc. 1990). Surveys were completed in both 1997 and 1998, during the spring season. The 1997 survey was described in an earlier Progress Report (June 1997). Below we present the results of the 1998 survey.

Between April 1 and June 6, 1998, we obtained concurrent estimates of transpiration rate for pairs of red and white mangrove trees. To measure transpiration, we attached Dynagage SGA-10 collars to stems 10-11 mm in diameter. The length of all leaves beyond the stem flow collar was recorded, and the total transpirational area was calculated on the basis of a previously established length:area regression (Ross *et al.* unpublished data); this allowed us to express sap flow in units of  $g/cm^2$  leaf area/hr. The temperature differential between the upstream and

downstream ends of the Dynagage collar – which is directly proportional to sap flow rate – was measured in millivolts. Voltage output was stored continuously on a Campbell CR-10 data logger, and averaged over half-hour intervals. In the Treatment block, Fringe and Dwarf forest transpiration were measured during the same period, but estimates for Control Fringe and Control Dwarf trees encompassed separate time intervals because of failure of one of the data loggers. The time course of water movement for each tree was carefully examined, and statistical analyses were based on 150 tree-days of record that exhibited good diurnal patterns (**Table C-8-1**). Typical diurnal transpiration patterns are illustrated in **Figure C-8-3A & B**, which track the transpiration of individual *R. mangle* and *L. racemosa* stems in the Fringe & Dwarf forests during a four-day period in April 1998.

<b>Site</b>	<b>Sampling Period</b>	<b>Total number of</b> trees sampled	<b>Number of tree-days</b> with good record
<b>Treatment Dwarf</b>	$4/3 - 4/17$	8	60
<b>Treatment Fringe</b>	$4/1 - 4/15$	8	42
Control Dwarf	$5/19 - 6/6$	6	36
Control Fringe	$5/13 - 5/16$	3	12

**Table C-8-1:** Mangrove transpiration sampling record during 1998.

**Figure C-8-4** summarizes the mean daily transpiration of 25 individuals over periods ranging from 3-9 days. The graph suggests that transpiration rates for *L. racemosa* exceeded those of *R. mangle* when calculated on a leaf area basis, and that within each species, transpiration was higher in the Fringe than the Dwarf forest. Because it was possible that species or site differences were affected by date, we applied a 2-way Model 1 analysis of variance to a subset of the entire data set – i.e., the 16 trees sampled in the Treatment block, censored minimally to secure a balanced representation of species and sites over the same time period. Data were log-transformed means of 4 or 6 daily totals for each tree during a common sampling period; the transformation was successful in homogenizing the variance among treatments. The analysis indicated significant effects of site  $(F_{(1,12)}=24.77, p=0.0003)$  and species  $(F<sub>(1,12)</sub>=13.19, p=0.0034)$ , while the species-by-site interaction was not statistically significant  $(F<sub>(1,12)</sub>=0.07,$  $p=0.795$ ).

In order to estimate transpiration per unit ground area, we multiplied the species-by-site estimates illustrated in **Figure C-8-4** (*R. mangle: Fringe forest, 0.270 g/cm<sup>2</sup> leaf area/day; Dwarf forest, 0.179 g/cm<sup>2</sup>; <i>L. racemosa*: Fringe forest, 0.546 g/cm<sup>2</sup>; Dwarf forest, 0.244 g/cm<sup>2</sup>) by species-specific estimates of leaf area (**Table C-8-2**) from vegetation plots in the two blocks. Estimates of leaf area were based on structural data from the 1997 census, in conjunction with regression equations described in **Section C-5.**



**Table C-8-2**: Estimates of leaf area ( $m^2$  leaf area/ $m^2$  ground area) of three mangrove species in the L-31E study area, Winter 1997.

Applying the estimated transpiration rates for *R. mangle* to the relatively uncommon and unsampled *A. germinans*, site estimates for transpiration were as follows:



These estimates appear to be quite reasonable, in light of measurements of pan evaporation from several South Florida sites. In Key Largo, for instance, pan evaporation during 1990 generally ranged from 3-8 liters/m<sup>2</sup>/day (Ross unpublished data). One may speculate that the large (3-6X) difference between Fringe and Dwarf forest may have important consequences at the ecosystem level, i.e., flooded conditions may persist for longer periods in poorly drained portions of the Dwarf forest, causing anaerobic conditions inimical to plant growth. However, this effect may be mitigated in part by higher rates of evaporation expected from the more exposed standing water surface in the Dwarf Forest.

# **Section D: Hydrology**

## **D-1.** *Introduction and methods.*

Beginning March-April 1996, hydrologic parameters were monitored at four wetland locations (CD, CF, TD, TF), and a tidal site (TT) (**Figure A-1-1**). A canal site (DC) was added the following year. Water levels were monitored in four-inch diameter PVC wells installed to bedrock and surveyed for elevation above mean sea level (amsl). Monitoring equipment initially included float and pulley devices, but these were replaced by pressure sensors in 1998. Water levels were measured at 15-minute intervals, and data were downloaded monthly. Measurements were verified during downloading of the recorders, and sensors were calibrated when necessary. Data gaps were occasioned by equipment failure, which we assumed to have occurred when the recorded water level differed by more than 1 cm from the measured water level. Hydroperiod (time inundated per period) was calculated for each month and year by superimposing water elevations on the mean elevations of nearby plots. Variation associated with microtopography was also assessed by considering the range of elevations within the plots. Water levels in the Control and Treatment Fringe forest, CF and TF Wells respectively, generally tracked the levels in the Tidal Recorder (TT) closely. Monitoring of the Fringe forest wells was therefore discontinued in 1999, and hydroperiods for both Fringe plots were calculated on the basis of water level at TT.

The hydrologic data described above (e.g., hydroperiod and the number and duration of inundation events) affect other physical variables, for instance, salinity conditions in local surface or ground water. Variation in such water quality parameters reflect a balance between the volumes of fresh and brackish water inputs to the sites, and the duration of those conditions. Hydrologic sources to the basins consist of: groundwater, precipitation, tidal intrusion, and, in the case of the Treatment Dwarf sub-block, freshwater discharge from the L-31E Canal. Models describing the overall budget for each site have proved difficult to develop. However, water levels in the two Dwarf basins exhibit interesting seasonal and diurnal associations with levels in the TT and DC wells, as well as with precipitation. The following discussion describes our attempts to detect hourly, diurnal, and seasonal correlations between monitoring wells, and to derive statistically significant relationships between them. Subsequently, we describe the general hydrologic and salinity conditions in the four wetland sites: TF, TD, CF, CD.

Site physiography varied between blocks, and between the Fringe and Dwarf basin locations. The average elevation in the Treatment Fringe plots was 17 cm above mean sea level, which is roughly 25 cm lower than in the Control Fringe. This topographic contrast creates disparities in the periodicities and volumes of tidal influx to these forests. The low surface elevations and close proximity to Biscayne Bay of the Fringe forests cause them to be easily and often inundated by high tides. Tidal influence decreases toward the interior, resulting in degraded hydropatterns that are less closely linked to tidal flux. The average plot elevations in sub-blocks CF, CD, and TD were all near 40 cm, with the greatest inter-plot variation occurring in CF. Despite the overlap in soil elevation between Dwarf and Fringe forest, the berm-like properties of the latter, whose soil is primarily organic, contrasts with that of the Dwarf basins, whose soils are of calcitic marl substrate overlaid by varying depths of organic, peaty material (**Section E**). The composition of these soils changes gradually with distance from the coast. The Fringe forests are separated from the Dwarf basins by a Transition forest that grades downward in overall size toward the Dwarf basins. The TD basin is broader and extends further east than the CD basin; consequently, the Transitional forest is narrow in this area. The relatively wide zone of Transitional soils and vegetation surrounding the smaller CD basin may dampen tidal inflows/outflows in comparison to TD or similar neighboring basins.

# **D-2.** *Flooding patterns.*

We determined hydroperiod in the Fringe plots based on tidal stage and amplitude, and mean plot elevation. Inundation events were defined as the period of time between water levels rising above the mean plot surface and falling below it. During some periods, tidal levels remain above the plot surface throughout the semi-diurnal oscillation; the result is fewer inundation events, but longer total flooding duration. The implications of small differences in elevation are apparent when comparing the average hydroperiod in the Treatment and Control Fringe plots (**Table D-2-1**), with the former flooded for more than twice as long in most months. In the spring and early summer, the Treatment Fringe also experiences more inundation events than Control Fringe, but during the fall

months, constant inundation of the Treatment Fringe by Biscayne Bay waters for multiple days result in fewer events (**Table D-2-1**). Control Fringe plots are rarely inundated for a complete diurnal cycle.

	<b>Variable</b>	<b>Number of Inundation Events</b> <b>Hydroperiod</b>															
	<b>Site</b>	TD			CD		TF		CF		TD		CD		TF		CF
	Year	1999	2001	1999	2001	1999	2001	1999	2001	1999	2001	1999	2001	1999	2001	999	2001
	Jan.	6	4			$\overline{\phantom{0}}$	31		30	100	6	54			52	$\overline{\phantom{0}}$	16
	Feb.	3	↑		0	54	$\,$	33	$\overline{\phantom{0}}$	83	5		$\theta$	53	$\overline{\phantom{a}}$	18	
	Mar.	4	4		4	59	59	37	26	61	40		9	49	43	13	9
	Apr.			$\theta$		58	52	43	51	54	18	$\theta$	18	53	69	17	32
	May			6	6	59		51	$\overline{\phantom{0}}$	98	100	10	86	61	$\overline{\phantom{0}}$	22	
	Jun.				-	58	49	53	18	100	$\overline{\phantom{a}}$	100	$\overline{\phantom{0}}$	58	40	21	6
Month	Jul.		⌒		$\overline{2}$	52	60	35	43	100	48		-	56	53	18	14
	Aug.				-	$\overline{\phantom{0}}$	60	$\overline{\phantom{0}}$	56	100	74	100	$\overline{\phantom{0}}$	-	65	$\overline{\phantom{a}}$	26
	Sep.						42	-	59	100	100	100	-		80	$\overline{\phantom{a}}$	40
	Oct.			10		35		45	37	100	100	88	100	86	98	42	74
	<b>Nov</b>			-		24	35	58	52	100	$\overline{\phantom{0}}$	$\overline{\phantom{0}}$	100	93	87	50	55
	Dec.				-	48	56	47	60	87			$\overline{\phantom{0}}$	65	68	23	31

**Table D-2-1:** Monthly number of inundation events and hydroperiod (percent of hours with surface inundation) at four sites in the L-31E study area during 1999 and 2001.

**Table D-2-1** also includes data from the two Dwarf forest sites during 1999 and 2001. These sites invariably experience fewer flooding events than their Fringe counterparts, but in most months total flooding duration is longer in the Dwarf forest. Inundation events in the Dwarf forests usually result from tidal intrusion, with peak water levels in the basins usually staggered from the tidal peaks in Biscayne Bay by one to two hours. **Figure D-2-1** illustrates tidal influence during the fall months in 1999 and 2001. At this time of year, the combined effects of high precipitation, high water level in the delivery canal, and high tidal elevation result in surface water in the basin tracking tidal oscillations very closely for extended periods. Multiple monthly inundation events during such periods are caused by brief dry-downs, followed by re-inundation by tide. In general, these cyclic oscillations are confined to the months of September through November, when mean basin stages rise to near or above the soil surface and mean tide levels are above average for the year. This pattern also occurs briefly during the high tide period of the late spring. However, when water recedes below the basin surface, tidal oscillation frequently becomes non-discernible in the Dwarf mangrove basins. The reasons for this are not entirely clear, but may be related to the large and spatially variable water holding capacity of the dwarf mangrove soils, which would act to dampen the tidal signal. Along with the contribution of ground water, the physical effects of the mangrove soils are critical and poorly understood components in the hydrologic dynamics of the L-31E study area.

The hydrologic regimes that affect the Dwarf and Fringe forests are examined further in **Table D-2-2.** In **Table D-2-2**, the percentage of days in which water level exceeds the mean surface elevation for at least one hour is reported. On this basis, the Fringe forest was flooded more frequently in both years and in both blocks. This conclusion appears to contradict our earlier discussion, which was based on the data reported in **Table D-2-1.** Here, flooding was accounted for on an hourly basis, and Dwarf forest sites were flooded a greater proportion of the time in most months. Clearly, both hourly and daily summaries are necessary to completely characterize the water regimes of these sites, as each presents a separate expression affecting relative soil drainage and soil redox potential.

		1999	2001			
<b>Site</b>	Percent # of Days <b>Flooded</b>	Days of Record	Percent # of Days <b>Flooded</b>	Days of record		
СE	64	302		191		
TD	92	352	62	305		
СF	83	270	-87	302		
TF	100	270	100	302		

**Table D-2-2:** The annual percent of days in which the soil surface was inundated at least once, at four L-31E sites during 1999 and 2001.

In comparison to the clear among-type differences discussed above, observed hydrologic patterns in the two Dwarf basins differed only subtly from one another. Average plot elevations in the two Dwarf blocks are nearly identical  $(CD = 41.7$ ;  $TD = 41.5$  cm amsl). Water levels were generally higher in the Treatment block than in the Control (mean water elevation: CD,  $1999 = 43$  cm,  $2001 = 42$  cm; TD,  $1999 = 48$  cm,  $2001 = 43$  cm), and flooding was more frequent in TD in both years, whether calculated on a daily or hourly basis (**Tables D-2-1** and **D-2-2**). Differences in duration of flooding in TD v. CD were most pronounced in the spring months (**Table D-2-1**).

The between-basin differences described above presumably resulted from differences in the hydrologic inputs to the two blocks. Freshwater inputs to the blocks are precipitation, delivery canal (DC) discharge volume, and groundwater seepage, especially from the L-31E Canal (**Figure D-2-2**). Discharge occurs only when stage exceeds 54 cm amsl, but it is reasonable to expect that groundwater seepage can be indexed by water level in the DC across a wide range of stages, i.e., higher stage equates to higher freshwater head. Canal levels for a typical year have a bimodal distribution due to water management regulations. The wet season schedule, when canal stage is maintained near the target elevation of 61 cm, begins May 15 and ends October 15. Discharge volumes during this period can reach 20,000 cubic meters per day. Sustained freshwater delivery during May and June increases freshwater inputs to the Treatment block only, and are responsible for a higher TD water table at this time of year. Delivery also appears to have a small but noticeable effect on surface water salinity (**Figure D-2-3**). In the CD block, water levels also increase slightly during May, most likely because of canal seepage and precipitation. High tide periods coincident with these raised water tables sometimes create brief tidal oscillations in TD and occasionally in CD, as discussed earlier.

We used simple linear regression to quantify the importance of the variables affecting hydrology in the two blocks. Coincident levels of inputs (independent variables) were regressed against water level in the wetland (dependent variable), and the data were analyzed separately within each basin and each month between January 1999 and May 2002. Independent variables were daily maximum tidal stage, maximum DC stage, and cumulative precipitation. The dependent variable was the daily maximum water level in the basin. We used maximum instead of mean values in order to better incorporate peak tides and canal surges.

**Table D-2-3** lists the coefficients of variation for each independent variable, as well as the mean monthly tidal, DC, and marsh stages. Strong correlations between daily tidal maxima and water levels in the Dwarf mangrove basins were observed in more than half of the months for which sufficient data were available in Block TD, but only four months in Block CD. The strongest associations were concentrated in wet season months in CD, but in TD strong correlations were also observed in the spring months of several years. In general, there appeared to be a strong positive relationship between mean monthly tidal elevation and the strength of the TT:TD association (**Figure D-2-4**). The influence of the Delivery Canal on water level in the basins exhibited a different pattern. Strong associations with DC level were equally likely to occur in either block, and were most consistently observed during the spring months, when basin water levels were lowest. Finally, no relationship between precipitation and mangrove water level was observed. These patterns suggest, most pertinently, that (1) the hydrologic connection between tidal waters and seemingly similar interior mangrove basins can vary widely, (2) seepage from adjacent canals is an important water source in current mangrove forests in the study area, and should be incorporated into hydrologic models developed for the Biscayne Bay Coastal Wetlands, and (3) water delivery that is restricted to high canal stages is likely to play only a minor role in the hydrologic budget of these basins.

	Adjusted $R^2$						Mean Water Elevation			
	TT:TD	TT:CD	DC:TD	DC:CD	PPC:TD	PPC:CD	<b>TT</b>	DC	TD	CD
Jan-99	0.08	0.66	0.32	0.00			11	47	45	42
Feb-99	0.76	0.05	0.24	0.44			20	49	46	34
Mar-99	0.32	0.02	0.84	0.92			18	47	40	31
Apr-99	0.72	0.08	0.08	0.58			20	40	36	21
May-99	0.68	0.00	0.18	0.17			24	50	46	36
Jun-99	0.60	0.07	0.03	0.02			23	57	46	47
Jul-99	0.11	0.08	0.24	0.13			22	67	47	46
Aug-99	NA	NA	0.14	0.06			NA	59	49	50
Sep-99	NA	NA	0.45	0.42			<b>NA</b>	61	59	54
Oct-99	0.88	0.73	0.38	0.36			37	58	60	55
Nov-99	0.53	0.11	0.05	0.12			40	49	55	52
Dec-99	0.49	0.17	0.61	0.23			25	42	45	42
Jan-00	0.46	0.05	0.46	0.15			21	51	39	31
Feb-00	0.00	0.11	0.75	0.11			18	53	41	33
Dec-00	0.89	0.37	0.44	0.45	0.01	0.09	28	47	48	43
$Jan-01$	0.06	0.34	0.15	0.56	0.10	0.07	19	48	33	33
Feb-01	0.09	NA	0.04	0.67	0.08	0.03	19	48	33	30
Mar-01	0.02	0.02	0.71	0.59	0.02	0.05	14	51	38	38
Apr-01	0.33	0.17	0.86	0.96	0.17	0.16	30	44	33	32
$May-01$	NA	$\rm NA$	0.71	0.48	0.01	0.02	84	61	52	47
$Jun-01$	0.58	NA	NA	NA	0.06	NA	13	NA	43	47
$Jul-01$	0.47	0.06	0.01	0.14	0.03	0.08	20	61	45	53
Aug- $01$	0.16	NA	0.24	NA	0.10	NA	26	46	44	50
Sep-01	0.87	NA	0.60	NA	0.03	NA	35	48	48	NA
Oct-01	0.90	0.89	0.48	0.47	0.1	0.06	54	54	54	58
Nov-01	NA	0.98	$\rm NA$	0.75	NA	0.34	44	48	49	59
Dec-01	NA	NA	NA	NA	NA	NA	28	41	NA	NA
Jan-02	NA	NA	NA	NA	NA	NA	6	44	NA	NA
Feb-02	0.81	0.10	0.46	0.03	0.07	0.12	11	50	35	33
$Mar-02$	0.56	0.22	0.57	0.44	0.00	0.12	15	50	40	39
Apr-02	0.26	0.00	<b>NA</b>	NA	NA	<b>NA</b>	23	51	43	31

**Table D-2-3:** Adjusted  $R^2$  values from simple linear regressions of hydrologic inputs (TT = daily tidal creek maximum, DC = daily delivery canal maximum, PPC = total daily precipitation) with maximum water level in the Treatment or Dwarf basins, January 1999 – April 2002. High  $R^2$  values (>0.40) are reddened for emphasis. There is a 9-month break in the hydrologic record between March '00 and November '00, inclusive. N.A. = not available.

# **D-3.** *Salinity/Conductivity***.**

Most salts are not actively taken up by primary producers, and are not transformed into the gaseous phase. For this reason, the salinity or conductivity of water may serve as an effective tracer of the balance between marine v. terrestrial sources in the mangrove hydrologic system. One may also expect the reverse to be true, e.g., months in which marsh water level and tidal stage exhibit a strong positive association should also exhibit higher overall salinity levels, while strong correlations with DC level should imply lower salinities on the wetland. Data presented in the previous section demonstrated that these correlation patterns were basin-specific (**Table D-2-3**). In the Control block, the Delivery Canal (fresh water) seemed to play a measurable role through groundwater seepage in the dry season, while the influence of tides (brackish or salty water) was concentrated in the wet season months. In the Treatment block, the seasonality of both of these sources was much less pronounced, due to a combination of factors, including the well-developed tidal creek system, basin topography, and complications associated with the passive fresh water delivery system. The following section describes monthly and seasonal salinity conditions in these two basins.

Salinity and specific conductivity (S.C.) were monitored for a seven-year period, beginning July 1995 and continuing through October 2002. Salinity and specific conductivity were measured using a handheld refractometer and conductivity meter, respectively. The longterm record for the salinity (not shown) and S.C. of surface and pore water reveal a strong seasonal pattern in both blocks (**Figure D-2-4**), and a slight, though significant, increase in conductivity in the Control block (**Figure D-3-1**).

Surface water was only intermittently present in TD and CD during January – April, resulting in many data gaps, while pore water was available almost continuously in both blocks. Despite the gaps in data, evidence of seasonality was apparent in both pore water and surface water S.C. With some variation among years, surface water conductivity usually increased from January to April-May, when peak concentrations were reached in both blocks. Pore water peaked about a month later, in May-June (**Figure D-3-1**). Surface water S.C. was lowest in July in both blocks (TD mean = 5.5 mS/cm; CD mean = 9.5 mS/cm), dropping again in October (TD mean = 9.9 mS/cm; CD mean = 10.9 mS/cm). In general, pore water S.C. was higher and demonstrated a less pronounced seasonal pattern than surface water, presumably because of the capacity of the soils to sequester cations on exchange sites.

**Figure D-3-2A & B** allow for a comparison of conductivity patterns in surface and pore water in both Dwarf mangrove blocks during the pre- and post-freshwater rediversion periods. Temporal variation differed with block and water type. Surface water S.C. decreased sharply in TD during the early wet season (June – August), indicating a treatment effect at that time of year, especially since no parallel change was observed in the Control block. The relative freshening of TD water during the wet season is paralleled by – and may be responsible for – lower pore water conductivities during the dry season. For instance, February - June S.C in the Control block increased by an average of 3-8 mS/cm between pre- and post-treatment periods, while TD pore water conductivity was unchanged.

Patterns of surface water conductivity within the TD block provided further evidence of diversion treatment effect. Monthly measurements began immediately after the initiation of the diversion treatment in August1997, and included stations at the TDWW, TDW, and TDI vegetation plots (50, 175, and 250 m, respectively, from the base of the levee). Conductivity increased sharply from west to east (means: TDWW, 10.5 mS/cm; TDW, 16.1 mS/cm; TDI, 16.7 mS/cm). The zone of influence was therefore relatively narrow, and may reflect not only discharge from the L31E canal, but also canal seepage affecting the areas closest to the fresh water source. In order to extend the effects of freshwater diversion further into the basin, increased canal volumes may be necessary.

In combination with the conductivity data presented in **Figures D-3-2A & B,** average monthly precipitation totals and water levels at DC, TT, TD, and CD recorders over the 1997-2001 period (**Figures D-3-2C**) hint at the dynamic balance between sources in their effects on marsh water quality. Marsh surface water conductivity was lowest in both blocks at the time of year when marsh water levels were highest, e.g., in July – October, a period of high rainfall, high canal stage, and increasingly high tides. The seasonal minimum in pore water conductivity (September – December) lagged behind these wet conditions by a few months. However, attempts at developing regression models to predict conductivity from the levels of the various sources were not successful. It may be that effective modeling of even this relatively simple hydrologic system requires a more extensive monitoring network, and the inclusion of potentially significant contributions of the regional ground water component.

# **Section E: Soils**

## **E-1** *Introduction & Methods.*

#### **Introduction:**

Soil constituents contain numerous environmental signals that permit the reconstruction of prevailing conditions during deposition. In the Southeast Saline Everglades (SESE), which includes the L-31E study area, a comparison of vertical soil sequences with surface soil constituents – which effectively reflect present plant communities – indicate that, in general, conditions have become more saline (Meeder *et al.* 1996). Fossil mollusk assemblages proved to be good indicators of salinity regime and are used at the L-31E site. Soils in the study area can be subdivided into two major types: carbonate mud (marl) and fibrous peat. Carbonate muds, composed of calcite, are produced in fresh-to-low salinity areas containing high dissolved calcium carbonate concentrations and abundant filamentous algae (Gleason 1974, Browder *et al.* 1994). Coastal peats are predominately made up of red mangrove root material (Cohen and Spackman 1974, Gleason and Stone 1994). Sawgrass root material is observed in the marl soils, but does not form fibrous peat in this study area.

Aerial photography dating to 1928 documents a fringing mangrove belt that was much thinner than today (approximately 250 m). By the early 1920-30's, ditching for coastal land reclamation, agricultural purposes, and mosquito control effectively drained most of the wetland areas found between the coastal ridge and the fringing mangroves. This reduced or eliminated freshwater sheet flow to Biscayne Bay. By the 1940's, salt-water encroachment became a problem in coastal areas, causing the abandonment of many fields (Parker *et al.* 1955). Parker *et al.* (1955), as well as many others, suggested placing salinity barriers in the mouths of major canals to reduce saltwater encroachment. In addition, during the mid 1960's, the L-31E canal and levee were constructed to minimize the effects of storm tidal waters. The construction of the levee resulted in the final reduction of sheet flow to the Bay. Thus, areas east of the levee were transformed in a few decades from coastal wetland ecosystems in which freshwater runoff was a significant part of the hydrologic budget to systems driven entirely by local rainfall and tidal processes. This change resulted in increased coastal basin salinities, which were eventually reflected in changes in both vegetation and soil characteristics.

Sea level has been rising continuously, but at different rates, during the Holocene, leaving an abundant record in the South Florida region dating back approximately 6,000 yrs. (Parkinson 1989). Tidal records from Key West indicate that the rate of sea level rise has accelerated during the last century (Maul 1993). Most researchers believe that the south Florida platform has subsided uniformly, and therefore differences in the rate of salt-water encroachment between coastal basins must be a response to changing freshwater discharge (Meeder *et al.* 1996). Given this assumption, the causes of salt-water encroachment can be further analyzed by comparing different basins with different histories of hydrologic alteration. A list of regional hydrologic alterations of note, with the date of origin and the area directly impacted (Meeder *et al.* 1996), was used in planning for the L-31E study.

Major objectives of our soil research were to: 1) quantify the major soil forming processes and their rates, 2) establish prehistoric environmental conditions and document their recent changes both temporally and spatially, and 3) establish criteria for the recognition of salt water encroachment in coastal sediments. Criteria for the recognition of salt water encroachment focus on paleoecological indicators such as fossil invertebrates, soil composition, and shifts in vegetation. The effects of mangrove colonization, stabilization, and eventual domination on the preexisting soils will be documented. Such factors as: 1) carbonate-to-organic carbon ratio, 2) surface microtopography, 3) accretion rates, and 4) mangrove density and standing crops are addressed. In addition, the role of ground water in coastal productivity will be addressed by the study of the more productive tree islands isolated within extensive dwarf mangrove habitats. The tree islands express positive topographic relief, have thicker peat deposits, and are located over karst features (dolines).

# **Methods:**

**Topography.** Survey lines were made using a Sokal 100 level and standard methods. Shots were closed and reshot with closure greater than 2mm/100m. Benchmarks established at structures on both the Military and Mowry Canals were used for elevation control. The elevation for the benchmark (R-26) at the Military Canal Structure (C-11) is 6.88 ft above MSL (1956 datum) and 6.8 ft for R-25 at the Mowry Canal Structure (C-12). The general topography of the 20-hectare block was established using 5 cm contours. The elevation of all core, water well, and vegetation sites were also established. Close interval surveys were completed: 1) at the vegetation sites to establish microrelief associated with the presence or absence of mangroves and the length of time of mangrove presence, 2) across mangrove tree islands to document peat mounding, and 3) both across channel and down tidal creek channels.

**Soil Depth.** Soil depth was measured by the use of a probe rod  $(3/8)$  in diameter steel rod) along survey lines. This was accomplished by pushing a probe rod of known length into the soil until it reached bedrock. The length of the remaining rod was then measured to give the soil depth. Probing was done at meter intervals along the tree island transect and every 10 m, throughout the basin.

**Soil Sampling**. Continuous soil cores were taken by hand driving or with the use of a tripod and piston-coring device. The piston-coring device was used in areas with soil profiles greater than 100 cm in thickness. This method is similar to the method described by Jarrett (1982) for peat extraction. It utilizes a rubber piston to draw a vacuum in the soil core tube as it is pushed into the ground. This is done to maximize recovery of the soils and to minimize compaction. The piston is placed initially in the bottom of the core tube located at the ground surface and held in place by a chain attached to the top of an aluminum tripod approximately 3.5 m in height. When the tube reaches bedrock notches cut in the bottom of the tube are bent over capturing the material. The tube is extracted from the ground utilizing a winch attached to the top of the tripod. The winch is connected to the tripod and the tube via a chain. When the tube reaches surface level the bottom of the core tube is capped to prevent water and soil loss.

Cores were collected in 3 in diameter Aluminum tubes. The tubes are prepared by cutting to an appropriate length for the depth of bedrock plus about 0.5 in extra. Once extracted, tubes were stored upright and sealed until soils were processed. Core tubes were cut lengthwise and the soil plug was carefully cut or pried apart in order to preserve sediment textural features. Cores were sampled at regular intervals and at changes in composition, color or texture.

Soil cores along the mangrove scrub basin were collected at 50, 200, 400, and 500 in from the L-3 I E levy. In the tree island soil cores were taken: at the center (deep core), at the exterior, and at the midpoint between maximum and minimum bedrock elevation.

**Soil Analyses**. The cores were split, photo documented and described (from the base to the top). Two 1-cm<sup>3</sup> samples were taken every 10 cm (from the top) in the longer cores (TD Dome 1, TD Dome 2, and TD Dome Intermediate) and every 5 cm in the shorter cores (TD Dome Exterior, TD 400-m, TDE 500-m). Sub-samples were taken every 2 cm in areas of significant color and morphological changes (unless other wise noted in the data). One cubic centimeter sample was weighed, dried at 70°C, and then weighed again to determine wet and dry bulk density. The same sample was then placed in a furnace and heated to 550°C for one hour to remove all organic material (Dean 1974). The sample was cooled and weighed to determine percent organic material lost. It was heated again at 1000°C for one hour, to remove carbonate fraction (Dean 1974), then cooled and weighed again. Weights of water, organic carbon, carbonate and incombustibles were recorded. Simple statistical measures were employed to determine weight percent organic, carbonates and water.

Organic constituents were determined by separation through a series of sieves (2.00 mm, 0. 84 mm and 0. 177 mm). Constituents were collected and separated into the following categories: fibrous, rhizomes, shells, amorphous organic, aboveground plant material (leaves, stems, seeds) and mud. In some samples, clastic material and "other" material were added to the categories. Rhizomes and roots were distinguished from fibers by size (greater than I mm in diameter) and definite root structure. Rootlets less than 1 mm in size were deemed fibrous and were placed into their respective category. All organic material collected in the 0.177 mm sieve was considered amorphous organic. Material smaller than 0.177mm (mud) was collected and placed in a beaker to dry at 70°C. Once dried, the samples were weighed.

**Faunal analyses**. Fossils >1mm in diameter were extracted from the soil sample by washing the sample through sieves. Uniform volumetric samples were collected. Most fossils recovered are mollusks that are fairly easy to identify. All mollusks were identified and counted. A salinity index was calculated based upon the known salinity tolerances from the literature and field observations (Meeder *et al*. 1996, Ross *et al*. 2000b).

## **E-2** *Soil Composition***.**

The two major constituents of all sediments processed are carbonate (mud, skeletal, and limestone clasts, in descending order of abundance) and organic residuals (usually fibrous root material, carbon films, or amorphous-togranular decomposed organic detritus). The ternary diagram illustrates the relationships, and commonalities of the soil components at the Dwarf sites (**Figure E-2-1A**). It was found that shell material never occurred in those portions of the core that contained clastic material. Clasts were found to be of two types: partially lithified red clay and limestone bedrock clasts. Lithoclasts occurred in the lower parts of the cores in soils high in calcite mud content. Shells occurred only in the upper portions of cores where carbonate content was greater than 50%. Red clays were associated with lower percentages of carbonates. Few shells were found in the mangrove peat soils, but those found frequently displayed severe signs of shell material dissolution.

When clastic material and carbonate mud was plotted with organic content three general trends were recognized (**Figure E-2-1B**). First, where clasts were in 75% or more abundance, organic and carbonate content was approximately 25%. Second, when clasts were under 50% abundance, carbonate content was generally greater than 50%, while organics were generally unchanged. This defined the lithoclastic calcitic mud of the bottom of the cores. Finally, where clasts were not present carbonate content was between 25 and 100% and organics made up the remainder of the sample.

Root material was plotted against amorphous organic material and carbonate in order to define the relationship between the types of organic material associated with carbonate mud content (**Figure E-2-1C**). Most carbonate marl contains approximately 10% organic material. Most samples plot either as organic rich marl (10 to 20 % organic material) or as marly peat (50 % carbonate or less). This illustrates the absence of peats in the dwarf sites. Most of the organic fraction in the marly peat is comprised of amorphous material.

Four major soils types are recognized: red lithoclastic calcitic mud, calcite mud, peaty carbonate mud, and mangrove peat. Contacts between soil types can be transitional or very abrupt.

Surface soils are characterized according to their content, thickness and distribution (**Table E-2-1**). This table summarizes soil characteristics and estimates of annual accretion rates of soil constituents along an east-to-west gradient in the Treatment block. Soil accretion rates are based upon estimates of the timing of salinization in the area, based on radiometric dates from similar soils in the SESE (Meeder *et al.* 1996). In addition, serial aerial photographs from 1928 to the recent were consulted to estimate the width of the mangrove belt at various times.

**Table E-2-1**: Soil attributes along the east-to-west gradient. DTB = Depth to bedrock or total soil depth. Soil type = Soil type of the marsh surface (pm = peaty marl, mp = marly peat, p = peat). Thickness = thickness of marsh surface soil type. Age = basal age of surface soil type (estimated from aerial photography, known time of salinity change, and numerous radiometric dates from the SESE).  $S =$  Soil accretion rate. Water content = mean water content of upper 10 cm of soil. Saturation volume = volume of water required to resaturate one square meter of soil to a depth of one cm. Carbon content = mean carbon content of upper 10 cm of soil. Carbon deposition = carbon deposition rate.  $CaCO<sub>3</sub>$  content = mean calcium carbonate content of upper 10 cm of soil.  $CaCO<sub>3</sub>$  deposition = Calcium carbonate deposition rate. \*Unlike other locations, carbonate source at 620 m is probably not freshwater marl but marine mud brought in by storm tides from Biscayne Bay.

	50 meters			200	400	500	620
	<b>High</b>	Low	<b>DOME</b>	meters	meters	meters	meters
DTB (cm)	97	89	235	101	130	180	260
Soil type	MP	PM	$\mathbf{P}$	<b>PM</b>	MP	MP	${\bf P}$
Thickness (cm)	15	7	34	15	19	25	125
Age	34	34	500?	74	100	$\overline{\mathcal{C}}$	1500?
$S \text{ (mm/y)}$	0.44	0.21	0.68	0.2	0.19		0.83
Water content (g/cc)	0.58	0.47	0.9	0.45	0.4	0.65	0.9
Saturation volume $(l/m^2)$	5.8	4.7	9	4.5	$\overline{4}$	6.5	9
Carbon content $(g/m^2/cm$ depth)	665	385	475	650	1013		1220
Carbon deposition $(g/m^2/cm$ depth)	0.802	0.222	0.885	0.356	0.527	۰	2.77
$CaCO3$ content $(g/m^2/cm$ depth)	520	470	20	445	303		$50*$
$CaCO3$ deposition $(g/m^2/d)$	0.627	0.27	0.037	0.244	0.158		$0.114*$

## **E-3** *Molluscan salinity index.*

Twenty-one species of mollusks were identified. Most are common species, with well-known habitat and salinity tolerances. From these known characteristics, a salinity index (between 1 and 6) was assigned to each species (**Table E-3-1**). Mollusks collected from core samples were identified, counted and an assemblage salinity index calculated. Vertical changes in assemblage salinity index number are recorded (**Table E-3-2**). Salinity index values of greater than 1.5 are considered to be indicative of seawater influence.

**Table E-3-1**: List of molluscan species and their salinity ranges. Salinity rankings used to weigh mollusk species abundances for calculation of salinity index. Rank  $1.0$  = Freshwater,  $1.5$  = freshwater species with tolerance for low salinity,  $2.0 =$  brackish species,  $2.5 =$  brackish species that tolerate marine conditions,  $3.0 =$ restricted marine with toleration for lower salinity, 4.0 = marine species with tolerance for low salinity, and 5.0 = marine species. Based on descriptions in Ladd 1957; Tabb and Manning 1961; Moore 1964; Turney and Perkins 1972; Abbott 1974; and Thompson 1984.



**Table E-3-2** documents several significant trends. The first is that the further from the Biscayne Bay shoreline, the thinner is the layer of marine-influenced sediments, signifying a shorter period of time spent under the influence of marine depositional processes. This observation fits the general South Florida trend associated with rising sea level. More significantly, the upper portions of cores reflect the changes in water management practices beginning at the turn of the century, with maximum impact in the mid-1960s (Meeder *et al.* 1996). The base of the peaty marls in the Treatment Dwarf site matches data from the late 1960s, when mangroves first colonized the area. The date of the base of the upper mangrove peat increases approaching the shoreline to the date of approximately 4,500  $^{14}C$ years before present (Meeder and Wanless, unpubl. data) at the depth of 265 cm below mean sea level.

<b>TD</b>	<b>DEPTH</b> (cm)	<b>TD</b> 400	<b>DEPTH</b> (cm)	<b>TD DOME</b> EXT.	<b>DEPTH</b> (cm)	<b>TD DOME</b> INT.	<b>DEPTH</b> (cm)
3.875	$\mathbf{1}$	1.5	$\mathbf{1}$	2.125	$\mathbf{1}$	2.125	$\mathbf{1}$
0.1	5	$\overline{\mathbf{3}}$	10	2.5	10	2.5	10
3.55	25	2.45	19	2.5	19	2.5	19
2.625	30	1.857	$20\,$	1.5	$20\,$	1.5	$20\,$
2.3	35	0.1	25	1.5	25	1.5	25
3.5	40	2.75	30	1.5	30	1.5	30
1.375	45	1.5	40	$1.5$	40	1.5	40
1.25	56	1.357	43	1.5	43	1.5	43
1.5	57	1.5	44	1.25	44	1.25	44
1.375	58	1.125	45	1.5	45	1.5	45
0.1	59	1.5	50	1.5	50	1.5	50
1.25	60	1.5	55	$\mathbf{1}$	55	$\mathbf{1}$	55
$\mathbf{1}$	$70\,$	1.334	60	$1.5\,$	60	1.5	60
0.1	75	1.5	65	$\,1$	65	$\mathbf{1}$	65
1.167	77	1.214	68	$\mathbf{1}$	68	$\mathbf{1}$	68
$1.1\,$	79	$\,1$	69	$\,1$	69	$\mathbf{1}$	69
1.5	81	$\mathbf{1}$	75		75		75
0.1	83	1.5	75(b)		75(b)		75(b)
$\mathbf{1}$	85	1.286	76		76		76
0.1	87	$\mathbf{1}$	77		77		77
0.1	89	1.334	80		80		80
$\mathbf{1}$	90	$\mathbf{1}$	85		85		85
$\mathbf{1}$	95	0.1	95		95		95
1.167	98	0.1	100		100		100
1.4375	99						
1	100						

**Table E-3-2**: Vertical soil salinity indices. Bold numbers in depth column are the lowest marine influenced sediments

A second important trend in **Table E-3-2** is an apparent buffering of the soils within the mangrove domes from the progressive salinization evident in the surrounding marsh soils. Under the mangrove domes, the salinity index is lower for the entire soil profile than that of the adjacent dwarf marshes. This is indicative of groundwater actively percolating upward through the karst features, or being wicked upward by capillary action in the peats and organic rich marls of the dome.

## **E-4** *Topography and Soil Thickness***.**

**Topography**. The Treatment Dwarf mangrove basin is a topographic depression (**Figure A-2-1**). The basin has approximately 30 cm of relief across its 250-m length. The lowest point of the basin is approximately 50 m east of the L-31E levee, and is just under 0.3 m in elevation. The toe of the levee provides the western basin boundary. Moving eastward, the elevation rises until mangrove trees of 3 meters in height and continuous peat soils are encountered. At this point, one also encounters the heads of tidal creeks, which permit more rapid water flow.

Soil under the Dwarf basin is thin, usually less than 100 cm thick, and is dominated by marl. Peat is rarely more than 15 cm thick in these areas. Sediment thickness increases from the edge of the dwarf basin (approximately 400 m) toward the coast, where soils may reach 3 m in thickness (**Figure E-4-1**). Basal marl is thin and is replaced by an increasing thickness of mangrove peat towards the coast. The highest surface elevations in the coastal area east of the L-31E levee are found along the coastal fringing mangroves (0.64 m).

**Surface Microtopography**. Several topographic surveys at 30 cm intervals through the Treatment Dwarf mangrove zone show remarkable differences associated with position within the basin. Marsh surfaces close to the basin topographic low have the lowest mean elevation and the greatest standard deviation. The higher the standard deviation, the greater the topographic irregularity. Areas with the highest topographic variability also have the lowest mangrove density, height, and leaf area index (**Table E-4-1**). Mangrove peat soils have the lowest standard deviation from mean elevation (by site).



**Table E-4-1**: Surface relief and macrophyte characteristics in the Treatment Dwarf basin.

**Tree Island Topography**. Tree islands exhibit positive topography and frequently are surrounded by a topographic low area that forms a shallow moat when inundated (**Figure E-4-2**). The difference in surface elevation between the dome interior and adjacent moat is 19 cm, whereas the dome interior is only 8 cm higher than the average marl marsh surface adjacent to the dome. There is usually a few cm of standing water in the moat, even when the adjacent marl soils are dry. Soils in the dome are saturated during most of the year. During the driest parts of the year only the upper few cm become desiccated, while in the lower marl soils, deep desiccation mud cracks develop. Tree island and adjacent surface and bedrock topography comparisons document: 1) dome soils began accreting earlier than adjacent areas, 2) in order to maintain positive topographic relief, mangrove peat production rates must have been more rapid than the rates of marl formation in adjacent areas, and 3) dome soils were influenced by standing water prior to adjacent Dwarf areas, thereby providing substrate for early mangrove colonization.

## **E-5** *Stratigraphy.*

Detailed core descriptions are provided in **Appendix C**.

# **Tree Island Cores**.

# **Core TD Dome:**

Core TD dome 1 is 325 cm long. The top 23 cm is mangrove peat. Below this the core is mostly marl of varying densities and colors. Shell layers are present in the upper third of the core at approximately 33 cm, 139 cm and 143 cm. Sharp color changes can be seen at 124.5 cm where the color goes gray to black towards the top. This probably represents the time when sea level rise was sufficient to maintain reducing soil conditions. Additional color change occurs from gray at the top (146.5 cm) to reddish brown lower in the core (173 cm). The reddish color is from oxidized iron. The first mangrove roots were observed at 184 cm. *Cladium* root material can be seen from base of the core (interwoven in clastic bedrock) to approximately 125 cm depth when mangrove root material dominates.

The bulk density of TD dome 1 generally increases with increasing depth (**Figure E-5-1A**). There is a sharp increase in dry bulk density below the 120 cm depth. This corresponds to a color and composition change from black peaty marl to gray marl. Density is  $0.1 - 0.4$  g/cm<sup>3</sup> prior to this transition and was between 1.0 and 1.5  $g/cm<sup>3</sup>$  afterwards. Wet bulk density also increases gradually with depth (except in the upper 20 cm). Dry bulk densities are approximately  $1.0 \text{ g/cm}^3$  below  $140 \text{ cm}$  in depth (red marl) and wet and dry bulk densities track one another closely.

Bulk analysis showed significant changes between 120 cm and 140 cm depth: 1) total organic material declines from approximately 60% in the upper 120 cm of the core to less than 10% in the central part of the core, where the color is gray (**Figure E-5-1B**). Increases in organic content to about 11-12 % of total sample weight are seen below 144 cm. Organic content remains at this level to the bottom of the core. One sharp peak of organic material (61.2% by weight) is seen at 300 cm depth and is thought to be due to root inclusion in the bottom clastic material. Carbonate trends are reversed. Above 120 cm, carbonate material is 10 % to 20 % by weight. Carbonate content increased between 120 cm and 140 cm to nearly 40% by weight. Below 140 cm carbonate material constituted only about 5 - 10 % of the sample.

**Figure E-5-1C** shows the major constituents of TD dome 1 (mud, amorphous organic, and clastic material). Amorphous organic content declines sharply in the gray region (122 cm - 144 cm) and averages less than 10 %. Gradual increases in amorphous content are seen from 140 cm downward (except in the segment between 270 and 290 cm) and measures 42 % by weight. An increase in mud content is apparent at 120 cm (up to 90 % of total sample weight) and gradually declines thereafter. Sharp declines in mud can be seen below 170 cm in depth where clastic material becomes prevalent. Also present are mangrove roots, which begin at 30 cm depth and continue, despite the small weight proportion, to the bottom of the core. Fibrous material is in abundance in the upper 60 cm of the core but becomes minor thereafter. Plant material was concentrated in the top 30 cm of the core and was totally absent thereafter. Small amounts of shell material were seen corresponding with the peaks in amorphous material.

# **TD Dome Exterior (200 m):**

Core TD Dome Exterior is 107 cm in length, the upper 12 cm of which is peat. Under the peat is a thin brown marl layer, which rapidly grades into gray marl, which continues to bedrock. The gray marl varies in content and color with darker, more organic-rich strata at 56, 81, and 96 cm. The first mangrove roots are observed at 92 cm. *Cladium* rhizomes can be seen to progressively increase in abundance from the center of the core to bedrock.

Dry bulk density is less than 0.1 g/cm<sup>3</sup> in the top 5 cm of the core (**Figure E-5-2A**), and increases to a maximum of about 0.6 g/cm<sup>3</sup>. Wet density is low in the top 5 cm of the core (<0.8 g/cm<sup>3</sup>) and gradually increases to about 1.2  $g/cm<sup>3</sup>$ .

At the very top of the core organic content rises from just over 40% to about 75% by weight. Carbonate content subsequently drops from just over 20 % to less than 10%. Unlike the other cores, this core exhibits only a single reversal, i.e., between 10 and 12 cm, where red-brown peat changes to gray marl. Here organic content declines from just over 75% to 10% or less. Conversely, carbonates increase from less than 10% to about 40% by weight. Bulk contents remain nearly constant throughout the rest of the core (**Figure E-5-2B**)

Constituents by weight percent are also fairly consistent below 12 cm. As seen in **Figure E-5-2C**, fibrous, amorphous and plant material constitute more than 50% of the top 10 cm of the core. Mud constitutes about 90% of the core material thereafter. Amorphous content can be seen to 90 cm depth and is 20% by weight. This core is quite similar to other soil cores sampled in the dwarf basin (see analyses below).

# **TDE 400-m:**

TDE 400 is 400 m east of the L-31E levee. It is similar to the TD Dome Exterior core in composition and color with variations. The top 23 cm is peat. The peat overlies a peaty marl (23 to 36 cm) that in turn overlies a gray marl, that continues to bedrock. The first mangrove root is observed at the depth of 88 cm and increase in abundance slowly upwards until approximately 36 cm where they dominate the soil constituents all the way to the surface. *Cladium* rhizomes are found between 51 cm and the bedrock. Significant shell beds are present at about 70, 76 and 80 cm depth. Also present are small, black, amorphous organic-rich strata at approximately 44, 67, 70 and 81 cm depth. Clastic material is observed from the base of the core to 94 cm.

Wet and dry bulk densities closely track one another down core and differ by only  $0.1$  g/cm<sup>3</sup> at the top of the core and  $0.6$  g/cm<sup>3</sup> at the bottom (**Figure E-5-3A**). Minimum dry densities in the upper 5 cm of the core average between 0.1-0.2 g/cm<sup>3</sup>. Density increases at 16 cm depth to 0.8 g/cm<sup>3</sup>. Dry bulk densities remain fairly constant down core with some minor variations. Dry density is highest at 86 cm depth, where it measures  $\sim$ 1.0 g/cm<sup>3</sup>.

Organic content in the upper 5 cm is 70% by weight. Organic content declines between 5 and 50 cm to between 10 and 20 % (except for peaks at 40 cm and 46 cm). Below 50 cm, organic matter comprises less than 10% by weight with the exception of two peaks at 68 and 100 cm depths, where organic content rises to slightly over 30% (**Figure E-5-3B**). In contrast carbonate content is highest in the bottom 90 cm of the core (30 - 40%) and is low in the top 5 cm ( $\leq$  10%). Constituent analysis shows that the core is dominated by organic material (e.g., aboveground, fibrous and amorphous) in the upper 20 cm, with each constituent being about 20% by weight. Below this, mud increases from 20% to more than 80% by weight. Amorphous material is concentrated at 45, 52, 68 and 78 cm depths, where it rises to maximal values of about 60% each time. Clastic material is found to constitute nearly 50% of the sample at the base of the core (**Figure E-5-3C**).

# **TD 500-m:**

TD 500 is in the distal end of the coastal swamp and is about 150 m from Biscayne Bay and has an overall length of 131 cm. Surface mangrove peats extend downward to 25 cm. The peat grades downwards into a peaty marl, which at 39 cm grades into a gray marl that contains some red mangrove roots, observed to the depth of 113 cm. Sharply delineated black beds of 1-2 cm thickness can be seen at 58, 70 and 106 cm depths. *Cladium* rhizomes are observed from 44.5 cm depth to the base of the core. Below 113 cm *Cladium* is the prevailing root material. As seen in other cores, root material is interwoven in the basal clastic material.

Bulk densities generally increase with depth, though there is a trend in the central 40 cm of the core for density to decrease (**Figure E-5-4A**). An abrupt increase in density is seen at 88 cm. Below this level, density remains nearly constant. In the top 20 cm of the core density measures approximately 0.2 g/cm<sup>3</sup> dry and is about 0.8 g/cm<sup>3</sup> wet. From 20 cm to 45 cm density increases to 0.8 g/cm<sup>3</sup> and 1.7 g/cm<sup>3</sup> respectively. From 45 cm to 85 cm density decreases to an average of 0.2 g/cm<sup>3</sup> dry, and 0.8 g/cm<sup>3</sup> wet. In the bottom part of the core dry density averages  $0.6 \text{ g/cm}^3$  and wet density is 1.1 g/cm<sup>3</sup>.

Numerous reversals in bulk constituents are present throughout the core (**Figure E-5- 4B**). Organic content is dominant between 0 cm and 20 cm depth (except at 5 cm depth), between 56 cm and 80 cm depth, between 98 cm and 102 cm depth and again briefly at 112 cm depth. Percentages of organic material are approximately 70%, 50-60%, 55%, and 40%, respectively. Carbonate material is higher in the intervals between organic layers. Between 20 and 56 cm depth carbonates make up approximately 35% of the sample. Between 80 cm and 98 cm carbonate content rises to about 40%. From 102 cm to 112 cm carbonate content is also about 40% by weight. It should also be noted that carbonate content decreases sharply at the very bottom of the core to less than 10% by weight. Minimum values for both carbonate and organic matter are between 10% and 20%.

Constituent analysis illustrates the reversals described above in terms of fluctuating amounts of amorphous vs. mud percentages (**Figure E-5-4C**). In the high carbonate intervals mud content nears 80%. Conversely, in the regions of organic material concentrations, amorphous, fibrous and rhizomes combined represent about 80% of the sample weight. An interesting feature is that at 65 cm depth a single piece of woody material constituted nearly 60% of the sample by weight. All other aboveground material is present only in the first 25 cm of this core.

### **Horizontal distribution of soil types.**

**East-to-west profile**. The surfacial peat layer of the Dwarf mangrove basin is nearly uniform and follows general surface topography to about 400 m from the L-31E levee. From this point it thickens gradually to the Bay. Peat measures approximately 15 cm in the western end of the basin and thickens to 26 cm by 500 m. The lower surface generally tracks bedrock topography. Marl layers comprise all the material between bedrock and peat, and generally maintain a constant thickness until 500 m, where they also thicken. At 200 m the marl measures 92 cm thick and then narrows to 73 cm as bedrock rises. Between 400 and 500 m the bedrock dips and marl thickens to 105 cm thickness (**Figure E-4-1**). Marl is further divided into peaty-marl and marl. Peaty-marl contains visible amounts of peat within the matrix. These can be seen to thin out in the center of the dwarf basin and in the fringe. The thickness of the peaty marl increases in regions of increased elevation.

**Tree Island**. Surface topography is depressed in the first nine meters of the tree island transect. Over the dome, a mounding of material raises the surface elevation to 2 cm above adjacent marsh (sea level). Bedrock shows the exact reverse trend. Bedrock elevation is highest and uniform under the dwarf and drops considerably under the tree island (**Figure E-4-2, Figure E-5-5**). Measurements of bedrock in the central part of the tree island average 225 cm below sea level. Total soil depth under the tree island is nearly 2.3 m deep and extends laterally almost 8 meters. Total length of the dome is about 18 m across. The tallest mangrove trees are found in the central 8 m, directly above the bedrock depression. Furthermore, tree height decreases more gradually to the south than it does in the northern portions of the transect. This corresponds with the gradual rise of bedrock to the south and sharper rise to the north. Figure E-5-5 shows the relative elevations of the peat, gray marl, red clay, and discontinuous clastic layers in the first 23 m of the transect (from TD exterior to TD dome 1). As shown, the layers increase in thickness in the middle of the dome. Red clay layers are not present anywhere except in the depression under the tree island.

## *E-6 Summary.*

## **Soil types:**

Soils are predominantly comprised of organically produced materials. The two end members are marl (freshwater calcitic mud) and mangrove fibrous peat. These soil types are generally the product of different plant community processes that are, in turn, controlled by different environmental conditions. Marls are produced in calcium carbonate hard waters of no or very low salinities, by the physiochemical processes associated with diurnal water column changes and with periphyton production (Gleason *et al.* 1974). Marl soils contain *Cladium* plant detritus, roots and basal culms, freshwater gastropods and ostracods, sponge spicules, diatoms and pollen.

*Eleocharis* (spikerush) material is also found occasionally but is poorly preserved. Limestone clasts are frequently abundant at the base. Aboveground plant material is rarely present.

Peats at the L-31E site are composed of mangrove root material, amorphous organic material, marl, and skeletal material. They vary in carbonate content considerably depending upon their location and specific site history. In areas of recent mangrove colonization the soils are marls with high organic content because of the root infiltration. The longer the period of mangrove dominance, the more organic-rich and fibrous are the soils. Some peats exhibit a gradation from marl to peats, and such profiles usually include an interval containing both sawgrass and mangrove materials. Mangrove peats usually exhibit a much higher molluscan salinity index (**Section E-3**) than do adjacent marl soils. In the Dwarf mangrove basin the contact between underlying marls and peats is distinct, indicating a rapid increase in salinity during the time when peat production was initiated. Besides salinity, a secondary influence on both plant community and soil is hydroperiod. As sea level rose throughout the Holocene, coastal Florida hydroperiods became longer and longer. Increased hydroperiods may not only favor one plant community over another but the preservation of organic material in the soils.

## **Typical vertical sequence:**

A typical soil profile can be described by basal limestone overlain by a limestone clast zone, grading into freshwater calcitic mud. More organic-rich marl or peat usually overlies the mud. The contact between mud and peat varies from gradual to very abrupt. Typical soil profiles for the tree island and the dwarf basin are distinct, and will therefore be described separately. In either case, these soil profiles document the change from exposed limestone to freshwater medium-hydroperiod marsh, and subsequently to either a longer-hydroperiod marsh or a marine-influenced mangrove swamp.

**Dwarf basin**. A typical soil profile in the Dwarf mangrove dwarf basin is approximately 100 cm in thickness, beginning with an unconformable contact with the limestone bedrock. The basal soils are frequently composed of a thin clast zone that contains a diversity of clast types. The matrix of the clast zone is calcitic mud which continues upward nearly to the surface, where the marl become increasingly organic rich (peaty marl about 10 cm thick). A red mangrove peat, with a thickness less than 12 cm, is formed under mangrove stands in the central part of the basin. In adjacent bare areas, the marl grades upwards into a peaty marl with a thickness of 10 cm. Microtopography is produced by the process of patchy mangrove colonization and concomitant organic soil production, i.e., it is a product of the longterm inland expansion of red mangroves with sea level rise and decreased freshwater runoff (Meeder *et al.* 1996).

Soil profiles vary little within the topographic basin except for the general trend of thinner peat surface layer nearer the basin center. This corresponds very closely to the decreased mangrove density and increased microtopography documented from the margin edge to its center (**Table E-4-1**). These trends indicate increasing marine influence to the dwarf basin. As described earlier, *Cladium* dominance in the bottoms of the Dwarf mangrove sediment cores gave way to mangroves at about 25 cm from the bottom of each core. This stratification is indicative of a transition from fresh water-dominated to marine-influenced vegetation. Marine mollusks can be see in the upper portions of the cores, while those in the lower parts are better adapted to fresh water environments (**Table E-3-2**).

In general, it can be seen that the peat layer at the top of each core increases in thickness approaching the Fringe forest. This is indicative of both higher productivity and a longer duration of mangrove soil accretion. A noticeable change in peat thickness occurs near the transition from dwarf to taller mangrove trees. As sea level rose, mangrove peat accreted with the rising sea level in the nearshore area. During the same interval, the interior basin was still a marl-forming soil environment characterized by lower soil accretion rates. Eventually, a topographic basin developed as a result of this combination.

Reversals in the carbonate and organic matter content and the variable thickness of the organic intervals are indicative of intermittent periods of higher organic production during the Late Holocene. The frequency and thickness of organic rich intervals increases towards the Bay. We conclude that alternating periods of higher and lower productivity are apparent throughout the Holocene, which may correspond to fluctuations in sea level or
climatic factors, especially rainfall. The highly organic tops of each of these cores attests to the more recent transgressive period, a period of increased organic productivity.

**Fringe mangrove**. The soils in the Fringe forest are much thicker, up to 3.1 m thick over limestone bedrock. The clast zone contains a high diversity of clast types and sizes, suggesting transportation. A marl layer is sometimes present. This layer usually is found with *Cladium* fossil material, and frequently grades upwards into a black peat or more organic-rich zone (freshwater peat), before rapidly changing to a red mangrove peat. The red mangrove peat thickness is frequently 200 cm. Thin shell beds may be present throughout the red mangrove section, and constitute evidence of a storm tide deposition of marine material in the coastal mangrove belt.

 **Dome**. Most mangrove tree islands exhibit three characteristics that distinguish them from the surrounding dwarf basin: 1) minor positive relief, 2) far greater soil depths, and 3) accelerated tree growth.

Soils from the cores of the tree islands are distinctly different from the cores of the Dwarf forest. The red mud at the base of each core attests to an oxygen rich environment at the time of deposition. The upward transition in soil color from red to gray carbonate-rich marl indicates a change to anoxic conditions as sea level rose. The general trend is for typical karst dissolution holes to fill with oxidized terrigenous soils that were subject to both aerial exposure and ground water influence. Continued marine transgression caused coastal groundwater levels to rise, making conditions favorable for sawgrass to grow, producing organic-rich marls that grade upwards from grey to black. As sea level continued to rise, mangroves invaded the depressions, which were surrounded by an exposed limestone substrate much like the rocky pinewoods and hammocks of the lower Florida Keys. As marine conditions moved farther west, upland plant communities were replaced by marl prairie vegetation. Hydrologic conditions continued to become wetter with sea level, until the South Florida drainage effort began near the beginning of the twentieth century.

The thicker peat interval at the surface and the positive topographic relief of the dome are a result of the higher productivity of the mangroves in the dome with respect to those in the surrounding dwarf area. Variations in these biogenic soils reflect the close connection between aboveground and belowground productivity, which is preserved in the current soil profiles.

In short, all soil profiles display a transition from freshwater influenced sedimentation processes to saltwater influenced processes. This is a result of combined sea level rise and anthropogenic changes in fresh water delivery (Meeder *et al.* 1996).

#### **Causes and effects of plant community succession (Transgressive model):**

The major difference in soil profile along the E-W gradient in the Treatment block is the increasing thickness and organic content in the surface soil layer towards the east. Throughout the study area, basal sediments are comprised of higher percentages of marl than organic material, and are dominated by freshwater plants and animals. Close to the coast, these freshwater deposits were replaced gradually, while closer to the levee the transition to marine-influenced, organic-rich sediments was very abrupt. With the increased influence of marine conditions, mangroves invaded and soon dominated the vegetation and, consequently, the soil forming processes. As mangroves became dominant, the change from marl to peat formation became the rule. The pattern described above is referred to as marine transgression. Marine transgression is a common occurrence during times of rising sea level (Holocene Transgression), or in areas undergoing subsidence. In the southern Biscayne Bay watershed, the decrease in freshwater sheet flow to the coast also resulted in saltwater encroachment. With less and less freshwater entering into the coastal wetlands, the coastal ecosystems began to become brackish at the turn of the century. By 1928 the coastal mangrove zone, thinner by about one half in comparison to its current extent, began to expand inland rapidly. During the 1960's all sheet flow was eliminated, and conditions became brackish all the way to the base of the L-31E levee. This transgression is marked in the soils by the change in salinity index as presented by fossil mollusks. The contact between the fresh and marine mollusks coincides with the change in soil type from marls to more peaty soils.

**Large scale settings**. The Dwarf mangrove basin has in the past century altered from a coastal freshwater marl-forming environment into a poorly drained red and white mangrove dwarf habitat. Approximately 150 m inland from the shoreline, the surface peat begins to thicken rapidly in the seaward direction. This was the transitional zone between coastal mangrove fringe and freshwater marl prairie at the turn of the century. Our core at 500 meters from the levee (230 m from the shore) is at the eastern lip of the basin, where peat forming processes have formed a surface layer 13 to 18 cm thick. This increased sediment accumulation in respect to the much lower rate in the dwarf basin interior actually produced the topographic basin conditions, resulting in stunted mangrove growth. During the Holocene transgression, the Fringe mangrove forest maintained its position with rising sea level by peat production. The coastal mangroves tend to be much more productive than dwarf mangrove (Lugo  $\&$ Snedaker 1974), whereas the marl formation process is a much slower accretion process. Therefore, a topographic basin was produced by the gradient in soil accretion rates. Interestingly enough, this basin produced by differences in biological sediment forming process rates (rapid accumulation of mangrove peats, slow accumulation of periphyton-associated marls) leads to a condition where the invading mangroves barely maintain themselves in the dwarf habitat.

Sea level rise produced the overall regional condition of marine transgression. However, anthropogenic alterations of freshwater delivery to the coastal system probably instigated the historic change from freshwater marl to marine peat.

**Tree islands**. Habitation by fresh water plants (*Cladium*) began early with roots extending into the oxidized red soils. During marine transgression these plants gave way to mangroves, which were much more tolerant of the increased salinity levels. Soil changes from oxidized iron rich soils (red) to anoxic iron rich soils (yellow) and eventually to gray or black marl show that the area was inundated by water during the Holocene and ultimately came under marine influence. This change from terrigenous soils to biologically induced production and then marine sedimentation clearly indicates that the karst was among the first area in the basin to feel the effects of the rising sea. Simply put, the karst served as a sediment trap when the area was dry. Upon inundation this area was subsequently filled first by oxygen-poor waters, and then by marine waters. The dominant plant species changed from fresh water *Cladium* to marine mangroves. Mangrove trees increase in height with the increased depth of soil and with increased surface elevation. The karst depression permitted more rapid mangrove growth than in the adjacent dwarf areas.

**Change in microtopography**. Mangrove seedlings are transported further inland as a function of the rate of saltwater encroachment (Meeder et. al. 1994). Initial colonization into former freshwater wetlands is patchy. In addition, as more time passes and mangroves move further inland, the fringing mangroves build positive topographic relief. This is because of the greater soil accretion rates of the mangroves. As the dwarf basin continues to develop a productivity gradient becomes established. The center of the basin (lowest elevation with corresponding longest hydroperiods) has 1) the most microtopography, 2) the lowest macrophyte percent cover, 3) the lowest leaf area index, and 4) the lowest macrophyte biomass (**Table E-2-2**). We suggest that throughout time as mangrove percent cover and productivity increases, microtopography decreases and soils become more organic.

**Basal Clast Interpretation**. Basal clasts are divided into two types: limestone lithoclasts and mixed limestone lithoclasts-bioclasts. The two types have different distributions. Limestone lithoclasts are found in bedrock depressions associated with red or tan-to-gray clays. These clasts rarely contain bioclasts or fossils such as mollusk shells. The second type of basal clast zone contains bioclasts, frequently including marine, transitional and freshwater mollusks. These basal clast zones are found in most dwarf mangrove areas. They are usually overlain by brown to tan to black carbonate mud soils, which do not permit upward leakage of fresh water. The composition and distribution of the two types of basal clast zones indicate different origins. The first type may be formed within an overlying soil profile, eliminating the presence of skeletal material. In contrast, the basal clasts found in the Dwarf basin are indicative of long-term exposure at the surface prior to soil development.

## **Section F: Invertebrates**

During the first two sampling periods, both infaunal and epifaunal samples were collected. All infaunal invertebrates caught in a 4 mm mesh sieve were collected. Because only a few nematodes were collected after many hours of labor, infaunal monitoring was discontinued. However, we continued to monitor both marsh surface and arboreal invertebrates. All invertebrates observed within each 0.5 m wide vegetation plot were counted, with a minimal count time of 20 min. Diversity is low and limited to two cerithids (*Cerithidea beattyi* Bequaert and *Batillaria minima* Gmelin), *Melampus coffeus* Linne and rare *Littorina angulifera* Lamarck, the marsh clam (*Cyrenoidea floridana* ), occasional *Brachidontes exustus* Linne, and the crab *Uca* sp. (recognized and counted by fresh burrow count). Arboreal mollusk counts were made in 30 cm height intervals beginning at the marsh surface. Very few mollusks were observed above 1m, except the rare *Littorina*.

*Melampus* was the most abundant mollusk in the Fringe sites and in the relatively heavily-vegetated Control Dwarf sites. *Melampus* was only occasionally found in sites with low vegetation cover and height and long hydroperiods, e.g., TDWW, TDW, and CDW. Except for *Melampus*, highest densities were usually found in late summer or fall, as a result of recruitment associated with higher spring-early summer tides. Very few mollusks other than *Melampus* appear to carry over from one year to the next, based upon their small sizes and lack of mature shell features.

Differences between stations are characterized in **Figures F-1-1** and **F-1-2**. January 1996 data presented in **Figure F-1-1** illustrates several trends: 1) Fiddler crab burrows (*Uca* sp.) and *Melampus* are much more abundant in Fringe sites than in the Dwarf forest ecosystem, 2) Rare *Littorina* and arboreal crabs were only observed in the Fringe forest, 3) Marsh clams are broadly distributed but low in numbers, and 4) Both cerithids are found at low densities throughout the study area, but are statistically much more numerous in both Treatment sites than in either site in the Control block. July-August 1997 data presented in **Figure F-1-2** documents several further trends: 1) *Melampus* were more numerous in summer than in January, and were most abundant in the Fringe sites, 2) *Uca* crab burrows were also more abundant and more common in the Fringe than Dwarf sites, though, uncharacteristically, no *Uca* burrows were found during this sampling period in the Control Fringe, 3) Cerithids changed little in numbers but did change in distribution, and 4) Marsh clams become much more abundant than in January.

Cerithid population density varies little seasonally but does vary from site to site. This variability is probably associated with changes in vegetative cover and periphyton cover, e.g., the less cover, the more periphyton and the more cerithids. *Batillaria*, especially, has the ability to increase in density very quickly with changing conditions, then disappear just as quickly. Marsh clam populations are maintained by larval colonization during spring-early summer high tides. Marsh clams are found in large numbers when very small, but only a few carry over the winter, probably because of soil desiccation during the late winter. Cerithids can handle desiccation better than clams, presumably because the clam is a filter feeder dependent upon water borne food.

*Uca* burrows were never observed at the TD site (**Figure F-1-3**) and were only observed at the CS-E vegetation plot during two sample periods (**Figure F-1-4**). In contrast, both cerithids were more abundant and uniform in TD than CD sites over two seasons of sampling. Marsh clams were found at both TD and CD sites, but are not found regularly in the latter, and are more common sub-block TD, where hydroperiods are longer. *Melampus* are found in low numbers and were not regularly observed during the two years of data presented.

*Uca* burrows are common at both TF (**Figure F-1-5**) and CF (**Figure F-1-6**) sites, and their populations appear to be stable. Cerithids are found at both sites in low numbers, and their populations vary considerably both spatially and temporally. The marsh clam also varies in numbers and distribution, but generally is more abundant at Fringe sites than Dwarf sites (especially CD). The Fringe sites are characterized by an abundance of fiddler crabs and *Melampus*. The *Melampus* population appears stable.

Rehydration of the coastal wetlands will probably result in larger and more uniform populations of most invertebrates, especially those most affected by desiccation events. Water delivery into the system may also shift both vegetation and invertebrates towards freshwater species that are not present east of the L-31E at this time. We predict that decreased salinities will cause an increase in pulmonate gastropods and other freshwater groups such as the *hydrobiids*.

#### **Section G: Algal Community Production and Composition**

#### **G-1.** *Methods.*

**Sites**. A second Control site was added for the periphyton study. This additional site (Block 2) was located in the hydrologic unit immediately north of the Treatment Block (see **Figure A-1-1**). For convenience, in this Section we refer to the three units as Blocks 1, 2, and 4, i.e., the Treatment, Additional Control, and Initial Control blocks, respectively. Periphyton was sampled in Blocks 1, 2 and 4 on a bimonthly basis from May 2000 through May 2002. Stations were located in the dwarf mangrove plots where periphyton was most abundant, at sites WW, W and I in Block 1, W and I in Block 2 and W, I and E in Block 4.

**Periphyton mat biomass**. To measure development and composition of the periphyton mat community on the natural substratum, we removed 15 small cores (each core  $= 3.8 \text{ cm}^2$ ) of benthic material from two locations at each station during bimonthly visits. The 15 cores were composited into a single sample. In the laboratory, samples were placed under a dissecting microscope and large debris (ie., plant material, large shells) were removed from the samples using forceps. The remaining periphyton was homogenized with a blender and subsampled for analysis of dry mass (mass after drying at 100ºC for 2 days), ash-free dry mass (AFDM, mass after drying at 500ºC for 1 hr.), chlorophyll a (extracted in 90% acetone and analyzed flourometrically), species composition (500 cells counted and identified per sample), total carbon and nitrogen (Carlo-Erba ® NA1500 autoanalysis) and total phosphorus (colorimetric analysis after after dry-combusting; Soloranzo and Sharp 1980).

**Periphyton production.** To measure biomass production we incubated 2 sets of 20 glass microscope slides at each station for a period of 2 months. In the laboratory, periphyton was removed from the slides, subsampled for species analysis and dried in a 100ºC oven for estimation of dry biomass. Although we had hoped to measure biomass production in terms of chlorophyll *a* and ash-free dry mass as well, accumulations were minimal and prohibited analyses that rely on larger quantities of material. Lack of appreciable accumulations on microscope slides appeared to be due at least in part to burial by sediment and leaf litter. In February 2001 we altered our production assessment protocol, changing the incubation substrate from glass slides to fine wire-mesh screens that were suspended above the sediment-water interface where periphyton accumulates. Fine rust-proof mesh screening was cut into squares approximately 56 cm<sup>2</sup> and were stretched across a plastic frame. Frames were then suspended just above the sediment-water interface within a larger (30 cm diameter) wire mesh corral that served to keep leaf litter from washing onto the substrate. Two screens were incubated at each station for the same length of time as the glass slides.

#### **G-2.** *Results and Discussion*

**Periphyton mat biomass.**Periphyton mat biomass, measured by dry mass, varied among sites, being highest in the westernmost plot in the mangrove scrub of treatment Block 1 (**Figure G-2-1A**). Besides receiving freshwater pulses, western sites of Block 1 are more open and less shaded by mangrove canopy than the eastern sites. The same pattern is true for Blocks 2 and 4 where shading from the mangrove canopy likely prohibits light penetration to the sediments that would stimulate periphyton growth. However, patterns in AFDM (**Figure G-2-1B**) were dissimilar from dry mass trends, showing increased organic accumulation in eastern portions of each blockand likely due to the contribution of leaf detritus to the cored material. Concentrations of chlorophyll a (**Figure G-2-1C**) were highest in Block 1WW and in Block 4, although these values were highly variable and among-site differences not significantly different*.* 

Mat biomass, measured by dry and AFDM of cored material showed little seasonal pattern (**Figure G-2-2A &B**). This is due partly to the inability to separate the periphyton from marl and benthic detritus.

**Nutrient content.** Concentrations of nutrients in Everglades periphyton mat tissue often provides a highly sensitive index of the quantities of nutrients delivered to the marsh system (Gaiser *et al.* submitted). Consistent patterns were evident in the concentration of P and N in mats in the L-31E marshes (**Figure G-2-1D-F**). Whereas seasonal changes were unclear (**Figure G-2-1C**), control block 2 had significantly less TP in the mat tissue than either Blocks 1 or 4 ( $p$ <0.01). A significant distance effect was detected in Blocks 1 and 4, where TP was lowest in

the western sites and increased eastward, a pattern observed in other coastal mangrove wetlands (Chen and Twilley 1999). Actual concentrations of TP in periphyton tissue were somewhat higher than measured for adjacent unenriched freshwater marsh (200-400 vs. 100-200 µg g<sup>-1</sup>, respectively; Gaiser *et al.* (submitted)). However, the N:P ratio in this study ranged from 80-120 (**Figure G-2-1F**), indicating P limitation throughout all sites, even though Block 1 had a significantly lower ratio than Blocks 2 or 4 (**Figure G-2-1H**).

**Periphyton production.** Periphyton production differed among sites, with treatment Block 1WW showing consistently greater accumulations than other blocks  $(p<0.01$ ; **Figure G-2-3A & B**). Accumulations were highest in the westernmost stations close to freshwater inputs. These patterns are likely due to a combination of water quality (i.e., conductivity, nutrient availability) and light availability. Low productivity easternmost sites (i.e., Block 1 I) was likely a result of the dense canopy of dwarf mangrove that prevents light penetration to the sediments where periphyton is most likely to grow. A shading effect was also evident in Block 4 where the mangrove canopy was dense and periphyton production low until leaf loss from the winter frost increased light penetration to the sediments. Recent periphyton production estimates from these sites suggest an increase due to the disappearance of this canopy.

Production on microscope slides was generally low during all visits and seasonal patterns were unclear (**Figure G-2-3C & D**). Accumulations on artificial screens were much higher than on glass slides, even during spring months when periphyton is typically least productive.

**Taxonomic Composition***.*A total of 358 diatom taxa representing 62 genera have been identified from material collected from the L-31E wetlands (**Appendix D**). The diatom flora of the L-31E wetlands includes both fresh- and saltwater taxa and overlaps considerably with the flora determined by Ross *et al.* (2002) from the Turkey Point basin approximately 10 km south of these sites. In addition, 34 taxa are commonly found in the freshwater Everglades (Gaiser *et al.*, submitted). However, the remaining taxa are part of a marine benthic flora that has been poorly documented taxonomically. Although we have gathered most of the relevant taxonomic literature pertaining to this flora, a large number of specimens from our samples remain unidentifiable. These taxa have been assigned species codes and have been archived in the diatom herbarium at FIU.

After deleting rare and infrequent taxa from the data-set  $(<0.1\%$  mean relative abundance;  $<2\%$  of samples), non-metric multidimensional scaling ordination was used to determine patterns in diatom distribution among sites. We used the Bray-Curtis dissimilarity metric to measure site differences based on taxon relative abundances and found a minimal-stress solution having 2 dimensions (**Figure G-2-4**). Each block had a unique taxonomic composition that was clearly denoted in the ordination. Of the environmental variables (conductivity, periphyton TP, TN, TC, N:P, water depth) only conductivity and N:P had significant correlation with the distribution of sites in the 2-d space  $(r^2 = 0.24$  and 0.58, respectively). Sites within Block 1 sorted by location and there was very little overlap among locality groups.

To determine the diatom taxa driving differences among sites illustrated in the ordination, taxa were first assigned to salinity preference categories (brackish, marine, freshwater) that were gathered from the literature (Hustedt 1930, 1927-1966; Krammer & Lange-Bertalot 1986-1997; Patrick & Reimer 1966, 1975; Van der Werff 1957; Van der Werff & Huls 1957-1974; **Appendix D**). Taxa without defined preferences were deleted from this analysis. The number of taxa in each preference category were summed within each block and location, and plotted in **Figure G-2-5**. Treatment Block 1 had the highest number of freshwater taxa, increasing in number toward the L-31E canal and decreasing toward the coast. Block 4 had the fewest number of freshwater taxa, indicating a persistent elevation in salinity, at least in periphyton porewater at these sites. The increase in freshwater taxa in the Treatment Block indicates an ecological effect of increased freshwater flows, suggesting that freshwater diatom taxa will perform well as early indicators of changes in water delivery.

#### **Section H: Benthic Community**

The results of the nearshore Biscayne Bay benthic community analysis was previously reported (Alvord 1998, Meeder *et al.* 1997). Below we summarize the significant results of that analysis, and their implications in respect to water management.

#### **H-1.** *Identification and distribution of nearshore benthic communities.*

Three macroalgae/seagrass zones were identified in the stretch of Biscayne Bay nearshore waters between Mowry and Military Canal, extending from the shoreline to 800m offshore (**Figure H-1-1**). *Halodule wrightii* was dominant near the coast, with *Penicillus capitatus* and then *Thalassia testudinum* becoming dominant with increasing distance from shore.

Using K-means clustering and the Twinspan classification procedures, we assigned each sample plot to one of three groups, roughly equivalent to the three zones suggested by the dominant plants cited above. The cluster analysis also suggested an additional group, which lacked a single dominant species. Sites assigned to this heterogeneous fourth group were inspected individually and assigned to one of the three major groups. Overall, there were approximately 40 plots in the *H. wrightii* group, 100 plots in the *P. capitatus* group and 45 in the *T. testudinum* group. There were some discrepancies between cluster analysis assignments and those suggested by the Twinspan procedure; for the most part these involved plots with no dominant species. *H. wrightii* was found to dominate the inshore community until approximately 200m offshore. *P. capitatus* dominates the area between 200- 600 m and the *T. testudinum* community is the most prominent 600-800m offshore. Locations of the long-term plots were chosen on the basis of these results, with each community type well-represented along three different transects.

#### **H-2.** *Biomass and productivity***.**

**Spatial patterns.** Neither the *H. wrightii* plots nor the *T. testudinum* plots showed a north-south difference in either biomass or productivity (**Figure H-2-1A & B**, **H-2-2a & B**). We had expected a north-south difference in the productivity of both seagrass species, with Transect 2 most impacted by high nutrient load associated with reestablished freshwater sheetflow and/or Mowry Canal outflow. Impact on the plant species from nutrient loading associated with these two sources was not documented. Results from our groundwater study (**Section B-2**) suggest that nutrient loads to nearshore Biscayne Bay from this source are high. This might imply that surface water nutrients may not be readily accessible for higher plants, but are sequestered immediately by phytoplankton and filamentous algae. In contrast, nutrients from groundwater may be more easily assimilated by rooted vegetation. The effect of groundwater as a source of nutrients in the nearshore area would tend to mask any north-south pattern associated with increased surface water discharge.

Groundwater influence can increase biomass and productivity of benthic algae and seagrass, and cause benthic zonation (Johannes, 1980 & Herrera-Silveria, 1994). The primary source of nutrients for seagrass is surface sediments, and sediment nutrient availability may have a direct effect on which seagrass species dominates (Short 1985; Fourqurean *et al.* 1995; Williams, 1987). The high groundwater nutrient load in the inshore vegetation zone may explain the dominance of *H. wrightii*. Fourqurean et al (1995) found that *H. wrightii* outcompetes *T. testudinum* in Florida Bay when nutrient availability increases. About 30 years ago, Kohout and Kolipinski (1967) documented the dominance of *T. testudinum* within 300 m of shore just north of the L-31E study area. At present, however, *T. testudinum* does not become abundant until 600m offshore. Our groundwater data indicates very little groundwater discharge beyond 400 m (**Section D-2**). The relative lack of *T. testudinum* inshore may be a response to a decline in coastal water quality parameters, which may increase nutrient loads and algal blooms.

A north-south difference was also not apparent in *P. capitatus*. Again, this may be a result of groundwater nutrient sources, because the *P. capitatus* sites were all between 300-425 meters from shore, which is still in the zone where groundwater discharge is present.

Seasonality. Based on the published literature, we expected a seasonal influence on seagrass growth, with highest growth rates in summer (Tomasko and Dawes, 1990; Barber and Behrens, 1985). In our studies, strong seasonality was documented for one of the major seagrass species, but not the second. *T. testudinum* growth was strongly seasonal (**Figure H-2-2A & B**), with productivity rates 58% higher and the biomass 72% higher in July than in February. Our measured productivity rates and biomass were similar to those reported for *T. testudinum* in Florida Bay (Tomasko and Lapointe, 1991). Unlike *T. testudinum*, *H. wrightii* did not show the expected seasonal trend (**Figure H-2-1A & B**). No seasonal difference was present in new leaf growth and the biomass actually decreased in the summer.

*H. wrightii* is reported to be dominant in areas close to a strong source of phosphorus, and *T. testudinum* is dominant further from the nutrient source (Powell *et al.* 1991; Forqurean *et al.* 1992a). *H. wrightii* is less efficient at utilizing nutrients when availability is low and has a much higher demand for sediment nutrients than *T. testudinum* (Fourqurean et al 1992b). *H. wrightii* is dominant in the inshore areas where salinities are lower and nutrient concentrations higher than further offshore.

The inshore nutrient load also encourages the growth of filamentous algae. In the summer, when the nutrient load increases, cover of filamentous algae increases to almost 100%, smothering the *H. wrightii* beds, and inhibiting growth (**Figure H-2-3**). This increased algal cover may explain the lack of seasonality in *H. wrightii* biomass and growth rate.

The *P. capitatus-*dominated macroalgae community likewise did not exhibit a seasonal difference. There was no significant difference between the biomass in February, March, and July, though biomass did drop in July. This drop might also be associated with increased algal cover. Filamentous algal cover increased from 38% in December to 60% in August in the *P. capitatus* zone. There was a significant difference in length measurements of *P. capitatus* among the three sampling periods, but the lengths decreased in July instead of increasing as expected.

Neither the Mowry Canal nor freshwater sheetflow in the experimental site had much of an effect on the biomass and productivity of the nearshore benthic communities. Instead, groundwater had the greatest effect on benthic communities. Groundwater flow is presumably evenly distributed in the inshore area, masking any northsouth trend during the period sampled. The expected summer increase in biomass and productivity was only apparent in the *T. testudinum* community. The *H. wrightii* and *P. capitatus* communities did not show this summer increase in either biomass or productivity. This is probably due to the increase of filamentous algal cover in the nearshore environments, which smothers the seagrass and inhibits its growth.

# **Conclusions and Recommendations**

#### **Conclusions:**

The purpose of the L-31E freshwater rediversion study was to document the ecological effects of re-establishing sheet flow through coastal wetlands. The treatment was expected to increase the volume of water and the load of nutrients delivered to the mangrove swamp and associated nearshore environments. Increased volume was expected to increase swamp hydroperiod while decreasing salinity, and elevated nutrient loading was expected to increase the ecosystem productivity. It is important to understand the implications of these changes before extending the scope of hydrologic restoration elsewhere along the coast of southern Biscayne Bay. The major findings of the study and their implications are summarized below.

#### **1. Biogeochemistry and Nutrient Dynamics**

- In the L-31E study area, Delivery Canal and adjacent Biscayne Bay waters had low levels of dissolved organic carbon, total phosphorus, total nitrogen, and NH3-N, and also were not polluted by heavy metals (copper, lead, zinc, and iron).
- In the mangroves, among-sites differences in water quality were attributable to topographic variation and distance from the coast, which modified the effects of various water sources. For examples, coastal Fringe forests, which are under more tidal influence, had 5-7 times greater pore water phosphorus than the interior Dwarf forests.
- Tidal influence on water quality was noticeable in both the Control and Treatment Fringe forests, where freshwater treatment had no effect. Pore water salinity increased while TN and TP significantly decreased over the study period.
- In the poorly drained Treatment Fringe, a decrease in pore water TN and TP was associated with an increase in physiological stress, as evidenced by a significant change in  $\delta^{13}$ C. However, this effect was not accompanied by a significant change in phosphorus content or N:P ratio in leaves.
- In the Fringe forests, the steady decrease in pore water nitrogen and phosphorus over the course of the study may have been due to the fact that sites were recovering from an earlier disturbance, perhaps Hurricane Andrew, that might have caused a temporary increase in pore water nutrients.
- In Biscayne Bay water, a strong pattern of increasing salinity and decreasing nitrogen concentration indicated that the volume of nitrogen-rich freshwater reaching the Bay, presumably through the Mowry and Military Canals, has probably decreased during the study period.
- There were no significant effects of freshwater delivery on surface and pore water quality in the Dwarf Forests at least during the study period, probably because the volume of freshwater was inadequate or the treatment was not extended far enough into the dry season to bring the significant changes in water quality.

### **2. Vegetation structure and production**

- The vegetation in the L-31E study area has changed considerably during the  $2<sup>nd</sup>$  half of the  $20<sup>th</sup>$  century. Tall mangrove forest has widened interiorward, and dwarf mangrove forest has replaced mixed graminoid marsh. The L-31E levee accelerated the process of the transition from open marsh to mangrove scrub by intercepting freshwater sheetflow.
- Spatial and temporal variation in vegetation structure and production over the study period were strongly influenced by Hurricane Andrew (August 1992), and two freezes (Jan 1996 and 2001). Their effects on vegetation represent an unavoidable complication in interpreting vegetation responses to the L-31E rediversion experiment.
- Hurricane Andrew caused extensive mortality and canopy damage in the Fringe forests, but had minimal effects in Dwarf mangroves probably because the low  $(1 \text{ m})$  tree canopy that prevailed in most of the zone in the later was submerged during the period of highest winds. Conversely, the two freeze events weighed heavily on the Dwarf forest, but did not penetrate the tall mangroves.
- The direct effects of the two disturbances were similar in being concentrated on the upper canopy strata of the impacted forests, and in both disturbances, the concentration of mortality among dominant individuals (1) released previously suppressed "advance regeneration", and (2) stimulated the establishment and development of new stems of seedling origin.
- Seedling recruitment and performance after these disturbances differed among sites and species. In the Fringe forests, new seedling regeneration was the primary source of stems for the developing canopy following the hurricane, while in the Dwarf forest, a dense, mixed-species cohort of advance regeneration was the first to take advantage of the resources made available when most stems in the canopy were freezekilled.
- Initial size of stems was important for subsequent growth in the early stages of recovery following Hurricane Andrew. As a result, the more productive Control Fringe forest reached the *competitive exclusion* stage of development more quickly than the less productive Treatment Fringe site.
- The relative stand growth patterns in the tree islands were closely related to underlying geomorphologic variables than to recent changes in hydrologic regime.
- Differences in biomass production between Fringe forests and tree islands in the Dwarf forests were affected by inherent site productivity, but also by differences in developmental stage occasioned by idiosyncratic responses to Hurricane Andrew.
- Incidences of salt stress were infrequent in the study area, and moisture stress was not responsible for the differences in Fringe and Dwarf forest productivity.
- Neither seedling establishment nor growth or survival of mangroves was influenced by the hydrologic treatment. This suggests that mangrove populations were insensitive to fresh water delivery, at least at the level of the individual plant. Instead, site productivity and disturbance history had discernible influences on population dynamics in a naturally developing mangrove.
- The lack of response to treatment observed in vegetation structural development and production may be because volume of water was either not sufficient or the treatment was not properly timed to alter the competitive balance within the resident Dwarf mangrove community.
- It is possible that year round freshwater delivery applied over a longer time frame may eventually bring significant changes in the habitat quality, and would allow for the further establishment of freshwater graminoid species.

# **3. Hydrology**

- Hydrology of the Dwarf mangrove forests in the study area represented the relative contributions of tidal events, freshwater delivery, canal water seepage, and precipitation.
- In the Treatment Dwarf, freshwater delivery has noticeable effects on the salinity and conductivity of surface water during the wet season, but the zone of influence was relatively narrow, thereby confounding these effects with the effects of freshwater input due to canal seepage.
- Seepage from adjacent canals is an important water source in current mangrove forests in the study area, and water delivery that is restricted to high canal stages is likely to play only a minor role in the hydrologic budget of these basins
- **4. Soils** 
	- Sediment profiles in the L-31E study include basal limestone overlain by a limestone clast zone, grading into freshwater calcitic mud, which is overlain by organic-rich marl or mangrove peat of varying thickness.
	- The peat layer at the top increases in thickness towards the coast. This pattern is probably due to both higher productivity and a longer duration of mangrove soil accretion in Fringe forests than in interior sites.
	- Decreased soil accretion rates from the coast towards the  $L-31E$  levee resulted in the development of a topographic basin where the invading mangroves maintained themselves in the Dwarf habitat.
	- In the Dwarf mangroves, the presence of *Cladium* roots and freshwater adapted mollusks near the base of the soils, and their gradual replacement by mangrove roots and marine mollusks, respectively, in the upper portions of the cores was strong evidence of a transition from fresh water-dominated to marine-influenced vegetation.
	- Replacement of freshwater vegetation by mangroves was associated with a change in soils from marl to peat formation, a pattern referred to as 'marine transgression'.
	- Marine transgression that occurred during the Holocene period due to sea level rise, contributed to in recent years by the elimination of freshwater sheet flow, was marked in the soils by a change in salinity index as presented by fossil mollusks.
	- As sea level rose, karst depressions in present basin settings were the first to be colonized by wetland species, e.g., *Cladium*. Later, *mangroves replaced Cladium* during marine transgression. The peaty marl soil formed from the growth of mangroves accelerated mangrove growth in comparison to adjacent dwarf areas, resulting into the formation of mangrove tree islands.
	- We hypothesize that the lower salinity index throughout the entire tree island soil profile in comparison to adjacent dwarf marsh soils may have resulted from the upwelling of groundwater through the karst, organic rich marls, and peats of the dome.

# **5. Invertebrates**

- Epifaunal invertebrate diversity in mangroves was relatively low and limited to 7 species.
- Invertebrate distribution and populations were related to hydroperiod, seasonal tides and vegetation cover.
- Rehydration of the coastal wetlands through year round freshwater sheet flow will probably result in larger and more uniform populations of most invertebrates, especially those most affected by desiccation events.
- Increase in populations of pulmonate gastropods and other freshwater groups such as the *hydrobiids* may serve as useful indictors of decreased salinity associated with freshwater delivery.

### **6. Periphyton**

- Periphyton cover and production were negatively related to the percent of vegetation cover and distance to the L-31E levee.
- Freshwater delivery had significant effects on periphyton production, as the periphyton mat production in the western plots of the Treatment Dwarf were significantly higher than in other Control and Treatment Dwarf plots.
- Higher number of freshwater diatom taxa in the plots near the L-31E canal in the Treatment block than in other plots also may be due to freshwater input through experimental delivery, possibly accentuated by canal seepage.
- Periphyton productivity and the relative abundance of freshwater diatom taxa can be considered as reliable indicators of changes in site characteristics due to freshwater delivery from the canal.

### **7. Nearshore benthic communities**

- Freshwater sheetflow in the experimental site had no significant effects on the biomass and productivity of the nearshore benthic communities. Instead, benthic sea grass community zonation, structure and production in the Biscayne Bay were mainly associated with nutrient loads in upwelling ground water.
- Groundwater flow is presumably evenly distributed in the inshore area, masking any north-south gradients in seagrass productivity in nearshore communities.
- Seasonality in productivity was only apparent in the *Thalasia testudinum* community, in the nearshore *Halodule wrightii* and *Penicillus capitatus* communities; seasonality was masked by growth of filamentous algae.
- Distribution and cover of marine algae appears to be related to Mowry Canal discharges. Therefore, an increase in nutrient loads in surface water through direct discharge from the canals will ultimately decrease sea grass biomass production. Nutrients associated with greater volume of freshwater sheet flow through the mangroves will probably be delivered in organic forms, which will have a different effect on nearshore ecosystems.

In the L-31E study area, background topographic variation, human modifications of drainage patterns or topography (e.g., roads, ditches, and canals), and natural disturbances (hurricanes and freezes) are the most important forces maintaining habitat variability in the mangroves along the coast of southern Biscayne Bay. Their effects on ecosystem processes present unavoidable complications in interpreting results of the freshwater delivery experiment, whose effects were limited, altering water salinity, periphyton productivity and freshwater diatom populations within a narrow zone near L-31E levee. Experimental freshwater delivery did not affect hydrology and nutrient loads in the basin water to an extent that would translate into a significant change in vegetation structure and production, probably because the volume of water was either not sufficient or the period of the treatment was not adequate. Therefore, year-round freshwater discharges in greater volume may eventually restore hydrology and bring significant changes in the habitat quality in the mangroves and adjacent bay waters.

#### **Recommendations:**

#### **Extend the timing of freshwater delivery**

Over the period of our treatment, water was delivered only during the wet season, when water level was already high in the basin. Biological responses to this delivery regime were restricted to a relatively narrow zone close to the delivery point. Therefore, if the objective is to change the nature of the Dwarf forest ecosystem, timing of freshwater delivery should be extended into the winter and spring. This would require actively pumping water into the basin or raising the water level in the canal during those times of year.

### **Prioritize the areas to be restored**

The purpose of freshwater rediversion is to restore the hydrology in the mangrove basins and to slow down the development of mangroves that have encroached in mixed-prairie vegetation. Our results suggest that the effects of rediversion are far more likely to be discernible in areas that still retain graminoids as major components of the vegetation. Therefore, future rediversion efforts whose objective is restoration of coastal marshes should focus on such basins, several of which are present north of the Pilot Project sites, within the Biscayne Bay Coastal Wetland (BBCW) project area.

#### **Increase the connectivity among blocks**

Decompartmentalization is important for the hydrology of the mangrove forests of BBCW, especially to provide a more even distribution of fresh water delivered into the recipient basins. At present, the east-west running ditches and canals in the mangroves divide the habitat into several blocks. When freshwater level in a basin is high due to diverted water or rainfall events, the ditches accelerate the drainage of water to the bay and disrupt the desired sheet flow. In cases of low water level in the basin, the ditches allow saltwater to enter the basin easily, thereby negating the effects of freshwater and promoting the growth of mangrove and exotic vegetation bordering the ditches. Moreover, a theme running through all of our results is that the ditches and canals that partition the wetland create smaller, artificial units with independent microclimatic, biotic, and hydrologic characteristics. To restore the BBCW as a functioning wetland, it is important to restore as much as possible the connectivity that existed in the pre-drainage ecosystem. Degrading the functionality of these ditches by partially or completely filling them should be one element in the restoration of the ecosystem.

#### **Consider rehydrating the mangroves via the major east-west canals**

Though not to be taken lightly, the possible placement of culverts east of the S-20F, G, and H structures to initiate controlled flooding of the Fringe mangrove forest should be considered. Properly designed, the project has the potential to improve water quality in the nearshore zone and expand the zone of tall forest, thereby providing more habitat variability and enhancing biological values. Any such actions depend on site-specific data and a more thorough understanding of the hydrology and physiography in the current forests adjacent to the canals.

#### **Reduce anthropogenic impact on mangroves**

As currently implemented, public access to Biscayne Bay and the adjacent mangroves forest via the Mowry Canal roads is entirely unmanaged, with sub-optimal results for both the ecosystem and its users. The development of a management plan that integrates recreational use, education, and ecosystem values is an important early step in restoring these coastal ecosystems. Management will not be cost-free, and should perhaps include some restrictions on public access. Procedures should be established to monitor and mitigate the environmental impacts that recreational users have on the mangrove forests and the bay at these access points. Mechanisms for cleaning and maintaining the access points to Biscayne Bay should be put in place.

#### **Establish long-term monitoring programs**

- Management activities in the area should be tied to a long-term monitoring program that would include climatic, hydrologic, biological, and water quality elements. To assess freshwater diversion effects, use should be made of a well-selected set of small, permanent plots, distributed among major community types already mapped in this project and related studies in the BBCW.
- Our hydrologic and biological data document that mangrove ecosystems in the L-31E area rely on seawater, rainfall, ground water, canal water seepage and diverted freshwater from the canal for hydrological subsistence, nutrients and sediments. However, determining the relative contribution of these source waters and their variability through time and space is a complex problem that requires more data and modeling expertise than could be provided in the Pilot Project. We recommend that such a study on hydrological regime be initiated, utilizing both a dense network of water level recorders and chemical signatures using hydrologic tracers.
- In Biscayne Bay water, our results show that salinity has increased, while total nitrogen and phosphorus has decreased over the study period. One possible reason for these changes is a decrease in the volume of freshwater delivered to the Bay from the canals. A monitoring program that quantifies the volume of water entering Biscayne Bay via the Mowry and Military Canals, as well as by ground water sources, is critical in interpreting ecological changes in the nearshore environment.
- Our results strongly suggest that several biotic populations and/or communities can be used effectively as bio-indicators of change in physical environments of the coastal area. In L-31E mangroves and adjacent bay waters, the relative abundance of diatoms, gastropods, freshwater graminoids, wading birds, and sea grass and filamentous algal communities are good indicators of temporal changes in the physical variables induced by rediversion of freshwater from the canal. Long-term monitoring of changes in these bioindicators will be helpful in assessing restoration efforts.

## **Acknowledgements**

The primary source of funding for the L-31E project has been the South Florida Water Management District (Contract C-12409). Financial support for the benthic monitoring was provided by the National Park Service, and the groundwater studies were done in collaboration with the U.S. Geological Survey. Gene Shinn (USGS) deserves special mention for installing the Biscayne Bay groundwater wells. The L-31E project was originally conceived at least a decade ago; Dewey Worth (SFWMD) and Richard Curry (BNP) were among those involved in the initial stages. Sarah Bellmund's (BNP) help was critical in ensuring that the project reached completion. And most importantly, the project would never have gotten off the ground or achieved what it has without the consistent efforts of Rick Alleman (SFWMD). We thank the staff of Biscayne National Park for allowing us to work efficiently within the Park boundaries. At FIU, we have enjoyed great support from the personnel in the Stable Isotope Laboratory, SERC Water Chemistry labs and the Periphyton Lab, specifically William Anderson, Pete Lorenzo and Franco Tobias, respectively. Many thanks to Dr. Leonel da Silveira Lobo Sternberg at the University of Miami. Others who made outstanding contributions to the work described above were Paulo van Breugel, Luz Romero, Diane Thurman, Anna Maria Rodriguez, Amanda Bern, and the too-numerous-to-name group of graduate students and other interested folks who helped on the two diurnal sampling periods for the flux study.

#### *Appendix A -* **The Seasonality and Survival of New Germinants**

**Germinant seasonality.** Counts of newly germinated seedlings were conducted in December/January and April/May of 1996 and 1997 in all fifteen plots. In analyzing total germinant densities censused independently in winter v. spring, it should be recognized that germination of new individuals and survival of old ones may be confounded.

We first analyzed the effect of seasonality without consideration of site interactions, i.e., across all four subblocks. In this analysis, neither *L. racemosa*, *R. mangle*, nor *A. germinans* demonstrated seasonal differences in germinant density (t=1.867, p=0.0728, df=27; t=0.140, p=0.890, df=27; t=0.827, p=0.416; df=27; respectively). Closer analysis of block and season interactions in the Fringe forest revealed that the Control Fringe had a greater abundance of *L. racemosa* germinants in winter when compared to Treatment fringe summer, Treatment Fringe winter, and Control Fringe summer ( $F_{0.05,22}=5.432$ , p=0.006). However, this difference appears to be a product of extremely high densities of *L. racemosa* germinants in the Control Fringe plots during a single winter census. In winter 1996 *L. racemosa* germinant densities were ca. 5x10<sup>5</sup> germinants per hectare, with Treatment or Control germinant densities ranging from ca.  $6x10^4$  to  $1x10^5$  germinants per hectare in other seasons and/or years.

*A. germinans* demonstrated no effects of season ( $t=0.827$ ,  $p=0.416$ ,  $df=27$ ), forest type ( $F_{0.05,27}=0.827$ ,  $p=0.416$ ), forest type by season ( $F_{0.05,26}=0.827$ , p=0.416), and plot by season ( $F_{0.05,22}=0.098$ , p=0.961) on germination. This result is at least in part due to the relatively small *A. germinans* dataset, as this species was rarely present as a germinant in any subplot. To confidently determine if there are any effects of season on *A. germinans* germination, further seasonal germination censuses would need to be conducted over larger subplots within the blocks to enumerate larger numbers of *A. germinans* germinants during each sampling period.

In conclusion, since we observed either maximal germinant numbers during winter or no seasonality, we can be confident that our germinant counts in December and/or January 1998-2000 were conducted at or near the time of peak germinant density. While these numbers can provide only a minimum estimate of total germination during the year, they may be used to provide an index of successful seedling establishment.

**Germinant success.** Based on the above data, we calculated *germinant success* as the ratio of enumerated germinants of one year to the successive year's newly tagged seedlings, multiplied by 100. The germinant years analyzed were 1996 to 2000, inclusive. As suggested above, In some cases a seedling might have germinated after the census, yet met the criteria of the seedling category by the time of the following census. Therefore, the following results must be interpreted with caution.

First, we explored annual variation in germinant success for each species and forest type. *R. mangle* demonstrated no difference among years in either the Fringe or Dwarf plots ( $F_{0.05,35}=0.738$ , p=0.572;  $F_{0.05,30}=0.602$ , p=0.664, respectively), whereas *L. racemosa* demonstrated significant annual variation in germinant success in both Fringe and Dwarf plots  $(F_{0.05,35}=3.516, p=0.016; F_{0.05,30}=2.800, p=0.044,$  respectively). In conducting post-hoc Bonferonni comparisons, the success of *L. racemosa* germinants was higher in 1996 than in either 1999 or 2000 within the Fringe forest (**Table A-1**). In the Dwarf forest, similar analyses revealed that *L. racemosa* success was lowest early in the study period, with rates in 1996 and 1997 significantly lower than in 1998 or 2000 (**Table A-1**). This reduced reproductive output in 1996 and 1997 may be a result of the freeze experienced by the Control Dwarf in early 1996, and 1998 and 2000 are demonstrating the reproductive outputs of more typical, undisturbed years. To determine the validity of this assumption, more focused analyses of freeze effects are needed.

Considering the Fringe forests, greater *L. racemosa* success rates in earlier years is not surprising (**Table A-1**). The six-year period of study has been one of steady recovery of canopy volume following Hurricane Andrew (**Figure A-1**). If canopy volume can be used as a surrogate for light extinction, these data suggest that germinants received lower levels of photosynthetically active radiation in later years, and as a result may have been shade stressed and less successful at becoming established.

			Year				
		Sub-block	1996	1997	1998	1999	2000
Freeze Effects	Frozen	<b>CSE</b>	95.7	100	100	$\theta$	100
		<b>CSI</b>	59.6	$\overline{0}$	100	100	100
	Unfrozen	TSE	39.3	33.3	100	100	100
		TSI	76	50	100	$\theta$	71.4
Freshwater Rediversion	Delivery	<b>TSW</b>	90.9	71.4	100	100	100
		<b>TSWW</b>	71.4	100	100	100	100
	Control	<b>CSW</b>	67.5	$\theta$	33.3	100	100
		<b>CFE</b>	$\theta$	$\theta$	$\Omega$	$\theta$	0
Hydroperiod and Elevation	High	<b>CFI</b>	$\theta$	$\theta$	$\Omega$	$\Omega$	0
	Elevation	<b>CFS</b>	78.3	23.9	$\Omega$	9.1	$\theta$
		<b>CFW</b>	7.7	$\overline{0}$	2.5	2	$\overline{0}$
		TFE	$\overline{0}$	$\overline{0}$	$\Omega$	$\Omega$	$\overline{0}$
	Low	TFI	51.4	50	12.5	$\theta$	10
	Elevation	<b>TFS</b>	24.6	33.3	4.3	$\theta$	$\theta$
		<b>TFW</b>	85.7	$\theta$	20	$\theta$	$\boldsymbol{0}$

**Table A-1:** *L. racemosa* annual seedling establishment percentages for each examined environmental factor

To examine if there are differences in germinant success between mangrove species, seedling establishment percentages for each species were pooled across all years. *R. mangle* and *L. racemosa* exhibited different success rates (F<sub>0.05,148</sub>=21.841, p=0.000), with *R. mangle* having higher success. Until *R. mangle* seedlings reach the two leaf stage, respiration rates are higher than photosynthesis rates (Lugo and Snedaker 1975). Thus, to support a seedling until such a well developed stage, *R. mangle* propagules must represent a significant energetic investment. They are produced in small numbers when compared with *L. racemosa* seeds, which are considerably smaller and produced in vast quantities by reproductively active plants. As a result, when the larger *R. mangle* propagules germinate they may be better supplied by nutritional reserves than the *L. racemosa* germinants, and thus more likely to survive the stress of becoming established.

# *Appendix B – Mangrove Biomass Regression Equations*

Intercept and slope coefficients ( $b_0$  and  $b_1$ , respectively) of regressions used to predict total, stem, branch, and leaf biomass (in grams dry weight) of individual mangrove trees from stem diameter (in mm) 30 cm above the ground  $(D_{30})$ . Equations are applicable to a range of sizes up to seven meters in height. Equations are of the form Ln(biomass component)= $b_0 + b_1 \cdot Ln(D_{30})$ .



# *Appendix C - Core Descriptions*

*Core description start at the base of the core* 





# **TD Dome 2:**





# **TD Dome Intermediate:**



209.5 cm Top layer. Large quantities of leaves, stems, rootlets, twigs, etc., are present interwoven in peat. Color and density of material is the same as written prior.

## **TD Dome Exterior:**





# **TDE 400-m:**





# **Transect Core T 500 A/B:**







129.0 - 13 1.0 cm Detritus is present in this region including stem, leaf and root debris and is all black colored.

# *Appendix D – Diatom Taxa of the Biscayne Bay Coastal Wetlands*

Diatom taxa collected from blocks 1, 2 and 4 in the Biscayne Coastal Wetlands shown with salinity preferences gathered from the literature (M=marine, B=brackish, F=freshwater).

















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