ESTIMATING PRIMARY PRODUCTIVITY OF RED MANGROVES IN SOUTHWESTERN PUERTO RICO FROM REMOTE SENSING AND FIELD MEASUREMENTS

By

María Vega Rodríguez

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
in
MARINE SCIENCE
(Biological Oceanography)

UNIVERSITY OF PUERTO RICO
MAYAGUEZ CAMPUS
2008

Approved by:

Roy A. Armstrong, Ph.D. — Date
Chairman, Graduate Committee

Fernando Gilbes, Ph.D. — Date
Member, Graduate Committee

José M. López, Ph.D. — Date
Member, Graduate Committee

Denny Fernandez del Viso, Ph.D. — Date
Member, Graduate Committee

Kurt Grove, Ph.D. — Date
Representative of Graduate Studies

Nilda E. Aponte, Ph.D. — Date
Director of the Department

ABSTRACT

Mangroves are considered dominant primary producers in many tropical and subtropical coastlines. In recent years, modeling of primary productivity (PP) and net primary productivity (NPP) in terrestrial ecosystems has been a subject of increasing interest because of the importance of the terrestrial carbon cycle in the global carbon budget and in climate change. Various studies have reported that leaf area index (LAI), litterfall and nutrient dynamics are some essential parameters related to the photosynthetic capacity of the mangrove ecosystems. The overall objective of this research was to determine PP of the red mangrove, *Rhizophora mangle,* in the Natural Marine Reserve of La Parguera, Puerto Rico, using both field measurements and remote sensing techniques.

Spatial and temporal trends in LAI, litterfall and nutrients exhibited a temporal variation that was mostly influenced by air temperature and salinity. Remineralized nutrients from leaf litter or exogenous nutrient inputs were the driving force for the observed spatial dynamics of primary productivity within these mangrove forests.

The remotely-sensed normalized-difference vegetation index (NDVI) was highly correlated with field-measured mangrove LAI. Accordingly, LAI maps of the study site were derived from IKONOS satellite imagery. LAI derived values were transformed to net primary productivity maps. Spatial variations of the NPP were clearly detected from remotely sensed images and can possibly be used to explain ecological patterns of LAI and leaf fall.

RESUMEN

Recientemente, los estudios para el modelaje de la productividad primaria (PP) y la productividad primaria neta (PPN) han cobrado mayor interés dado a la importancia que tienen los ecosistemas terrestres en el presupuesto global del ciclo de carbono y el cambio climático. El índice de área foliar (IAF), la caída de hojarasca y la dinámica de nutrientes son parámetros fundamentales que promueven la capacidad fotosintética del manglar. El objetivo principal de este estudio fue determinar la PP del mangle rojo, *Rhizophora mangle*, dentro de la Reserva Marina Natural de La Parguera, Puerto Rico, utilizando no sólo datos de campo sino también la tecnología de percepción remota.

Los patrones temporales y espaciales en el índice de IAF, la caída de hojarasca y los nutrientes demostraron ser influenciados principalmente por variaciones en temperatura del aire y salinidad. La remineralización de nutrientes provenientes de la hojarasca y la entrada de nutrientes exógenos resultó ser el elemento influyente en la dinámica espacial de PP observadas en estos bosques de mangle rojo.

El índice de diferencia normalizada de vegetación (NDVI por sus siglas en inglés) obtenida con la percepción remota está altamente correlacionado con las estimaciones tomadas en el campo del IAF del mangle rojo. Consecuentemente, mapas del IAF fueron derivadas de una imagen de satélite de IKONOS. Luego se transformó el mapa de IAF a uno de PPN. Las variaciones espaciales para la PPN fueron claramente detectadas a través de las imágenes satelitales y esto podría servir para explicar patrones ecológicos tales como IAF y caída de hojas.

If tears could build a stairway
and memories were a lane,
I'll walk up right up to heaven and
Bring you home again",
Unknown Author

For the one man that believed in me
since my first day of life and up to our last day together…my father
Julio C. Vega Ortiz (1954-2007)

“Y gloria a las manos, a todas las manos que hoy trabajan
por que ellas construyen y saldrán de ellas la
Nueva Patria Liberada”
J.A. Corretjer

ACKNOWLEDGEMENTS

I am entirely grateful to my chairman Dr. Roy Armstrong, for the absolute support of this research. Your academic teachings will be always treasured. I am also very grateful to a professional who has been a big influence on my academic endeavors and has walked with me up to the accomplishment of my master's thesis, my undergraduate research advisor: Dr. Denny Fernandez del Viso.

I want to thank Dr. Yasmín Detrés from the Bio-Optical Laboratory for her support and critical review over the presentations that came out of this and other projects. Thanks to Dr. Jorge Corredor, Julio Morell and Valentine Hensley from the Chemical Oceanography Laboratory for the instrumentation support and for the effort and valuable suggestions giving within the achievement of the C:H:N chemical analysis. Thanks to Dr. Ernesto Otero for the instrumental support used in the collection of the litterfall data. I would also like to thank my committee for the critical review of this project.

I am grateful to the entire Bio-Optical Laboratory for their friendship and support along the evolution of this research. I want to specially thank Luis Lugo (alias Vitamina) and Sara Rivero for their disinterested and extensive help with the field work. Without you guys this project would have been impossibly difficult. Suhey Ortiz, Rosalinda González and Alex Mercado are graduate students from the department who also helped at different stages of the mangrove field work.

I would like to thank the Sea Grant Program from the UPR, Mayaguez Campus for supporting me with travel grants that gave me the opportunity to

attend the 2007 AMLC conferences at St. Thomas and the 2008 Light and Photosynthesis course held at the Autonomous National University of Mexico.

I appreciate the administrative assistance from the Marine Science Department secretaries, Taty, Zulma and Lily. You are great women that always try to do the best to help. I am also very grateful to all the workers within the Magueyes Island Research Station, specially to the “boteros” for making possible the 40 second travel from La Parguera to the Research station, Marcos Rosado for aiding me during my first field work sections, Negrito for always having the Whaler boat ready for my adventurous field work and for aiding me in the mangroves every once and a while, Wiche for using some of his time to prepare the 40 wooden litterfall traps used during 13 month research, and Godo for preparing great food for us every time he has a good excuse to do so.

A special thanks to my friends from the Marine Science Department and to the ones that traveled with me from the UPR Humacao campus for the unique moments held together and to dearest friends Angela, Ixia and Sol for all the support. We have all walked a long journey together and have been successful.

Most importantly, I am more than grateful to my beautiful family, Mami, Julito and Angélica who without contemplations have always supported and demonstrated their love for me in every way. I want to give special thanks to Gaby for his help with some field work, for his patience, total support, and for not letting me give up. Without a doubt, I also dedicate the success of this work to you guys for being part of me and for giving me the most valuable teachings of all, the way of life.

TABLE OF CONTENTS

CHAPTER 3: Remote Sensing of LAI & Primary Productivity

CHAPTER 4:

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

1.1 Background:

Mangroves are tropical and subtropical marine plants that used to cover up to 75% of tropical coastlines. The most recent estimates suggest that mangroves presently occupy about 15.2 million ha of tropical and subtropical coastlines which are mostly threaten by anthropogenic factors (FAO 2007). Among tropical marine ecosystems, mangroves rank second in importance after coral reefs in terms of gross productivity (Wafar, 1997). Therefore, understanding their ecological importance is critical for the social and economic benefits of a progressed country. Two centers of diversity exist: the Indo-West Pacific, with the highest diversity and the Caribbean/Florida region with low generic diversity (Rogers, 1997). There has been over 54 species identified in 20 genera, belonging to 16 families. Furthermore, *Avicennia* and *Rhizophora* dominate mangrove communities worldwide. Three different “true” species of mangrove trees have been classified for the Caribbean: the red mangrove (*Rhizophora mangle*), the black mangrove (*Avicennia germinans*), and the white mangrove (*Laguncularia racemosa*). A fourth species, buttonwood (*Conocarpus erectus)*, is transitional between the true mangroves and non-mangrove species (Feller, 1996).

1.2 Primary Productivity

Mangrove productivity is often compared to that of other terrestrial forests. Their resources become significantly important for many marine vertebrates, invertebrates and terrestrial organisms. Productivity of the major families of mangrove trees (e.g. Rhizophoraceae) over the Caribbean and Indo-West Pacific regions has been the subject of many studies.

One of the first studies completed for mangrove productivity in the Caribbean region was conducted in a red mangrove, *Rhizophora mangle*, forest located in La Parguera, Puerto Rico (Golley et al., 1962). They reported that the mangrove average biomass for two years consisted mainly of leaves, 778 g/m^2 and wood, 5507 g/m^2. Total gross photosynthesis and leaf respiration was about 8 g C/m^2/day. Net day-time photosynthesis totaled 0.12 g C/m^2/day for seedlings, 0.24 g C/m^2/day for shade leaves, and 5.2 g C/m^2/day for sun leaves. It was concluded that the red mangrove community is more productive than most marine and terrestrial communities, although they are not as efficient as the mountain rainforest or the coral reef in the conversion of sunlight into organic matter in a similar light regime.

Furthermore, Miller (1970) reported his results for a mathematical model that predicts bioclimate, leaf temperature and primary production in red mangroves canopies of South Florida. The objective of that study was to measure primary production and transpiration of the forest canopies through different measurement parameters of individual leaves in the canopy. Net photosynthesis calculated with the model was 5.6 g organic matter/m^2/day for sunny days and 3.5 for cloudy days in June. Gross photosynthesis per unit leaf area was greater at the top of the canopy than at the bottom, but the middle levels of the canopy had the greatest production. The model predicted that the maximum photosynthesis for mangrove stands occur with a leaf area index (LAI) of about 2.5 if no acclimation to shade within the canopy occurs. A LAI greater than about 2.5 may decrease production. Net photosynthesis increased with leaf inclination at all leaf area indices. It concluded that production and transpiration increased with increasing LAI with steeply inclined leaves and leaf absorption.

Therefore, primary production assessments provide valuable information on the functional status of mangrove ecosystems. LAI, litterfall and nutrient dynamics are essential parameters related to the photosynthetic and productive capacity of the mangrove ecosystem.

1.3 Leaf Area Index (LAI)

Various definitions have been published for leaf area index (LAI). Chen (1997) has referred to LAI as one half the total green leaf area per unit ground surface area. It is a measure of the photosynthetic biomass or size of the photosynthetic system which converts solar energy to chemical energy (Pool, 1972). As a result, it drives both within and below the canopy microclimate, determines and controls canopy water interception, radiation extinction, water and carbon gas exchange and is, therefore, a key component of biogeochemical and physical cycles (Chen, 1996; Breda, 2003; Wythers, 2003).

Many direct and indirect methods have been developed to quantify LAI from the ground. All direct measurements have the disadvantage of being time-consuming; they are two-step processes consisting of leaf collection by either harvesting (e.g., destructive sampling) or non-harvesting (e.g., litter traps) methods, and subsequent leaf area calculation based on either planimetric (e.g., scanning planimeter LI-3000, LICOR, Lincoln, NE, USA) or gravimetric (e.g., predetermined green leaf area-to-dry weight-ratios) methods (Sonnentag, 2007). Indirect methods include techniques based on gap-fraction analysis which assume that leaf area can be calculated from the canopy transmittance (the fraction of direct solar radiation which penetrates the canopy) (Green, 2000). Four instruments have been developed to measure the fraction of light transmitted through the canopy. Two of them have been developed to use the photosynthetically active radiation (PAR) waveband (e.g. SunScan, ACCUPAR) and other instruments measure the gap fraction in different zenithal angles (e.g. LAI 2000, DEMON). Hemispherical photography (which is a technique based on canopy photography) can also be used from above the canopy looking downward. Thus, the calculation of LAI can be time-consuming and has been replaced by canopy analyzers. (Breda, 2003).

1.4 Litterfall Production

Various studies have addressed the use of litter production as a measurement of mangrove productivity. Litterfall, consisting of both vegetative and reproductive structures, represents a fraction of net primary production that can be accumulated on the forest floor, remineralized through decomposition or exported (Snedaker, 1984).

Lugo and Snedaker (1974) found that the average annual litterfall in a fringe mangrove forest of red mangrove was 896 g dry wt m^{-2} yr^{-1} for a contribution to the ecosystem of 224 g C m^{-2} yr^{-1} leachate and an equal amount of particulate detritus. Pool et al. (1986) studied the litter production in mangrove forests of southern Florida and Puerto Rico and reported that most of the litterfall corresponded to peaks of wet seasons and frequent wind storms. The composition of the litterfall was 68-86% leaves, 3-15% wood, and 8-21% of miscellaneous structures (e.g. twigs, stems). These authors also found that between Florida and Puerto Rico there were no significant differences in the rate of total litterfall, although there were significant differences of litterfall within each geographical region and between mangrove forest types.

Navarrete and Oliva-Rivera (2002) studied the litter production of *Rhizophora mangle* in Mexico and found that total litterfall (one year cycle) was 2.61 t dry wt ha^{-1} $year^{-1}$. The 99.83% of the total litterfall biomass was comprised of leaf production. They demonstrated that there are significant differences in litterfall between study sites and months. The maximum peaks for litter production and reproductive phases were in July and September and were attributed to stress (lack of water), dry periods and an increase in precipitation and wind. These results are compatible with Juman (2005) who found that red mangrove productivity in the Bon Accord Lagoon, Mexico, varied seasonally and spatially. Leaf fall contributed 67% of total litterfall.

As the rate of litter production provides an indirect estimate of primary production, total litterfall may reflect the nutrient status of the mangrove forest and surrounding watersheds (Pool, 1986).

1.5 Nutrient Dynamics

In tropical oligotrophic marine environments, low temperatures and water availability are not likely to limit decomposition, so the availability of oxygen and nutrients are likely to play important roles (Fourqurean, 2003). Little is known about how nutrient availability affects ecological processes related to nutrient retention and cycling in mangrove ecosystems (Feller, 1998). Thus, knowledge of nutrient cycling in mangroves is required to assess their potential role in regulating water quality, in understanding the coupling of the forest ecosystem with upland and marine ecosystems, and for learning how mangroves maintain nutritional homeostasis while being subjected to high rates of water turnover (ocean and freshwater) that certainly must leach large amounts of nutrients (Lugo, 1998). Moreover, one of the most important factors affecting degradation of organic matter is nutrient content (Raulerson, 2004). Since leaf litter comprise the main bulk of litterfall, its nutrient content may be indicative of the health of mangrove ecosystems and thus serve as an indication of the primary productivity capacity of the ecosystem. Both nitrogen and phosphorus are limiting nutrients within mangrove forests (particularly those that are located in arid environments). Variations in nutrient content (nitrogen and phosphorous) can also be an indicative of nutrient use-efficiency per unit biomass (Lugo, 1998). Nutrient enrichment on within-stand cycling in a mangrove forest greatly affected the C:N, C:P, N:P, and lignin:N ratios in leaf litter produced by the trees that received P and NPK fertilizers (Feller, 1999)

Furthermore, decomposition in detritus within the mangrove system represents a source of nutrients for photosynthesis [Lugo, et. al 1973]. A convenient indicator of the nutritional value of a food is their carbon to nitrogen (C:N) ratio. Nutrient enrichment of *Rhizophora mangle* leaf litter results from loss in carbon content and an increase in final nitrogen; the C:N could change from 120 in senescent leaves to 43 in partially decomposed leaves (Fell, 1981). Thus, it has been proposed that the lower the ratio the higher the nutritive value of mangrove leaves. It remains questionable whether increases in the concentration of nitrogen, and decreases in the C:N ratios during the decomposition of mangrove leaf detritus reflect increases in the nutritional status of detritus for higher consumers (Robertson, 1988).

CHAPTER 2

Primary productivity of red mangrove in semi arid environments

2.1 Abstract

Mangroves are considered essential primary producers in tropical coastal marine environments. Primary production (PP) assessments, which are an accounting of the forest organic production (total biomass) within a specific area and over a time period, give valuable information on the functional status of these ecosystems. Leaf area index (LAI), litterfall, and nutrient dynamics are essential parameters that drive the productive capacity of the mangrove ecosystem and deserved a detailed attention. Three specific objectives have been defined for this research: (1) to determine relationship between direct (LAI_d) and indirect (LAI_e) estimations of true LAI for red mangroves in La Parguera; (2) to determine spatial and temporal patterns of litterfall and LAI; (3) to determine landscape level patterns of nutrients in mangrove leaves. LAI_d and LAI_e had high correlations for almost all study sites. Spatial patterns were observed with the highest LAI_e annual average values ranging between 5.0 and 5.7. Variation in sampling dates was an important factor when taking into consideration LAI_e changes. Temporal patterns for LAI_e were related to changes in leaf fall, air temperature, salinity, barometric pressure and C:N ratios. Inverse relationships with leave fall peaks were observed for all study sites. A positive increase of LAI_e was observed with an increase of nitrogen within all study sites.

Moreover, the total estimated PP for all study sites was 1406.4 g dry wt/m^2/y. Leaf and propagules production comprise over 80% of the litter production, being propagules the mayor litterfall component. Total litterfall exhibited temporal and spatial patterns mainly related to leaf and propagules temporal variations, air temperatures, salinity fluctuations and temporal changes of LAI$_e$. Nutrient parameters obtained from senescent leaves C:N ratios, and percent nitrogen demonstrated to have a distinct spatial variation that influences to a greater extent the leaf and seed production. Percent nitrogen of senescent leaves peaked mainly between May 2006 and December 2006. Green leaves had higher values of C:N ratios and percent nitrogen that were independent of seasonality variations. Study sites with higher litterfall and LAI$_e$ are the most productive mangrove forests in La Parguera. Overall, remineralized nutrients from leaf litter or exogenous nutrient inputs were the driving force for the observed spatial dynamics of primary productivity within these mangrove forests.

2.2 Introduction

Two of the most conspicuous primary producers in coastal marine environments of the Caribbean and tropical Atlantic Ocean are the seagrass *Thalassia testudinum* and the mangrove *Rhizophora mangle* (Fourqurean et al., 2003). Mangroves are tropical and subtropical marine plants that used to cover up to 75% of tropical coastlines. The most recent estimates suggest that mangroves presently occupy about 15.2 million ha of global coastlines (FAO, 2007). Mangrove ecosystems are the habitat for many species of bacteria, protists (including algae), vertebrates, and invertebrates and are characterized for being highly productive. For instance, total photosynthesis and leaf respiration in a red mangrove forest at the Natural Marine Reserve of La Parguera, Lajas, Puerto Rico, estimated from CO_2 analyzer measurements, were in the order of 8 g C/m^2/day (Golley, 1962). Mangrove forests drive many ecological functions and their resources become significantly important for many marine and terrestrial organisms.

Primary production assessments are an accounting of the forests organic production (total biomass) within an established area over time and its estimation can give valuable information on the functional status of these ecosystems. Harvesting, gas exchange, and litterfall are direct methods commonly used to estimate primary productivity (Odum, 1982). Furthermore, to determine the mangrove primary production of any given forest it is also vital to understand the critical functions that drive the ecological processes. Leaf area index (LAI) and nutrient dynamics are essential parameters that drive the photosynthetic and productive capacity of the mangrove ecosystem and deserve detailed research.

Within forest canopy structures, light is the most important physical parameter that is required for plants to provide the energy needed for photosynthesis (Feller, 1996). Consequently, leaves are the active interface for energy, carbon and water exchange between plants and the atmosphere. Therefore, LAI is a key variable in most of the models developed for the simulation of carbon and water dynamics and the most important indicator of forest status, due to the role of green leaves in controlling many biological and physical processes driving the exchange of matter and energy flow (Stroppiana, 2006; Rautiainen, 2004). Leaf area index (LAI) is correlated with total photosynthesis (of individual plants or entire ecosystems) and thus primary productivity and mangrove health. It is defined as one half the total green leaf area per unit ground surface area (Chen, 1997). Spatial and temporal patterns of LAI have been associated with various factors including nutrients and meteorological (e.g. precipitation) patterns (Miller, 1971; Maas, 1994; Bouriaud, 2003; Emmons, 2006)

Many direct and indirect methods have been developed to quantify LAI from the ground. All direct measurements have the disadvantage of being very time-consuming (Sonnentag, 2007). Indirect methods include techniques based on gap-fraction analysis which assume that leaf area can be calculated from the canopy transmittance (the fraction of direct solar radiation which penetrates the canopy) and hemispherical photography (Green, 2000, Breda, 2003).

Furthermore, mangroves high productivity is often attributed to high litter degradation rates and efficient recycling of nutrients, which are supplied by both autochthonous litter and allochthonous inputs from natural and anthropogenic sources (Bosire, 2005). Litterfall is an important source of energy that achieves its role in the ecosystem because it expresses the functionality of the vegetation *in situ* and it influences the recycling of nutrients (Musa, 1986). It consists of both vegetative and reproductive structures and represents a fraction of net primary production that can be accumulated on the forest floor, remineralized through decomposition or exported (Snedaker, 1984). Litterfall production can be established as a proxy for mangroves productivity, which followed by decomposition processes and nutrient enrichments, forms an essential food source for most estuarine animals (UNESCO 1984).

Thus, productivity in marine and coastal ecosystems is essentially influenced by availability of nutrients, particularly nitrogen (Roger, 1996). Since leaf litter comprise the main bulk of litterfall, its nutrient content (e.g. nitrogen and phosphorus) may be indicative of the health of mangrove ecosystems and thus serve as an indication of the primary productivity capacity of the ecosystem A convenient indicator of the nutritional value of a food is the ratio of the carbon to nitrogen (C:N) content in mangrove leaves. The higher nutrient quality the smaller will be the C:N ratios. Onuf et al. (1977) reported that the characteristics of nutrient enrichment of red mangroves are: increased primary productivity, increased percent nitrogen in leaves (=higher nutritive value of vegetation for consumers), and therefore increased losses to more kinds of consumers. It has also been reported that the nutritional balance of plant detritus plays an important role in the control of material flow in ecosystems (Enriquez, 1993).

Based on this information, the following hypotheses are proposed: (1) indirect estimates of LAI are highly correlated to direct measurements of LAI, (2) LAI and litterfall show spatial and temporal patterns that are directly correlated to wind speed, wind gusts and precipitation, (3) foliar nitrogen values reflect the existing patterns of exogenous nutrient sources, and (4) patterns of primary production can be inferred from *in situ* rates of litterfall and LAI.

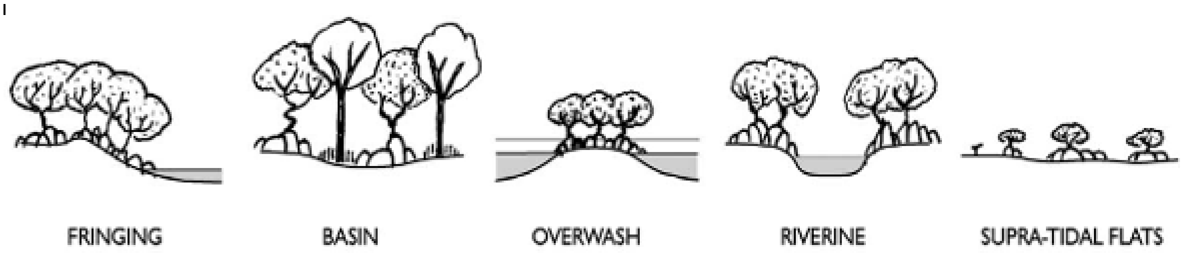
The overall objective of this research was to determine spatial patterns of primary production of the red mangrove, *Rhizophora mangle,* in La Parguera, Puerto Rico. The specific objectives are: (1) to determine the relationship between direct and indirect estimations of LAI for red mangroves, (2) to determine spatial and temporal patterns of LAI and litterfall, and (3) to determine landscape level patterns of nutrients in mangrove leaves.

2.3 Methodology

Study Sites

The original total area of mangroves in Puerto Rico was estimated at 30,000 ha by the 1930's. (UNESCO, 1998). The most recent reliable mangrove area estimate for Puerto Rico and adjacent islands is 8,870 ha. (FAO, 2007). These mangroves have been classified by their climate regime as mangrove forests of the north coast (higher humidity) and the arid mangrove forests of the south coast (Lugo, 1989). La Parguera mangrove forests are located in southwestern Puerto Rico, the most arid zone of the island. The southwestern coast of Puerto Rico contains approximately 996 ha of mangroves, representing 15.3% of the total mangrove area in Puerto Rico. *Rhizophora mangle* (known commonly as red mangrove) is the dominant species within the Natural Marine Reserve of La Parguera. It is followed by *Avicennia germinans* (black mangrove) in dominance.

La Parguera which is one of the driest and hottest areas along the coast of Puerto Rico reported an average annual rainfall of 74.52 cm in comparison to 132.74 cm reported at San Juan between the years 1961-1990. The “rainy season” occurs during the July to December (average 35.61 cm), the “dry season” occurs in January to June (average 9.12 cm) (UNESCO, 1998). Mangrove forests, within La Parguera Marine Reserve, are subject to low-wave energy and low precipitation and runoff (Armstrong, 1990). Red fringe and overwash mangrove forest are most commonly encountered within the marine reserve and although they are usually exposed to extreme environmental conditions, they are highly productive ecosystems (Figure 1).



Source: After Lugo and Snedaker (1974). Their scrub category has been dropped as it is just a variant of the basin one. Similarly, the hammock category has been dropped as it is considered only to be a minor variant within basin environments.

Figure 1. Different physiographic classifications for mangrove ecosystems. Two types are encountered within the Marine Reserve of La Parguera, Puerto Rico (Murray 2003).

Ten monospecific study sites were selected within the Natural Marine Reserve in order to have a representative data set of red mangroves exposed to the existing range of exogenous nutrient sources (Figure 2). For instance, one site closed to shore receives the effluent waters of a sewage treatment plant, another site directly receives nutrients from a resident bird population, and the other sites are at various distances from shore influenced either by pulses of exogenous nutrients (e.g. birds) or no exogenous nutrients (see Table 1).

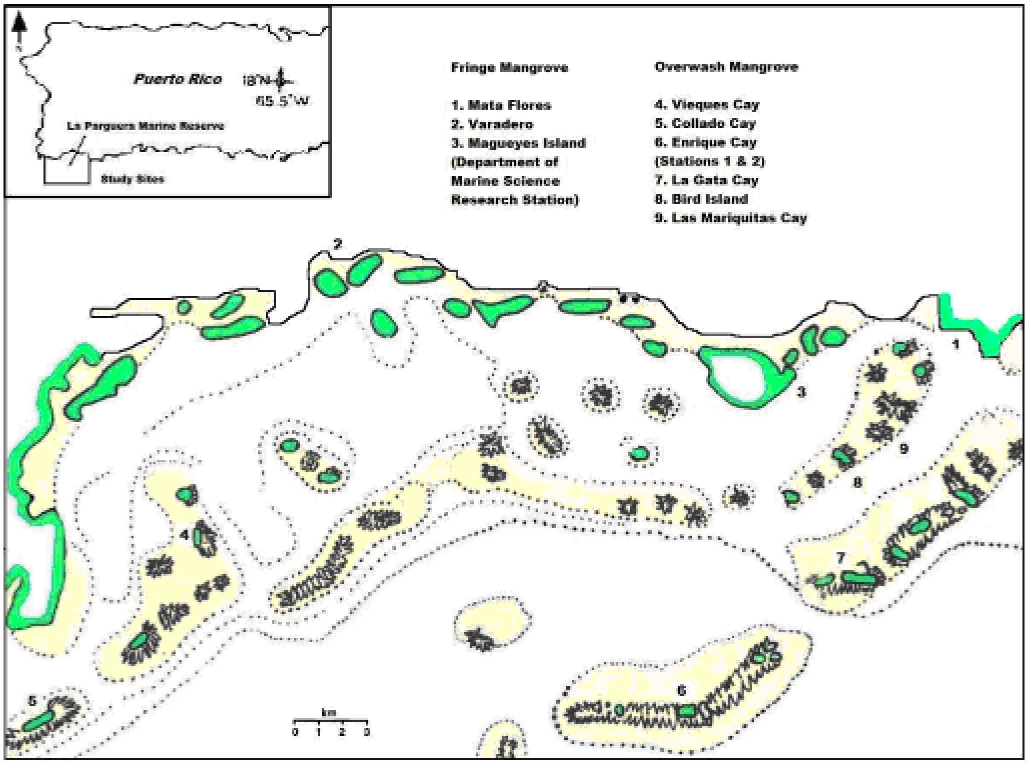


Figure 2. Detailed map illustrating the fringe and overwash mangrove study sites within the La Parguera Marine Reserve.

Within all study sites, three substations were positioned randomly at the "center" of the forests and the site coordinates were measured with a Trimble ProXR global positioning system (GPS).

The GPS was configured in NAD83 datum, UTM and Zone 19. In general, all the substations were positioned and marked with an accuracy of <1 m except for Varadero, Vieques Cay and Bird Island. The canopy density for these stations did not allow for sub-meter accuracies. These were 1.02, 1.6, and 1.34 m, respectively. 15 m linear transects were established with a distance of 7.5 m between substations. Each substation was properly marked and identified for future visits throughout this study. The purpose of these substations was to obtain three replicates for each study site. This research was conducted during 13 months between May 16, 2006 and May 24, 2007.

Table 1. Geographical description of the study sites in La Parguera Marine Reserve.

Study Sites	**Coordinates**	**Physical Description**
Mata Flores Cay	N 17° 58’ 18’’ E 67° 2’ 4’’	Close to shore; fringe mangrove
Varadero	N 17° 58’ 32’’ E 67° 3’ 47’’	Close to shore; Fringe mangrove; Near sewage treatment plant that discharges effluents following secondary treatment
Vieques Cay	N 17° 57’ 45’’ E 67° 4’ 14’’	Overwash mangrove cay
Collado Cay	N 17° 57’ 16’’ E 67° 4’ 39’’	Overwash mangrove cay with occasional bird presence
Enrique Cay (Station 1)	N 17° 57’ 15’’ E 67° 2’ 50’’	Overwash mangrove cay; coral reef area
Enrique Cay (Station 2)	N 17° 57’ 16’’ E 67° 4’ 39’’	Overwash mangrove cay; coral reef area
La Gata Cay	N 17° 57’ 36’’ E 67° 2’ 25’’	Overwash mangrove cay;
Bird Island	N 17° 58’ 2’’ E 67° 2’ 15’’	Overwash mangrove cay with birds presence
Las Mariquitas Cay	N 17° 58’ 12’’ E 67° 2’ 9’’	Overwash mangrove cay
Magueyes Island	N 17° 58’ 10’’ E 67° 2’ 33’’	Close to shore; fringe mangrove

LAI Estimations (LAI_e)

Indirect LAI estimations (LAI_e) were a useful tool for this research. Within each substation of each study site LAI_e were measured using an AccuPAR Linear PAR/LAI ceptometer, Model PAR-80, Decagon Devices, Inc. This instrument consists of an integrated microprocessor-driven data logger and probe. The probe contains 80 photodiodes, spaced 1 cm apart. The photodiodes measure photosynthetically active radiation (PAR) in the 400-700 wavelength range. PAR is displayed in units of micromoles of photons per meter squared per second (µmol m^{-2} s^{-1}). AccuPAR measures light interception in crop and forest canopies and calculates LAI by using the following relationship (equation 1):

$$LAI=[(1-1/K)f_b-1] \ln \tau /A(1-0.47 f_b) \qquad (1)$$

Where K is the extinction coefficient for the canopy, f_b is the fraction of incident PAR which is a beam, τ is the ratio of PAR measured below the canopy to PAR above the canopy and $A=0.283+0.785a-0.159a^2$ (a is the leaf absorptivity in the PAR band, AccuPAR assumes this value to be 0.9 in LAI sampling routines).

At each substation, one above canopy reading of PAR and 30 below canopy PAR measurements were collected in a circle. The above canopy reading was obtained assuming that all of the light received at the canopy was homogenous. Where as, below canopy readings were repeated assuming that the light intercepted by the canopy is affected by the canopy gaps and therefore, the light distribution is not homogenous. These readings were automatically averaged by the instrument. All readings were taken during daytime (7:30 am- 2:00 pm- local time) and only under sunny conditions. LAI_e are then calculated by the instrument using equation 1. LAI_e used in this study are the result of the monthly averaged replicates for each substation. The estimates were made during an annual cycle.

In order to validate the LAI_e, direct LAI measurements (LAI_d) was estimated. At each site, 30 leaves were selected randomly and the specific leaf area (SLA) was calculated from these samples. The SLA was calculated as the ratio of cumulated leaf area to total dry weight of the 30 leaves (Bouriaud, 2003). LAI_d were calculated according to Breda (2003):

$$LAI_d = SLA * \text{Total dry weight leaves}^a \qquad (2)$$

[a] Where the total dry weight leaves were calculated from the leaves collected within the litterfall traps. Taking into consideration the leaf life span of *Rhizophora mangle* leaves, a time interval of 9 months was used for the calculation of LAI_d (Suárez, 2003).

Further conversion of the SLA into LAI is necessary in order to determine the relationship that exists between LAI obtained with a direct method (LAI_d - destructive harvesting) and the LAI_e obtained from an indirect method (the AccuPAR ceptometer estimation).

Litterfall Estimations

Within the 15m line transects, litterfall was collected bi-weekly during the 13 month research period. Wire baskets of 0.23 m^2 were constructed with treated wood and placed within each substation at each study sites at a height of 1.50 m above the ground surface (Snedaker, 1984). This was done in order to minimize the inundation of the baskets at high tide periods. A maximum of four baskets per study site were placed in the mangrove forests, resulting in a total of 40 baskets used for this research. For each bi-weekly collection, the materials in the baskets were separated into various categories: leaves, propagules, wood, fragmented leaves, miscellaneous (which included flowers, dead insects, etc.) and placed into individual aluminum baskets individually made for each study site. This material was then dried at 70°C for 72 hours (Musa, 1986). Subsequently, the material were weighed and reported in units of $g/m^2/d$.

Nutrients

Monthly samples of senescent leaves (obtained from the litterfall) were collected in every study site and throughout the 13 month research. Green sun leaves samples were collected (for comparisons with senescent leaves) within each study site and only for two months, October 06 and February 07 (wet and dry season, respectively). All samples were dried at 70°C for 72 hours, pulverized with a mortar and encapsulated in tin capsules (with specific weights of three milligrams) for chemical analysis. Acetanilida (CH_3CONHC_6HF) was used as a standard for the instrumental analysis. Determination of the amount of carbon (C) and nitrogen (N) were achieved with an EURO EA 2000 Series C:H:N analyzer. Further calculation for C:N ratio of leaves were achieved with regression analysis. Monthly percent N analysis for senescent leaves was achieved at every station for accurate temporal comparisons. Phosphorous content in mangrove leaves was not measured.

Statistical Analysis

Meteorological data were obtained from the Integrated Coral Reef Network/Coral Early Warning System station (ICON/CREWS) deployed at Media Luna Cay (17° 56.317' N, 67° 03.117' W) in La Parguera Marine Reserve. Linear regression analyses were used to establish the relationship between LAI_e and LAI_d. Furthermore, Kruskal-Wallis tests were performed to determine the spatial patterns of LAI_e. An analysis of variance (ANOVA) was used for the determination of its temporal patterns. A stepwise linear regression was useful to determine the relationship between LAI_e and other variables such as: litterfall, C:N ratio, % N, leave fall and meteorological data. An ANOVA LSD Fisher test ($p<0.05$) was used to establish the spatial patterns of litterfall for each study site. The temporal patterns for litterfall were determined with non parametric Spearman correlations and relationships of litterfall and litter composition with meteorological, oceanographic and chemical parameters were established with stepwise linear regressions. InfoStat and Statistix were used for the spatial and temporal analysis.

2.4 Results

Meteorological Data

During this study, the Natural Marine Reserve of La Parguera reported an average annual air temperature of 27 °C and an average annual wind gust and speed of 13.5 and 9.6 knots respectively. Average annual wind direction was 108 degrees. Annual accumulation of precipitation was of 934 mm with high peaks during the "wet season" (August – November) and low peaks during the "dry season" (January – April) (Figure 3). December and May are considered transitional months within season changes.

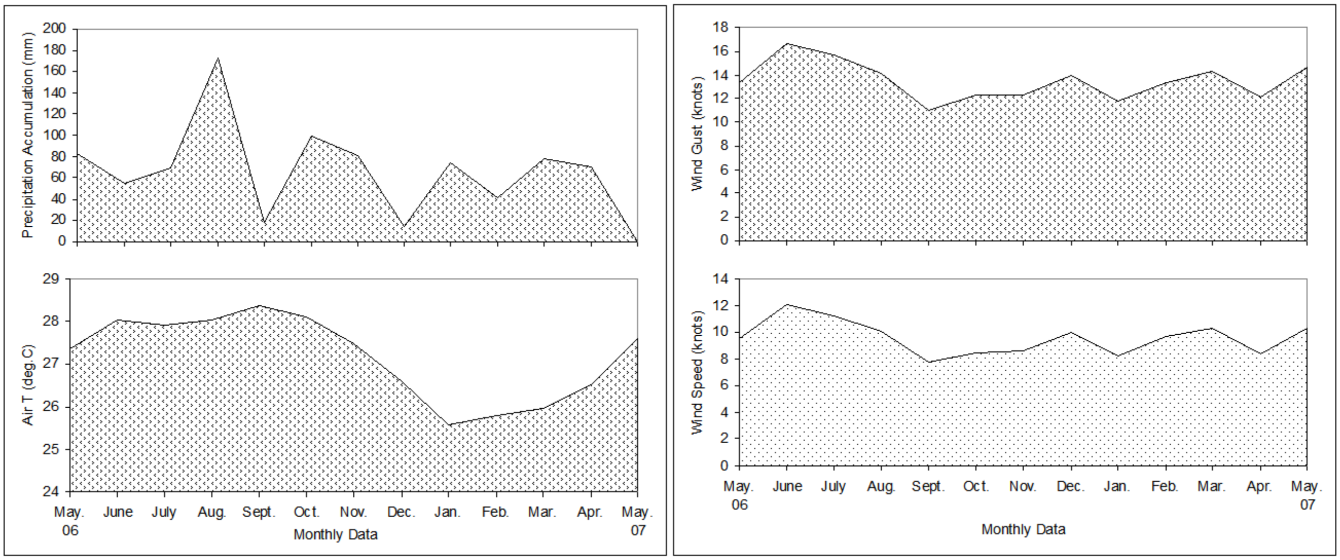


Figure 3. Monthly averages of meteorological parameters. Data collection was obtained from May 2006 to May 2007.

Primary Productivity

LAI Estimations

Variations in SLA and LAI reflect the non homogenous canopy structure of all mangrove forests. SLA resulted in values that ranged between 46.5 and 73.7 cm^2/g. The lowest value reported was for La Gata Cay and the highest was for Vieques Cay. Correlation analyses were used to assess the relationship between direct (LAI_d) and indirect estimated LAI (LAI_e). High coefficients of determination for these variables (R^2 = 0.51- 0.95) were found at all of the study sites, except for Mariquitas Cay indicating that the use of the LAI_e technique is adequate for these mangrove forests (Table 2).

Moreover, almost all measurements of LAI_e suggest a slight overestimation over LAI_d except for Mariquitas Cay where a significant underestimation of the LAI_d was found. LAI_e measurements for all study sites ranged from 1.69 to 7.43 and when compared to LAI_d it resulted to have a site dependent percent of error that ranged between: 0.23% and 50.72%.

General spatial and temporal LAI_e trends

Due to the non-normal distribution of LAI_e detected by a Shapiro-Wilks test (mean: 4.09; $p < 0.0001$) a non-parametric test of Kruskal-Wallis was applied to determine the significant differences of LAI_e between study sites and time periods.

Table 2. SLA, LAI_d, LAI_e values and the relationships between the LAI indices.

Study Sites	**LAI_e**	**LAI_d**	**SLA(cm^2/g)**	**R^2**
Magueyes Island	3.54	2.63	61.58	0.94
	3.53	2.70		
	3.62	2.49		
	3.66	2.43		
	3.70	2.20		
Mata Flores Cay	2.72	2.24	52.45	0.93
	2.69	2.79		
	2.67	2.67		
	2.60	2.56		
	2.51	2.42		
Las Mariquitas Cay	3.82	7.66	52.22	0.19
	3.74	7.50		
	3.82	7.13		
	3.80	6.83		
	3.73	6.31		
Bird Island	5.25	5.52	68.31	0.51
	4.96	5.43		
	5.20	5.04		
	5.26	4.60		
	5.40	4.26		
La Gata Cay	3.63	2.28	46.45	0.67
	3.51	2.31		
	3.62	2.11		
	3.68	1.98		
	3.69	1.82		
Enrique Cay (St.1)	3.42	3.08	50.67	0.81
	3.53	3.15		
	3.78	2.85		
	3.80	2.74		
	3.86	2.50		
Enrique Cay (St.2)	3.46	2.31	48.32	0.68
	3.64	2.39		
	3.80	2.20		
	3.87	2.08		
	3.90	1.95		
Collado Cay	4.46	4.13	62.63	0.64
	4.63	4.08		
	4.75	3.82		
	4.85	3.60		
	4.83	3.11		
Vieques Cay	5.44	4.29	73.71	0.93
	5.73	4.48		
	5.94	4.64		
	6.08	4.82		
	6.18	4.74		
Varadero	5.10	6.17	68.25	0.96
	5.06	6.24		
	5.18	5.40		
	5.24	4.97		
	5.37	4.45		

Study sites exhibiting high LAI values (Varadero and Vieques Cay, respectively) were significantly different from all other stations. Mata Flores Cay exhibited the lowest LAI value of 2.5 and was significantly different from all study sites. Results indicated that LAI$_e$ had a clear spatial variation being Bird Island, Vieques Cay and Varadero the study sites with the highest reported values. No significant differences were found within these study sites. Whereas, Mata Flores Cay reported the lowest average LAI$_e$ values and was significantly different from all of the other sites (Table 3).

Table 3. Mean values of LAI$_e$ within each study site (Kruskall-Wallis, H = 73.99). Different letters indicate significant differences between study sites.

Study Sites	**Mean**	**Ranks**			
Mata Flores Cay	2.5	11.54	A		
Magueyes Island	3.6	47.35		B	
La Gata Cay	3.6	49.73		B	
Enrique Cay (St.2)	3.6	51.04		B	
Enrique Cay (St.1)	3.7	53.65		B	
Las Mariquitas Cay	3.7	56.35		B	
Collado Cay	4.6	88.58			C
Bird Island	5.0	90.04			C
Varadero	5.0	94.65			C
Vieques Cay	5.7	112.08			C

A Kruskal – Wallis (all pair wise comparison) test determined that changes within sampling months were not significant for a determination of temporal patterns in LAI$_e$. In general, significant temporal patterns for LAI$_e$ were inferred with an ANOVA repeated measurements tests (F: 4.71, $p<0.05$).

A stepwise linear regression for LAI_e in La Parguera suggests that temporal patterns have a significant but low and inverse relationship ($R^2 = 0.20$, $p < 0.05$) with air temperature, salinity, barometric pressure and C:N ratios (obtained from senescent leaves). The percent N is also a critical parameter to take into consideration, although its temporal relationship with LAI was not significant.

Precipitation, wind gust, and wind speed had no significant relationships with LAI_e. Furthermore, maximum LAI_e peaks for all study sites were mostly observed during early and low precipitation events (March and May of 2006) and during late low precipitation events (December and January of 2007). Within study sites, Bird Island was the exception, thus it reported a maximum LAI_e during the high precipitation events reported for November of 2006.

In general, LAI_e maximum peaks have a low but significant relationship ($p < 0.05$) with leave fall (Figure 4). Inverse relationships with leave fall peaks were observed for all study sites. A positive increase of LAI_e was observed with an increase of nitrogen within all study sites, even when the relationship was not significant.

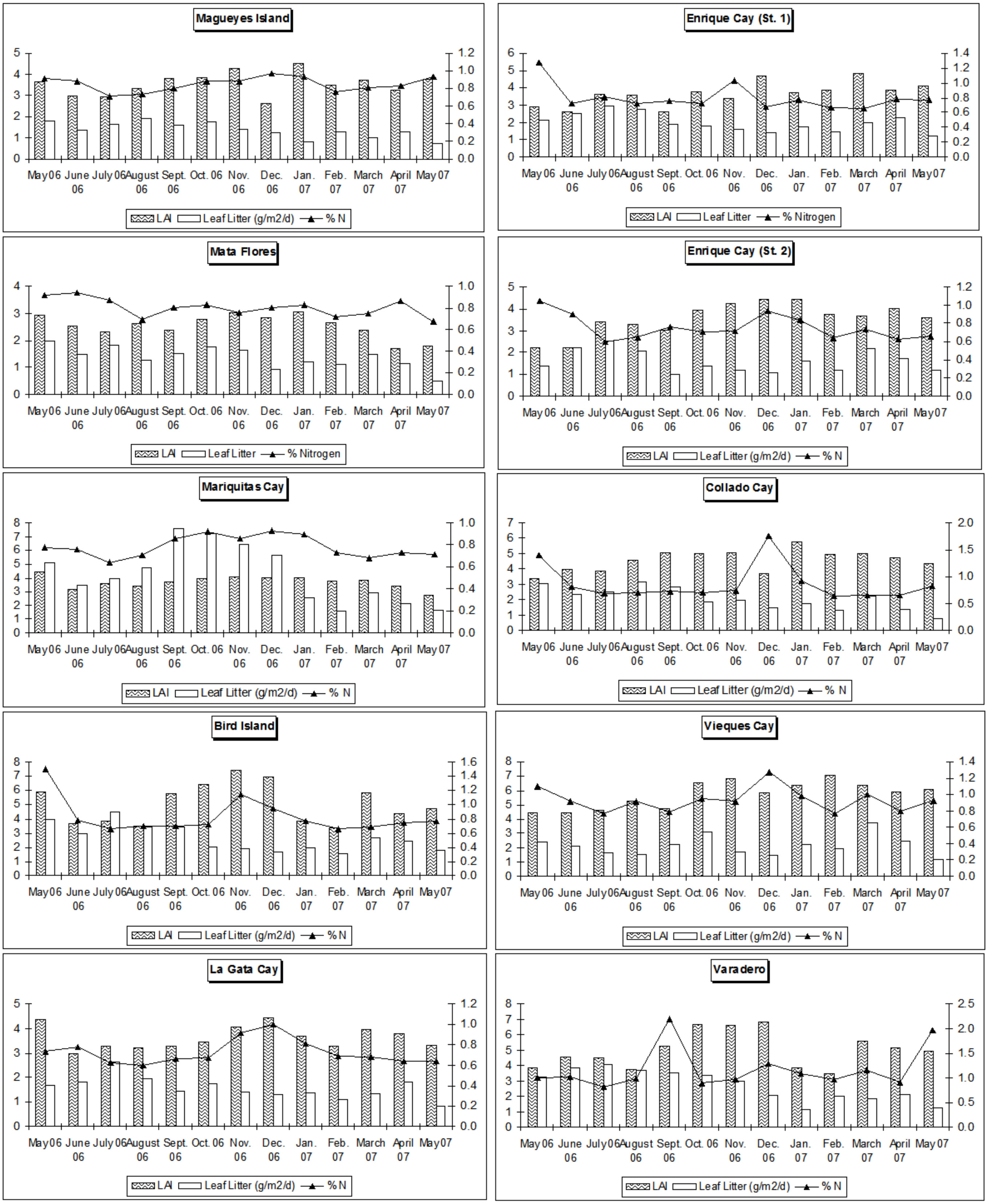


Figure 4. Time series for LAI_e, Leaf Litter, and % N in all study sites.

Litterfall Production & Nutrient Availability

The total estimated primary productivity for *Rhizophora mangle* for all study sites in La Parguera was 1406.4 g dry wt/m^2/yr. Estimated litterfall ranged between 53.08 – 331.93 g dry wt/m^2/yr being Magueyes Island the site with the lowest litterfall production and Mariquitas Cay the one with the highest production (table 4). Bird Island and Varadero sites also reported high primary productivity values.

Table 4. Total litter production within study sites (g dry wt/m^2/yr).

Study Sites	Litterfall	Miscellaneous	Wood	Leaves Fragments	Leaves	Propagules
Magueyes Island	53.08	6.79	1.31	1.69	35.39	7.90
Mata Flores Cay	81.42	27.83	3.97	2.60	41.51	5.51
Mariquitas Cay	331.93	34.88	12.65	4.35	108.48	171.57
Bird Island	218.69	15.65	1.25	3.66	67.47	130.66
La Gata Cay	67.39	9.30	7.74	0.90	40.69	8.76
Enrique Cay (St.1)	217.28	10.75	6.85	1.03	51.92	146.73
Enrique Cay (St. 2)	68.77	4.94	3.56	1.01	42.52	16.74
Collado Cay	72.9	6.99	0.62	1.32	52.61	11.36
Vieques Cay	148.76	8.52	1.11	1.60	55.15	82.38
Varadero	146.21	7.73	4.48	2.28	70.92	60.81

In general, leaf litter and seed production comprised about 87% of the litterfall for all study sites. Seed production resulted to be the mayor litterfall component, followed by leaf litter. Study sites which reported the highest annual leaf litter production were associated with lower total annual litterfall, while sites that reported higher annual seed production were associated with higher total annual litter fall production (Figure 5). Only one study site (Varadero) associated with high litter production was an exception to this tendency. This site reported a higher leaf litter production (48%) over seed production (42%) and it's considered one of the most productive mangrove forests.

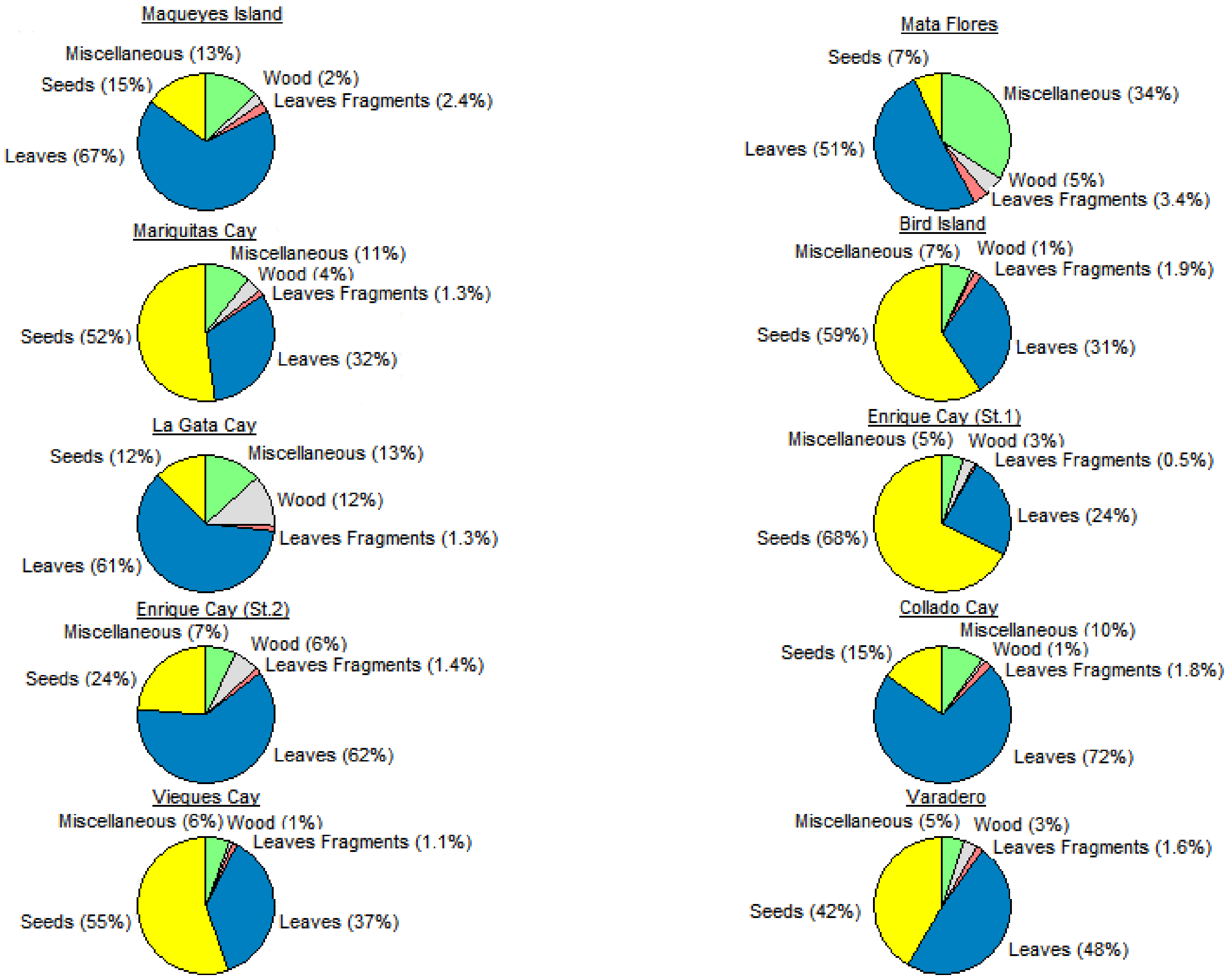


Figure 5. Percentages of litter fall components at all study sites.

General temporal litterfall trend

Litterfall has been found to have temporal patterns that may be related to various physical and chemical parameters (Golley, 1962; Lugo, et al., 1973; Lugo et al., 1978, Pool et al., 1986; Twilley et al., 1986; Clough et al., 2000; Narvarrete, 2002). An ANOVA repeated measurement determined that the variation in litter production is significantly related ($p < 0.05$) to seasonal variations (Table 5).

Table 5. ANOVA (repeated measurements) for litterfall production

Source	DF	SS	MS	F	P
Sites	9	7.16	0.80		
Dates	12	1.71	0.14	4.2	0.0000
Error (Study*Dates)	107	3.63	0.03		
Error	1	0.00	0.00		
Total	129				
Grand Mean	0.64	CV(Study*Dates)	28.81	CV(Error)	5.53

Accordingly, temporal patterns for litterfall production were observed (Figure 6). Total litterfall production was markedly seasonal with highest peaks between June 06 and November 06 (“wet season”). High peaks were also reported during May 06 and December 06. Specifically, the highest total leaf litter peaked mainly between June 06 and October 06. Likewise, additional peaks were also reported for February 07 and April 07, during the dry season. Propagules peaked between June 06 and November 06 with some exceptions during December 06 and wood parts peaked mainly between June 06 and October 06 with some exceptions during February 07 and March 07.

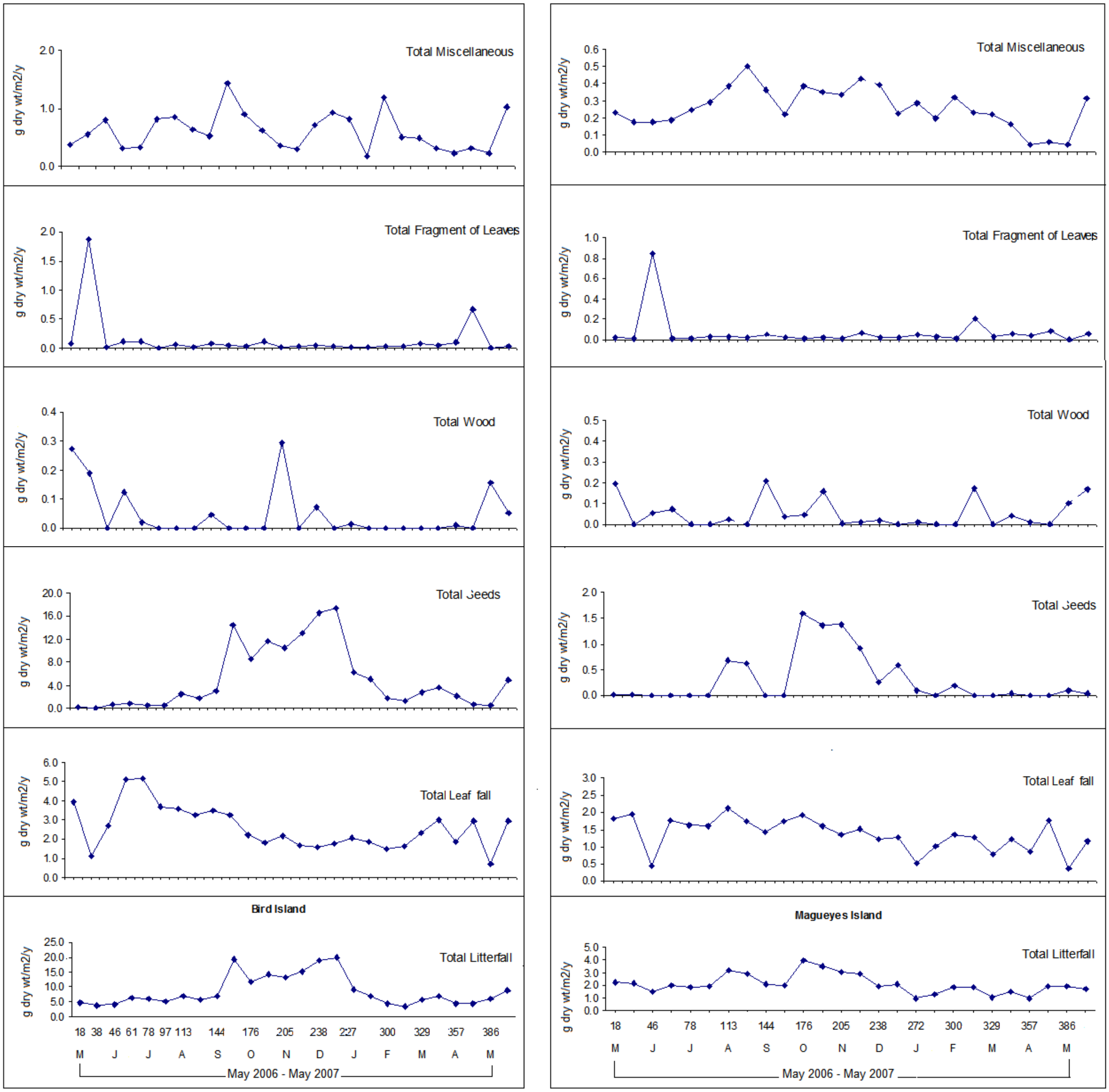


Figure 6. Temporal patterns for two study sites in La Parguera Marine Reserve (g dw/m2/yr).

In general, a non parametric Spearman Rank correlation indicated that total litterfall has a low correlation with the total wood but a very good correlation with leaves and propagule production (correlation coefficients equal to 0.23, 0.67 and 0.85, respectively). It also highlights the low relationship to some meteorological factors such as: air temperature, salinity (negative relationship) (coefficients equal to 0.27 and -0.12, respectively). On the other hand, low and non significant relationships between nutrient parameters (obtained from senescent leaves) such as C:N ratios and % N with litterfall seasonality were detected (coefficients equal to 0.32 and 0.20, respectively). No clear significant relationship between total litter fall and precipitation could be established.

Furthermore, when independently analyzing the response of the different litter components to meteorological, oceanographic and physical parameters, low but significant relationships were observed for all litter parts. A stepwise linear regression was used in order to determine the relationship between the leaf, seed and wood production with air temperature, wind gust and speed, precipitation, salinity, % nitrogen and LAI (Table 6). Leaf litter had a significant correlation to precipitation (correlation coefficient = 0.74, $p < 0.05$). This stepwise regression model also includes very low but significant relationships with air temperature, LAI, wind gust (negative relationship), and wind speed. Seed production is significantly related to air temperature (coefficient = 0.40). Relationships were also established with salinity (coefficient = -0.23) and LAI (coefficient = 0.13). Seed production was not significantly related to wind gust, speed or % nitrogen. Additionally, wood production was significantly related to wind gust, speed and direction, air temperature, salinity and LAI. In general, senescent leaf nitrogen content and C: N ratios had poor relationships with total litter fall (including leaf, seed and wood production) and its temporal influence seems to be non significant.

Table 6. Linear regression models of litter components with significant meteorological, physical and oceanographic variables ($p < 0.05$).

Litter components ($g/m^2/d$)	Variables	Coefficient	Std. Error	p-value	Model R^2
Leaf	Precipitation	0.74	0.35	0.04	0.20
	Air temperature	0.09	0.03	0.002	
	Wind Gust	-0.08	0.03	0.007	
	Wind Speed	0.10	0.04	0.009	
	LAI	0.04	0.02	0.002	
Propagules	Air temperature	0.37	0.11	0.0008	0.24
	Salinity	-0.23	0.08	0.01	
	LAI	0.13	0.06	0.04	
Wood	Wind Gust	-0.31	0.11	0.006	0.24
	Wind Speed	0.52	0.16	0.002	
	Air temperature	0.29	0.11	0.008	
	Salinity	-0.35	0.15	0.02	
	LAI	-0.12	0.05	0.03	

Spatial litterfall trend

Mangrove litterfall can also exhibit variations due to site-specific factors. An ANOVA LSD Fisher test was used in the determination of the spatial patterns for La Parguera Marine Reserve. The ANOVA test indicated that litter fall production varied significantly between study sites. Sites with the lowest litter production (e.g. Magueyes Island and Mata Flores Cay) were significantly different from sites with higher litter production (e.g. Mariquitas Cay and Bird Island) (Table 7).

Table 7. ANOVA litterfall test: LSD Fisher. Alfa: 0.05 DMS: 0.16525. Error: 0.045 Different letters indicate significant differences between study sites.

Study Sites	**Mean**	**n**				
Magueyes Island	0.31	13	A			
Mata Flores Cay	0.34	13	A			
Enrique Cay (St.2)	0.4	13	A			
La Gata Cay	0.4	13	A			
Collado Cay	0.44	13	A			
Varadero	0.66	13		B		
Vieques Cay	0.71	13		B	C	
Enrique Cay (St.1)	0.86	13			C	D
Bird Island	0.88	13				D
Las Mariquitas Cay	0.96	13				D

More over, analyses within groups of sites were achieved. Non-parametric Spearman correlations indicated that variations in total litterfall and litter compartments (leaf, propagules or wood production) correlate very well with meteorological parameters (air temperature, wind gust and wind speed), salinity, LAI_e, and most importantly to nutrient variations (C:N ratios and % N obtained from senescent leaves) according to the study site evaluated. A detailed description for litterfall variations and its mayor influential parameters within each homogenous group (see table 7) is herein reported:

I. Group A:

   a. Fringe and overwash mangrove forests with little to no exogenous nutrient input.
   b. Litterfall mainly related to leaf litter (correlation coefficient > 0.80) for all study sites, except for litterfall in Enrique Cay (St. 2) which correlated better with propagules production (0.81).
   c. Litterfall mainly triggered by air temperature (correlation coefficient > 0.20). Other meteorological parameters such as: precipitation

salinity and wind gust and speed have good correlations with study sites.

d. Senescent leaves C: N ratios and % N content correlate very well with leaf litter.
e. In general, leaf litter have moderate to low and inverse relationships with LAI_e.

II. Group B:

a. Fringe and overwash mangrove forests with constant to occasional exogenous nutrient input.
b. Litterfall is mainly related to propagules production (correlation coefficient > 0.90). Its variation is essentially triggered by air temperature, salinity and precipitation.
c. Litterfall and leaf litter have no correlation with LAI_e.
d. Senescent leaves C: N ratios and % N content correlate with both leaves (Varadero) and propagules production (Vieques Cay).

III. Group C:

a. Overwash mangrove forests with low to none exogenous nutrient inputs.
b. Litterfall is directly related to propagules production (0.81), followed by wood production (0.25). Its variation is mainly influenced by air temperature, followed by salinity and precipitation.

c. Litterfall and leaf litter has no correlation with C: N ratios and % N.

d. Litterfall has a very low correlation with LAI_e (0.13), thus leaf litter has a good and negative correlation (-0.48) with $LAI_{e.}$

IV. Group D:

a. Overwash mangroves with continuous to occasional exogenous nutrient inputs.

b. Litterfall is mainly related to propagules production (0.89), followed by leaf litter and its variation is triggered essentially by air temperature, salinity, wind speed and wind gust. A low correlation was found with precipitation (0.24).

c. Litterfall has very good to moderate correlations with C:N and % N. Leaf litter, propagules and wood production all have good correlations with C:N ratios and % N.

d. Leaf litter has good and negative correlations with LAI_e.

Results indicated that nutrient availability obtained from senescent leaves seems to be a determinant parameter for spatial litterfall trends. A non parametric Kruskall- Wallis ANOVA test demonstrated that nutrient availability (% N) has a significant spatial variability ($p<0.05$) (Table 8). This test highlighted that study sites with scarce inputs of exogenous nutrients are significantly different (e.g. La Gata Cay) from those with continual exogenous nutrients inputs as the Varadero site.

Table 8. Mean C:N values within each study site (Kruskall-Wallis, H = 41.07). Different letters indicate significant differences between study sites.

Trat.	**Ranks**				
La Gata Cay	38.42	A			
Enrique Cay (St.2)	46.35	A			
Collado Cay	53.77	A	B		
Enrique Cay (St.1)	55.62	A	B		
Bird Island	55.92	A	B		
Mariquitas Cay	57.42	A	B		
Mata Flores Cay	65.12	A	B	C	
Magueyes Island	78.42		B	C	
Vieques Cay	92.96			C	D
Varadero	111				D

Overall, results indicated that there is an inverse relation between C:N ratios and % N. Senescent leaves percent nitrogen content seemed to peak between May 06 and December 06 (Figure 7). Green leaves had more % N (2.1 – 4.0) than senescent leaves and no significant differences (except for the nutrient content in green leaves of Enrique Cay, station 2 for February 2007) were reported between wet or dry seasons. (APPENDIX 2).

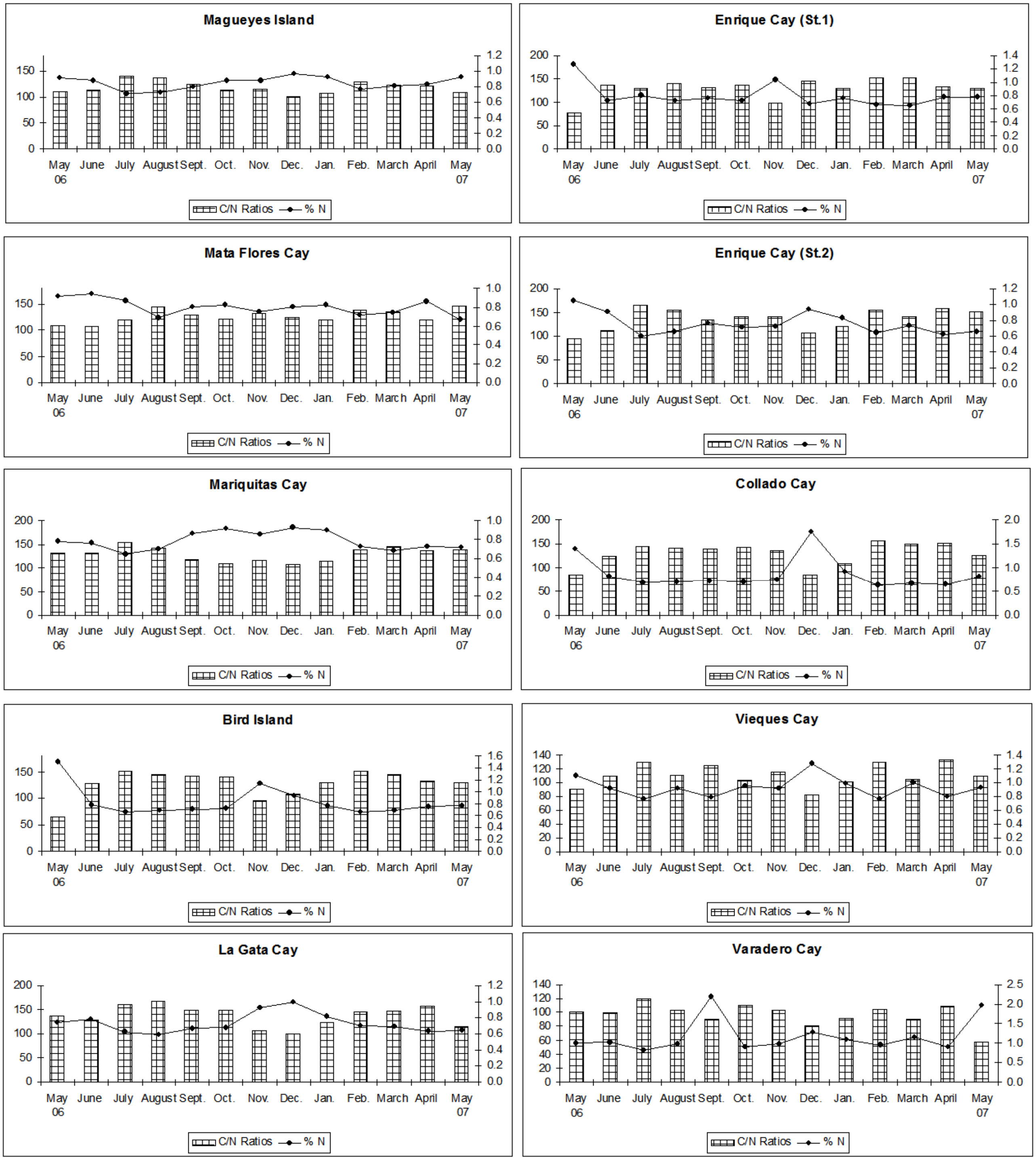


Figure 7. C: N ratios and % N temporal patterns for all study sites.

2.5 Discussion

Primary productivity of red mangroves in La Parguera

The primary productivity values reported within this study are consistent with other reports for *Rhizophora mangle* for the Caribbean and Mexican coasts (Table 9). Moreover, results are also comparable with primary productivity reported for other mangrove species. Bunt (1995) studied the continental scale patterns in mangrove litterfall in Australia for the species *Rhizophora stylosa*, *Ceriops tagal* and *Avicennia marina*.

Table 9. Primary productivity values reported for mangrove forests in the Caribbean and Mexico coasts.

Monospecific Sites	Forest Type	LAI	Litterfall (g dwt/m2/y)	% N	References
La Parguera, Puerto Rico	Overwash Fringe	1.6 – 7.4 (mean:4.09)	1406.4	0.6 – 2.2	This study
Bon Accord, Tobago	Fringe	-	1273*	-	Juman (2005)
Agua Brava, Lagoon Mexico Pacific	Fringe	2.49	-	-	Kovacs et. al. (2005)
Vacía Talega, Puerto Rico	Fringe Riverine	-	810 - 1278	-	Pool et. al. (1986)
West Mexico	Fringe	3.3 – 5.4	-	-	Maass (1995)
La Parguera, Puerto Rico	Overwash Fringe	1.2 – 4.3	-	0.87 – 1.5	Armstrong (1990)
Teacapán , Agua Brava, Mexico	Basin	-	1417	-	Flores-Verdugo et. al., (1990)
Laguna Joyuda, Puerto Rico	Basin	2.0 – 3.30	511 - 919	0.9 – 1.3	Musa (1986)

* estimated value, calculated by a daily average value.

He reported litterfall measurements of 1598 g dry wt/m^2 for *Avicennia marina*, 2369 g dry wt/m^2 for *Rhizophora stylosa* and 1290 d dry wt/m^2 for *Ceriops tagal*, being *R. stylosa* the most productive mangrove forest for arid zones. He concluded that the capacity of litter production at individual sites must depend heavily on controls such as salinity regime, nutrient inputs and topographic characteristics of the substrate operating at relatively local scales.

LAI_d and LAI_e estimations

Canopy phenology can be inferred from LAI by estimating the amount of intercepted light through the forest canopy. LAI can be achieved either directly or indirectly for any given forests and its accuracy is dependent on the errors that can accumulate upon any chosen method. Moreover, caution is needed when using indirect methods because underestimations of LAI can be achieved. This has been previously reported for different vegetation canopies but has been poorly documented (e.g. Bréda, 2003, Chen, 1997, Sonnentag, 2007).

Within the LAI_e data set used herein, Mariquitas Cay was the only study site with a tendency to underestimate LAI_e values. The two main causes previously reported for LAI underestimations are leave clumping and contribution of stem and branches (e.g. wood). When not taken into consideration, these forests parts can lead to the over estimation of the Plant Area Index (PAI). In the intent to overcome this inconsistency, one can take into consideration the Plant Area Index (PAI) and calculate the LAI with the input of the woody to total leaf ratio and foliage clumping effect or validate the indirect LAI estimations (acquired with the use of any canopy light intercepting instrument) with direct LAI estimations (e.g. harvesting, litterfall, SLA measurements).

For this study, all indirect data (LAI_e) were validated with direct data (LAI_d) calculated from SLA measurements. Consequently, Mariquitas cay had the highest LAI_d to LAI_e error, indicating that maybe the PAI for this study site had a major contribution to the LAI_e.

However, the majority of LAI_e reported here tended to slightly overestimate true LAI. This overestimation can be attributed to the input of an incorrect value for the leaf distribution parameter within the ceptometer LAI calculation. Leaf distribution refers to the distribution and orientation of leaves within the canopy. Its importance for calculating LAI is fundamental since it determines the amount of photosynthetically active radiance that is being intercepted by the forest canopy (AccuPAR, Operators Manual). Miller (1971) demonstrated that the importance of leaf orientation within mangrove canopies was determinant when establishing the optimum productivity for mangrove forests. He found that with steeper inclined leaves, gross photosynthesis continued to increase up to a LAI of 8; but with more horizontally inclined leaves the gross productivity would occur at lower LAI values.

Overall, these results show that LAI_d and LAI_e had good correlations for almost all study sites. The percent of error ranged between 0.23% and 50.72% which is within the range previously reported by Chen (1997) and Boriaud (2003).

Spatial and temporal LAI_e trends

.Annual averages for LAI_e ranged between 2.5 and 5.7 being Mata Flores Cay the lowest reported value and Vieques Cay the highest one. In general, mangrove LAI tends to be relatively low in comparison with other tropical forests, thus maximum LAI of up to 5 had been reported for the Caribbean mangroves (Pool, 1972). Odum (1982) attributes the low LAI estimates for mangrove forests to: (1) effective light interception in the canopy, (2) incapacity of lower mangrove leaves to flourish at low light intensities and (3) the absence of low light adapted plant layers on the forest floor.

Moreover, sites in La Parguera indicated that the response of red mangroves to light availability was enhanced by nutrient availability. In general, there was a tendency of LAI_e to increase after the maximum or very high peaks of % nitrogen for senescent leaves. Whereas spatial LAI_e trends were highly sensitive to exogenous nutrient input demonstrating that study sites which received constant to very frequent exogenous nutrients either from bird guano or from a sewage water treatment discharge (e.g. Collado Cay, Bird Island, Vieques Cay and Varadero) reported the highest LAI_e. This agrees with Onuff (1977) who demonstrated that red mangroves are capable of assimilating the nitrogen excess, producing a higher rate of biomass (through rapid growing) and reported that there was a 33% more nitrogen accumulation in mangrove leaves in a high nutrient environment. This accumulation enhances the nutritive value of leaf litter increasing its consumption. Furthermore, Rogers (1997) documented that nutrient inputs from bird guano stimulated plant growth and increased the percent nitrogen concentrations in forests. Armstrong (1990) determined that structural parameters as LAI where higher with exogenous nutrient input. Therefore, the resulting nitrogen per unit area from mangrove leaves can be considered a key parameter for photosynthesis.

Temporal patterns exhibited in La Parguera indicated that variations were mostly correlated with air temperature and salinity. The variations of these parameters may have either a positive or negative effect on productivity rate. Miller (1971) indicated that measurements of air temperature and humidity are critical since they directly affect leaf temperatures, transpirations and net photosynthesis. Interesting, maximum LAI peaks for mangrove canopies in La Parguera were correlated with minimum peaks for photosynthetically active radiation irradiance (Ed_{PAR}), minimum peaks of leaf litter and were usually expressed during the dry seasons (APPENDEX 1). A tendency for canopy densities to increase were observed after the rainy (and high cloud cover) season, high nutrient inputs from litterfall and minimal leaf abscission, meaning that perhaps mangrove forests in La Parguera have adapted to achieve optimum productivity under water stressed environments. After reporting a similar LAI seasonality in two semi-deciduous forests in South America, Emmons (2006) suggested that maximum LAI is achieved because the ground water stored (after rainfall periods) are sufficient to prevent leaf abscission due to water stress. He concludes that the high LAI values, during dry seasons and maximal irradiance, correspond to high primary production of the forests before maximal desiccation of ground water. Moreover, Lugo (1978) stated that soils in subtropical dry forests in Guánica, Puerto Rico reached field capacity after prolonged periods of rain and therefore, plants quickly develop a full set of leaves and primary productivity reached its maximum rate. The relationship between LAI_e and litterfall can result to be a bit complex, and the results herein may be contradictory to previous reports. Thus, this study clearly indicated that LAI_e showed maximum peaks during the dry season when minimum peaks for leaf abscission were achieved and a possible explanation for this phenomenon has been described.

Temporal and Spatial litterfall trends

Litterfall is an essential source of renewing nutrients for mangrove ecosystems and its importance can be critical especially for forests in poor nutrient and harsh environments. Within all study sites in La Parguera Marine Reserve, litterfall was mainly composed of leaves and propagules (seedlings). Wood was an important litterfall component but its percentage was only up to 6%. Paradoxically, the major dry weight component in litterfall was of propagules. Interesting, Clough (2000) studied the LAI and litterfall of *Rhizophora apiculata* within mangrove stands of different ages in Vietnam and proposed that propagules would increase with an increase of forest age. He found that 1 ha of forest aged 21 produced sufficient propagules each year to plant about 40 ha of new forest, while a 36 year old forest would produce 20 ha more. Maturity in forest age could probably explain the amount of propagules that mangrove forests in La Parguera are producing.

Subsequently, clear temporal litterfall patterns were observed. Highest rates of litterfall (leaf, propagules and wood production) corresponded to the “wet season" in Puerto Rico. Some of the highest peaks were observed within the transitional months of May and December 06. It has been speculated that possible resistance to leaf abscission during rainy periods (which decreases salinity rates) could become an energetic cost of maintaining photosynthetic tissues and hence the mangrove prefers to eliminate the leaves in order to overcome the stress (Pool, 1986). Moreover, Miller (1971) stated that cool moist conditions generally support higher productivity, thus wind may be less important. Hence, litterfall in La Parguera was significantly correlated with air temperature and inversely correlated with salinity measurements. Wind gusts and speed may be more influential in the final removal of tree parts when the abscission is definitely in process.

Moreover, high peaks of leaf production during the dry season can be attributed to the normal life span of mangrove leaves which have been reported to be 9 months (Suárez, 2003). Furthermore, high peaks for propagules production within the wet season has been poorly documented, but two main hypotheses are reported: (1) red mangrove propagules mature and fall from trees between June and September and (2) the tendency to fall within the rainy season is a mechanism of seed dispersal (Odum, 1982; Navarrete, 2002).

Spatial patterns for litterfall were also established. Results indicate that variations in total litterfall and litter composition (leaf, propagules or wood production) were in response to meteorological parameters (air temperature, wind gusts and wind speed), salinity, LAI_e, and most importantly to nutrient variations (C:N ratios and % N obtained from senescent and leaves) according to the study site evaluated. Sites with significant higher litterfall were associated with higher propagules production and higher LAI_e, whereas sites with lower litterfall were associated with higher leaf production and lower LAI_e. Thus, recently (Feller, 2007) reported that upon nutrient availability maximum photosynthetic rates per unit leaf area of *A. germinans* increased.

Overall, exogenous nutrient inputs played an important role in litterfall dynamics, leading to higher litterfall rates with higher % N and lower C:N ratios in mangrove senescent leaves. This highlights the essential relationship between nutrient availability and mangrove productivity. Whereas the nutritional balance of plant detritus plays, therefore, an important role in the control of material flow in ecosystems (Enriquez, 1993).

Nutrient Availability

Various researches have focused on the importance of nutrient availability within mangrove primary productivity. Mangrove forests are usually exposed to limited nitrogen and phosphorus. Knowledge on the carbon and nitrogen ratios highlights the importance of leaf quality. Thus the higher the ratio, the lower is the nutritive value for consumption.

Twilley et al. (1986) studied litter production and turnover in basin mangrove forests in southwest Florida and found that leaf nitrogen decreased during senescence, and absolute nitrogen increased in leaf litter during decomposition on the forest floor. Green leaves in comparison with senescent leaves had lower C: N and higher %N, independently of the rainfall seasonality. This means that the plant undergoes reabsorption or translocation of nutrients before leaf senescence in order to reduce nutrient loss. Within La Parguera, study sites with exogenous nutrients (e.g. Bird Island and Varadero) the lowest C:N ratio and highest % N in leaves were observed. Thus, % N in senescent leaves is an important parameter in ecosystems dynamics. The lack or availability of nutrients seemed to trigger both the canopy leaf density inferred by LAI_e estimations and the dominance of leaf litter or seed litter within the total litterfall of mangrove forests in La Parguera. Decomposition of detritus within the mangrove ecosystem also represents a source of remineralized nutrients for other trophic levels (Lugo, et al, 1973).

2.6 Conclusions

High correlations between direct and indirect LAI estimations were observed. As a result, I conclude that the LAI of R. mangle forests can be adequately determined using indirect, optical methods. Temporal trends of LAI_e and litterfall were influenced, for the most part, by variations in air temperatures and salinity. Wind gusts and speed are of secondary importance and mainly influences the leaf and seeds abscission processes. The maturity of forests within La Parguera Marine Reserve may be an indication of the amount of leaf and propagule production obtained within the litterfall. Moreover, spatial trends in LAI_e and litterfall are mostly influenced by exogenous nutrient inputs. Lower C:N ratios and higher % N within the study area resulted in higher LAI_e and litterfall. The nutritional leaf content may also trigger the dominance of either leaf or seed production within the total litterfall.

Overall I conclude that study sites with higher litterfall and LAI_e are the most productive mangrove forests in La Parguera. Therefore, management and conservation is of fundamental importance within the survival of these fragile ecosystems in this new era of global climate change.

CHAPTER III

Remote Sensing of LAI and Net Primary Productivity

3.1 Abstract

Mangrove forests are highly productive ecosystems that are located within tropical and subtropical coastlines. They serve as habitat to many bacteria, protists (including algae), vertebrate and invertebrate marine organisms. In recent years, modeling of net primary productivity in terrestrial ecosystems has been a subject of interest because of their capacity to sequester atmospheric carbon. Net primary productivity (NPP) is defined as the new carbon stored in living plants per unit time (usually annually) per unit surface area (Chen, 1999). Leaf area index (LAI) and litterfall are two of the essential parameters needed to estimate primary productivity. Various methods have been used in the determination of LAI, thus only recently remote sensing has gained popularity among ecology studies. The general goals of this study were to estimate LAI and NPP using remote sensing techniques.

Four spectral bands (blue, green, red and NIR) were obtained from a 2006 IKONOS satellite image. Field estimates of LAI ($LAI_{in\ situ}$) were used for validation purposes. $LAI_{in\ situ}$ had better correlations with the spectral red and near IR bands. The normalized difference vegetation index (NDVI) and simple ratio (SR) were also derived from the satellite image and related to $LAI_{in\ situ}$ measurements. Results indicate that the relationship between NDVI and $LAI_{in\ situ}$ is the highest and most significant (R^2= 0.72, n=10). The NDVI linear equation model

produced with the previous correlation was useful in the NDVI transformation to a LAI map. $LAI_{in\ situ}$ had a high and significant correlation with the IKONOS LAI map (R^2 = 0.65, n=10). As a final product, an IKONOS NPP map was generated. A spatial tendency of NPP was observed to be similar to the spatial $LAI_{in\ situ}$ at the La Parguera Marine Reserve. This spatial tendency was not observed in accordance to leaf litter. This research shows that accurate high spatial resolution LAI and NPP maps can be obtained and spatial variations of the NPP can be detected from remotely sensed images.

3.2 Introduction

Mangrove ecosystems are the habitat for diverse populations of bacteria, protists (including algae), vertebrates and invertebrates and are characterized for being highly productive. Subject to rapid daily, monthly, and annual variation in their physical environment, they have a remarkable ability to cope with wide variety of stressors (McLoad, 2006). Quantification of process rates and their regulation could provide a useful perspective to our understanding of system dynamics and enables predictions to be made for planning and management (Lee, 1990).

Primary production assessments quantify the forests organic production within an established area over certain time periods give valuable information on the functional status of these ecosystems. In recent years, modeling of net primary productivity (NPP) in terrestrial ecosystems has been a subject of increasing interest because of the importance of terrestrial carbon cycle in global carbon budget and climate change. NPP is defined as the new carbon stored in living plants per unit time (usually annually) per unit surface area (Chen, 1999). Historically, net day-time photosynthesis for mangrove sun leaves has been reported to range between 5.2 and 5.7 g C/m^2/day (Golley et al., 1962; Miller, 1970; Lugo and Snedaker, 1973; Edwards, 1997).

Leaf Area Index (LAI) is one of the essential parameters measured in studies of forest primary productivity. LAI is defined as half the total green leaf area per unit ground surface area and is correlated with total photosynthesis (of individual plants or entire ecosystems) and thus with primary productivity and mangrove health. It is a measure of the photosynthetic biomass or size of the photosynthetic system which converts solar energy to chemical energy (Pool, 1972).

There are various methods for obtaining leaf area index (LAI), which include the time consuming but precise planimetric techniques and the indirect methods which include techniques based on gap-fraction analysis. These assume that leaf area can be calculated from the canopy transmittance (the fraction of direct solar radiation which penetrates the canopy) (Green, 2000). Four instruments have been developed to measure the fraction of light transmitted through the canopy. Two of them measure the incident photosynthetically active radiation (PAR) (e.g.

SunScan, ACCUPAR) and other two measures the gap fraction in different zenithal angles (e.g. LAI 2000, DEMON) (Breda, 2003). Hemispherical photography (which is a technique based on canopy photography) can also be used from above the canopy looking downward. Thus, the calculation of LAI can be time-consuming and has been replaced by canopy analyzers (Breda, 2003). Continual measurements of LAI can give valuable information concerning the canopy photosynthetic efficiency and mangrove productivity.

Satellite and airborne remote sensing (RS) techniques have been developed to obtain spectral information from the earth's surface. An important advantage of RS is that it allows quantitative and qualitative assessments of ground conditions over large and inaccessible areas (Aschbacher, 1995).

Green leaves are selective absorbers of solar radiation. Compared with non-vegetative surfaces, green leaves absorb more visible radiation for photosynthesis and less near infrared radiation. Reflectance in the red and near-infrared wavelengths have been used to formulate various vegetation indices (VI) as spectral indicators of the conditions of vegetated surfaces (Wythers, 2003). Vegetation indices are usually ratios of spectral data. The most commonly used VI's are the Normalized Difference Vegetation Index (NDVI) and the Simple Ratio (SR).

The information content of the high spatial resolution satellite images (e.g. IKONOS, Space Imagining Corp., Thornton, CO, USA) may be useful in large-scale quantitative assessment of biophysical attributes, such as LAI. LAI can be estimated from remotely sensed data through VI's (Fang, 2003). Validating indirect methods of LAI with direct methods will help determine the accuracy of indirect methods. Major issues facing LAI product validation may include: (1) consistency in ground-based LAI measurement methods and protocols since there have been different definitions of LAI and diverse methods of LAI estimation; (2) methods for spatial scaling from ground plot to pixel; and (3) accuracy assessment for coarse-resolution LAI images (Chen, 2002).

Different multispectral high-spatial resolution (e.g. IKONOS and Landsat) data sets have been used to estimate LAI and Net Primary Productivity (NPP) models for mangrove forests. An advantage of using high-spatial resolution images is that the range of 1-15 m is the ideal spatial resolution for mangrove characterization and mapping. The disadvantages are the high spectral reflectance variation, the large data storage requirements, the extensive processing time, and the higher acquisition cost (Bettinger, 2006). The use of multispectral images has proven to be a promising tool for LAI modeling in mangrove forests

Johnson (2003) obtained remotely sensed NDVI values from IKONOS satellite images during the 2001 growing season and compared them with ground measurements of vineyard LAI during that same time period. These two variables were strongly related in six vineyard blocks on each of four occasions (R^2 = 0.91 to 0.98), suggesting the temporal stability in this relationship and the possibility at least on a localized basis, of minimizing (or even eliminating) subsequent ground calibration.

The following hypotheses were tested in this study that: (1) there is a positive relationship between LAI_e and vegetation indices (e.g. NDVI, Simple Ratio) obtained from satellite images, (2) accurate LAI and net primary productivity estimates can be derived from high resolution satellite images, and (3) patterns of net primary production can be inferred from spatial changes in LAI as determined by satellite data.

The overall objective was to assess spatial trends of NPP, LAI and litterfall in *Rhizophora mangle* forests at La Parguera Natural Marine Reserve, Puerto Rico, using remote sensing. The specific objectives were: (1) to determine relationships between *in situ* estimations of LAI, spectral data and VI (e.g. NDVI and SR) obtained from satellite images, (2) to produce accurate LAI and net primary productivity maps of the study sites.

3.3 Methodology

Study Sites

In Puerto Rico, mangroves have been classified into two major categories according to climatic conditions: the humid mangrove forests of the north coast and the arid mangrove forests of the south coast (Lugo, 1989). La Parguera mangrove forests are located in southwestern Puerto Rico, the most arid zone of the island. During this study, La Parguera Marine Reserve reported an average annual air temperature of 27°C and an average annual wind gust and speed of 13.5 and 9.6 knots, respectively. Average annual wind direction was 108 degrees. Annual accumulation of precipitation was 934 mm with high peaks during the “wet season” (June – November) and lowest values during the “dry season” (January – April).

Ten monospecific study sites (overwash and fringe mangrove forests types) were strategically selected within the Natural Marine Reserve in order to have a representative data set of red mangroves exposed to the existing range of nutrient conditions (Table 1, Figure 2). For instance, a site close to shore receives the effluent waters of a sewage treatment plant, another site is exposed to nutrients from a resident bird population, and the other sites are at various distances from shore influenced either by residues of exogenous nutrients (e.g. birds) or no exogenous nutrients. *Rhizophora mangle* was the dominant specie within all overwash mangroves in La Parguera Marine Reserve, Puerto Rico. One study site (Magueyes Island) also had the presence of *Avicennia germinans*.

Within all study sites, three substations were positioned randomly at the "center" of the forests and the site coordinates were determined with a Trimble ProXR global positioning system (GPS). 15m linear transects were defined, each had three substations with a 7.5 m distance between each one.

Field estimates of LAI ($LAI_{in\ situ}$) were obtained using the AccuPAR Linear PAR/LAI ceptometer, Model PAR-80. AccuPAR measures light interception in forest canopies and calculates LAI by the PAR inversion equation (see equation 1).

Within each substation, one above canopy reading of photosynthetically active radiation (PAR) was made and 30 circular below canopy readings of PAR were recorded. These readings were automatically averaged by the instrument while assuming that the light intercepted by the mangrove canopy is non homogeneous. All readings were taken during daytime between 0730 – 1400 hrs. They were mostly under sunny conditions. $LAI_{in\ situ}$ used in this study is the average of all replicates at every study site. Although LAI estimates were measured throughout the 13 month study, for the purpose of this discussion only the data for October 25, 2006 is included.

Downwelling irradiance data (for day length estimates) were obtained from the Integrated Coral Reef Network/Coral Early Warning System station (ICON/CREWS) deployed at Media Luna Cay (17° 56.317' N, 67° 03.117' W) in La Parguera Marine Reserve.

Remote sensing of LAI & Net Primary Productivity

IKONOS multispectral image

A high resolution multispectral IKONOS (Space Imagining Corp., Thornton, CO, USA) satellite image of the Natural Marine Reserve at La Parguera (67° 5’ 55’’ W, 17° 58’ 12’’ N) from October 25, 2006 was used. IKONOS data provides the finest spatial resolution with 1 m panchromatic and 4 m multispectral (blue, green, red, and near-infrared) with high radiometric fidelity and geometric accuracy (Rodríguez, 2004) (table 10). The image was referenced to the same UTM, Zone 19, and NAD83 datum as the GPS data. Georeference and atmospheric corrections corrects for geospatial and atmospheric errors in the derivation of the vegetation indices were performed as part of the IKONOS image pre-processing. Although the image acquired was previously georeferenced, GIS was used to verify its accuracy. The atmospheric correction method used was the dark subtraction with the minimum band value. Water masks were performed prior to the creation of the NDVI and SR images using the band minimum of 0.1 and the band maximum of 1.8 respectively. All masked pixels were identified by a -1.0 value. Each study site was delimited within regions of interest of 3 x 15 pixels of information per site.

Only $\text{LAI}_{in\ situ}$ data taken at the same time as the satellite image were used. The field data was used with validation purposes. Spectral data were derived from the 2006 IKONOS satellite image, compared to $\text{LAI}_{in\ situ}$ and the best correlation within spectral an *in situ* data was established. ENVI 4.2 (Research Systems Inc., Boulder, Colorado USA) image processing software was used.

Table 10. Specifications of the multispectral IKONOS imagery

Bands	**Spectral Range**	**Spatial Resolution**
Blue	0.45-0.52 µm	4 m
Green	0.51-0.60 µm	4 m
Red	0.63-0.70 µm	4 m
Near Infrared	0.76-0.85 µm	4 m
1 m black and white (panchromatic)		

Vegetation Indices Calculation

The Normalized Difference Vegetation Index (NDVI) is sensitive to changes in the amount of green biomass, pigment content and concentration and leaf water stress (Gong, 2003). This vegetation index correlates near infrared (NIR) and red (R) bands according to the following equation:

$$\text{NDVI} = (\text{NIR band} - \text{Red band})/ (\text{NIR band} + \text{Red band}) \qquad (3)$$

The Simple Ratio (SR) also compares the amount of green biomass, pigment content and concentration and leaf water stress (Gong, 2003). SR was calculated according to equation 4:

$$\text{SR} = \text{NIR band/R band} \tag{4}$$

LAI & Net Primary Productivity maps

Red and near IR spectral data were derived from the IKONOS image and used to calculate both vegetation indices. A correlation between indirect field estimations of LAI$_e$ and the VI's were achieved and the model with the highest R^2 and lowest standard error was used for deriving the LAI maps (Kovacs et al., 2004). Once this relationship is known the VI values for the remainder of the image is converted to LAI (Edwards, 1997) using the linear regression:

$$\text{LAI} = m\ (\text{VI}) + b \tag{5}$$

where m is the regression model's slope, VI is the most appropriate vegetation index and b is the intercept.

The derived LAI image was then used to generate a map of net primary production (NPP) for the study area. This NPP map is produced with estimated net primary production values reported historically for red mangroves. The NPP of the mangrove canopy per m² of ground area over a day can be described by the following equation (Edwards, 1997):

$$\text{NPP} = A \times d \times \text{IKONOS LAI map} \tag{6}$$

where A = average rate of net primary productivity (gC m^2 hr^1) calculated from previous reports (Golley et al., 1962; Miller, 1970; Lugo et al., 1973; Edwards, 1997), d = day length (12 hrs reported for Puerto Rico during October 25, 2006), and LAI is the leaf area index IKONOS derived map already estimated using equation 5.

Statistical Analysis

Regression analyses were used to relate the image-based VI to the field-based LAI measurements. The statistical program, InfoStat was used for the determination of linear correlations and ANOVAS for the determination of the models significance.

3.4 Results

The monthly average $LAI_{in\ situ}$ ranged from 2.8 to 6.7 and showed a high spatial variation within the study sites. In the intent to validate the use of spectral bands for subsequent NDVI and SR image processing, linear regressions between average LAI_e and individual spectral bands (bands 1-4) were performed. Results indicated that all spectral bands had low correlations with $LAI_{in\ situ}$ (Table 11). Bands 3 (red) and 4 (NIR) produced the best correlations with field measurements (R^2= 0.20, 0.32 respectively).

Table 11. Correlations of individual spectral bands with LAI_e

Bands	Spectral Range	R^2	Standard Error
Blue	0.45-0.52 µm	0.15	1.9
Green	0.51-0.60 µm	0.14	4.7
Red	0.63-0.70 µm	0.17	3.6
Near Infrared	0.76-0.85 µm	0.32	22.2

.

Subsequently, NDVI and SR were derived from the IKONOS imagery and correlated with $LAI_{in\ situ}$ (Figures 8 and 9). The highest NDVI and SR values were related to the highest LAI_e measurements (e.g. Bird Island, Collado, Vieques and Varadero) (Table 12). Spectral data obtained from both vegetation indices and compared with linear regressions to LAI_e, indicated that the best possible fit with field measurements were achieved using the NDVI (R^2=0.72, $p < 0.05$). The NDVI regression also produced the lowest standard error. The SR had low correlations with LAI_e measurements, and its standard error was higher (Figures 10 and 11).

An IKONOS LAI image was generated based upon the NDVI values using the following equation:

$$LAI = 33.21\ (NDVI) - 14.63. \tag{7}$$

Accordingly, a derived IKONOS LAI image of La Parguera was produced (Figure 12). These LAI spectral values were related to field-based LAI_e measurements in a linear regression analysis (R^2 = 0.65, standard error: 0.74)

An ANOVA (SC type III) indicated that the correlation was significant ($p<0.05$) (Figure 13).

Table 12. Vegetation indices values for each study site within La Parguera Marine Reserve

Study Sites	LAI (Oct. 06)	NDVI (IKONOS)	SR (IKONOS)
Magueyes Island	3.85	0.57	3.80
Mata Flores Cay	2.78	0.55	3.42
Mariquitas Cay	3.96	0.58	3.67
Bird Island	6.37	0.65	4.07
La Gata Cay	3.46	0.56	3.59
Enrique Cay (St.1)	3.74	0.55	3.65
Enrique Cay (St.2)	3.96	0.53	3.29
Collado Cay	4.99	0.59	3.41
Vieques Cay	6.53	0.60	4.12
Varadero	6.67	0.62	3.45

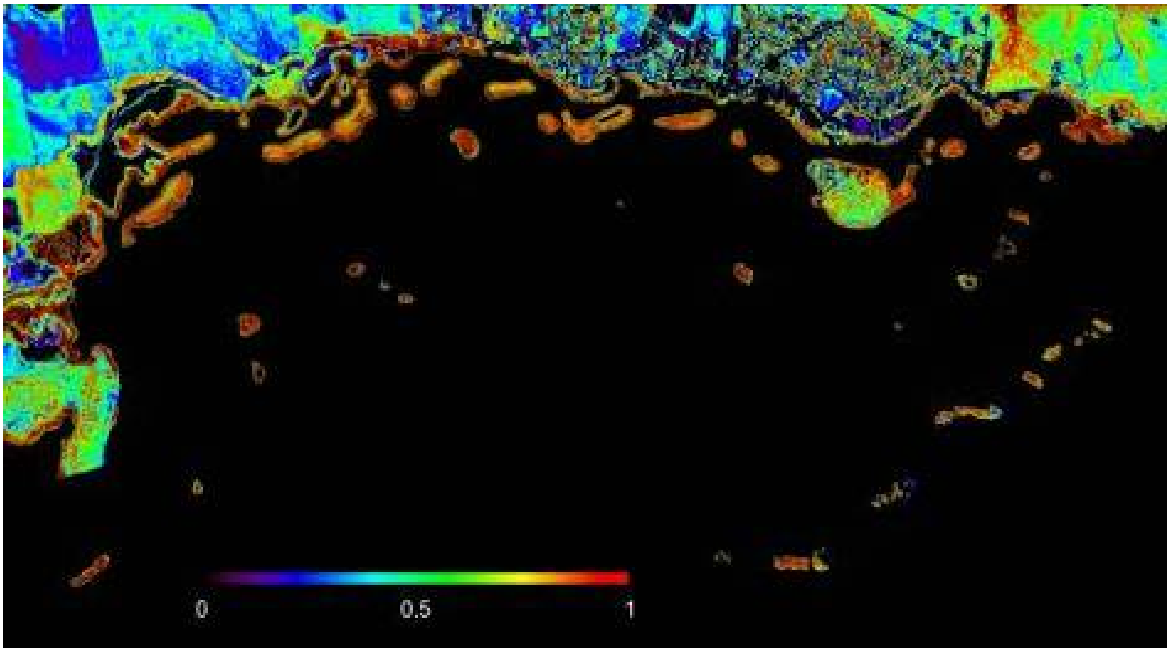


Figure 8. IKONOS 2006 NDVI image of La Parguera Marine Reserve.

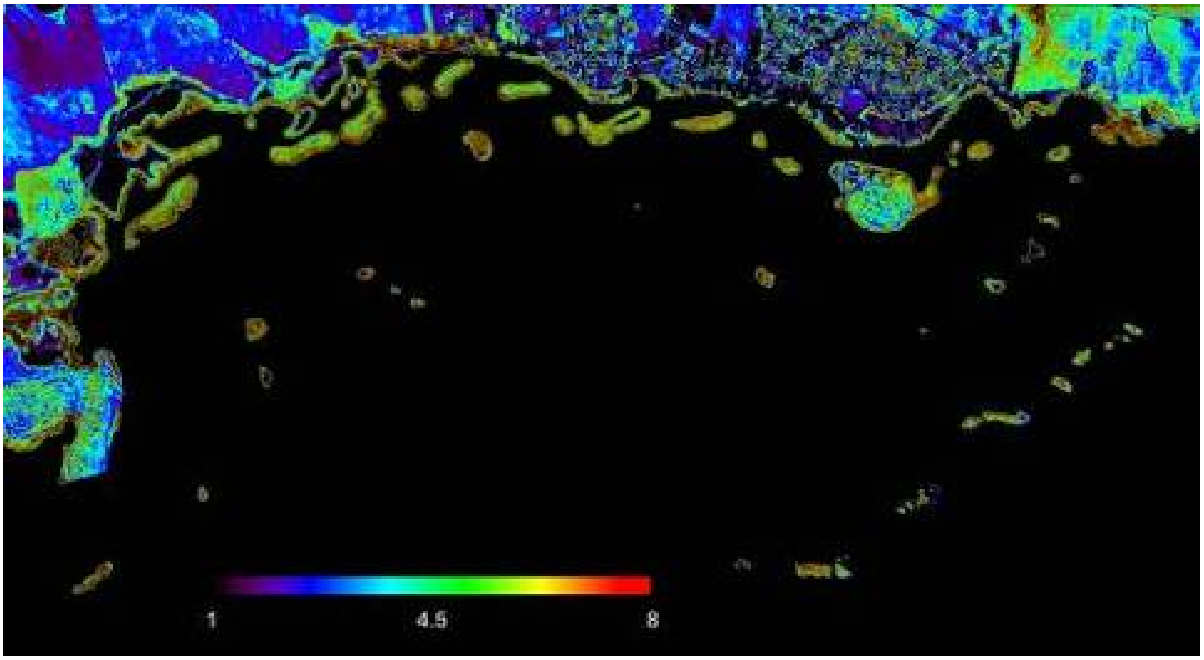


Figure 9. IKONOS 2006 SR image of La Parguera Marine Reserve.

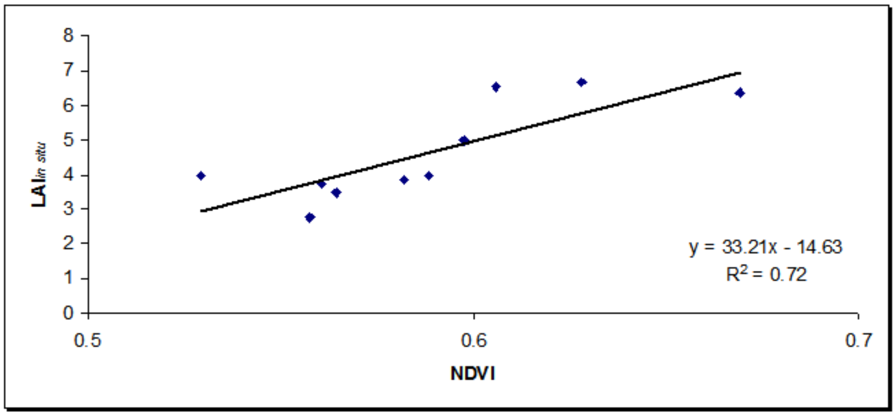


Figure 10. Regression analysis for the NDVI model vs. LAI$_e$ for all study sites ($p<0.05$)

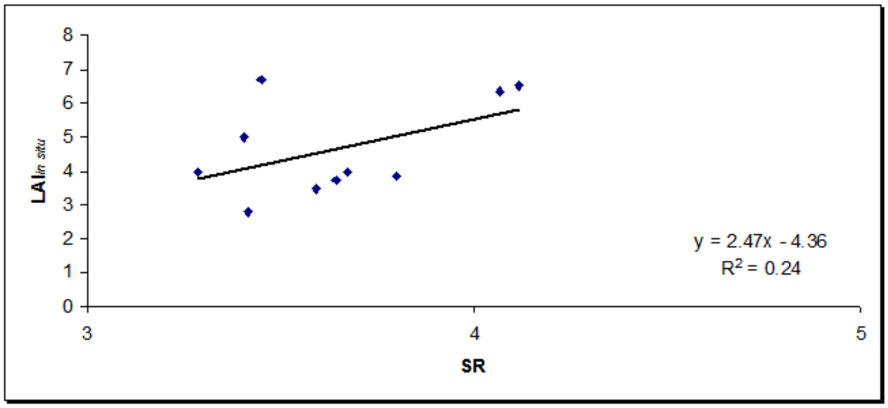


Figure 11. Regression analysis for the SR model vs. LAIe for all study sites ($p>0.05$

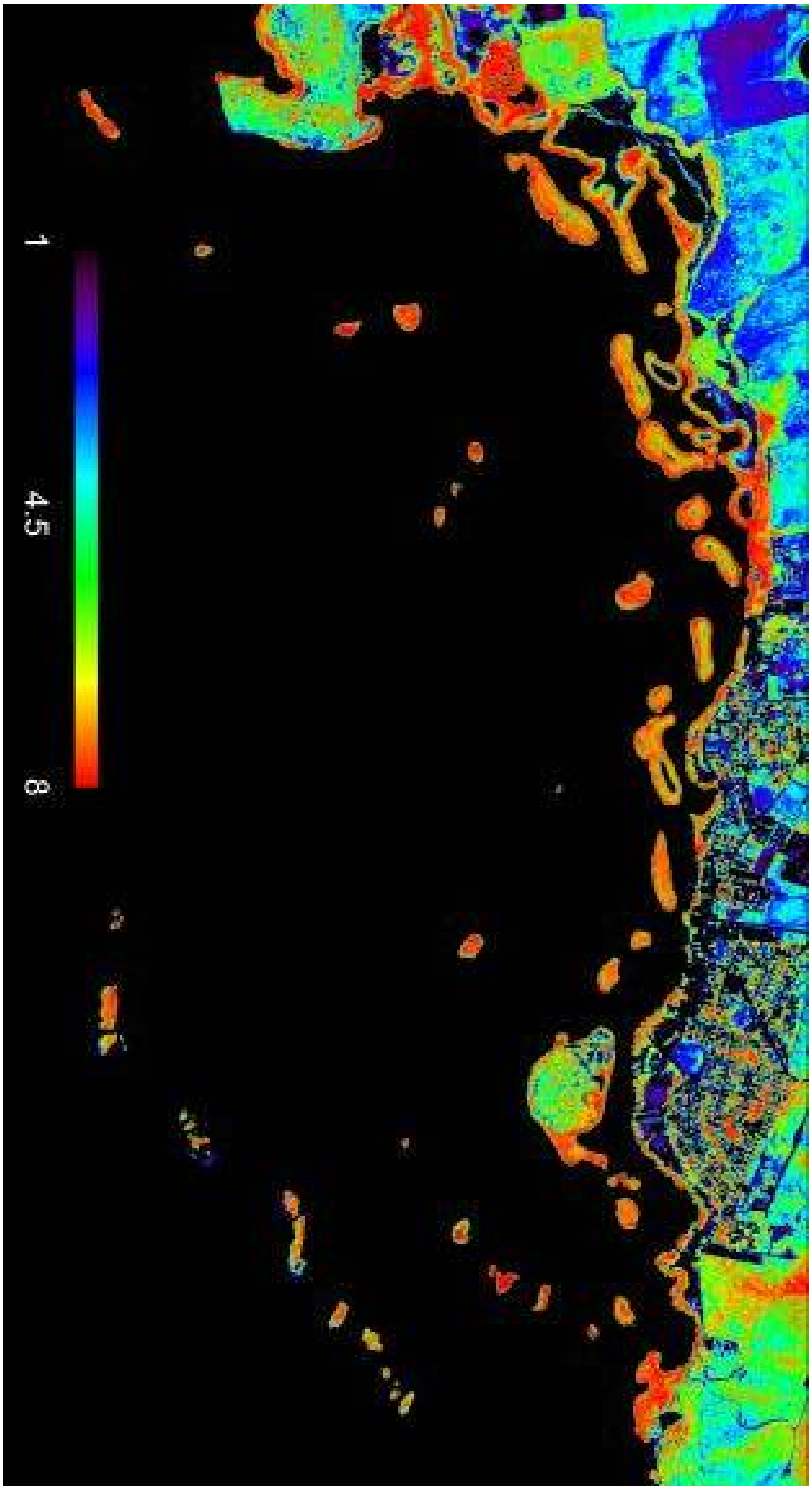


Figure 12. IKONOS estimated LAI image for La Parguera Marine Reserve.

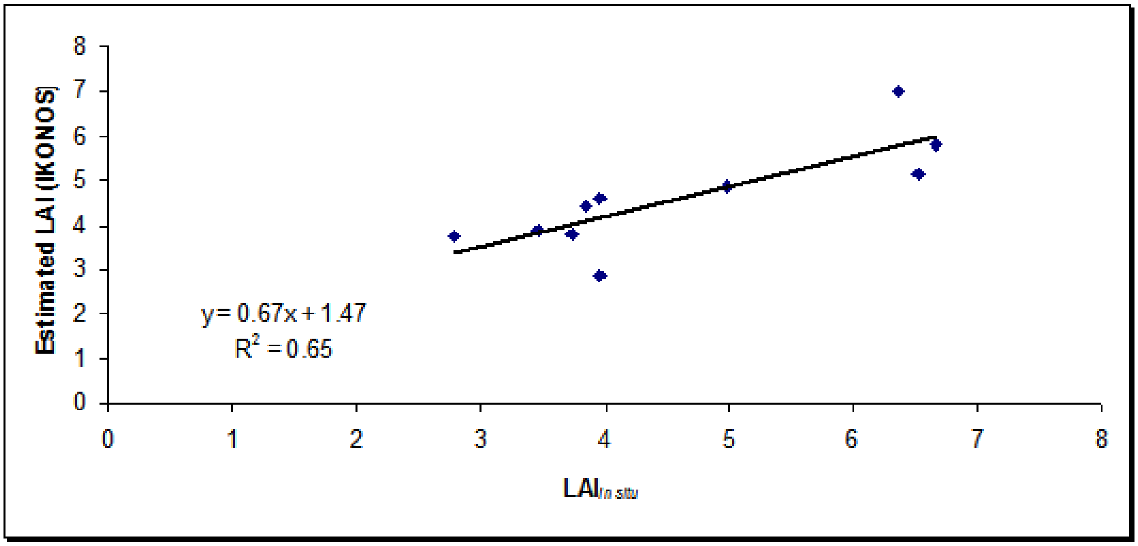


Figure 13. Regression analysis for LAI$_e$ vs. estimated LAI (IKONOS)

Equation 6 for NPP was then, applied to the IKONOS LAI image and a net primary productivity image of La Parguera was produced (Figure 14).

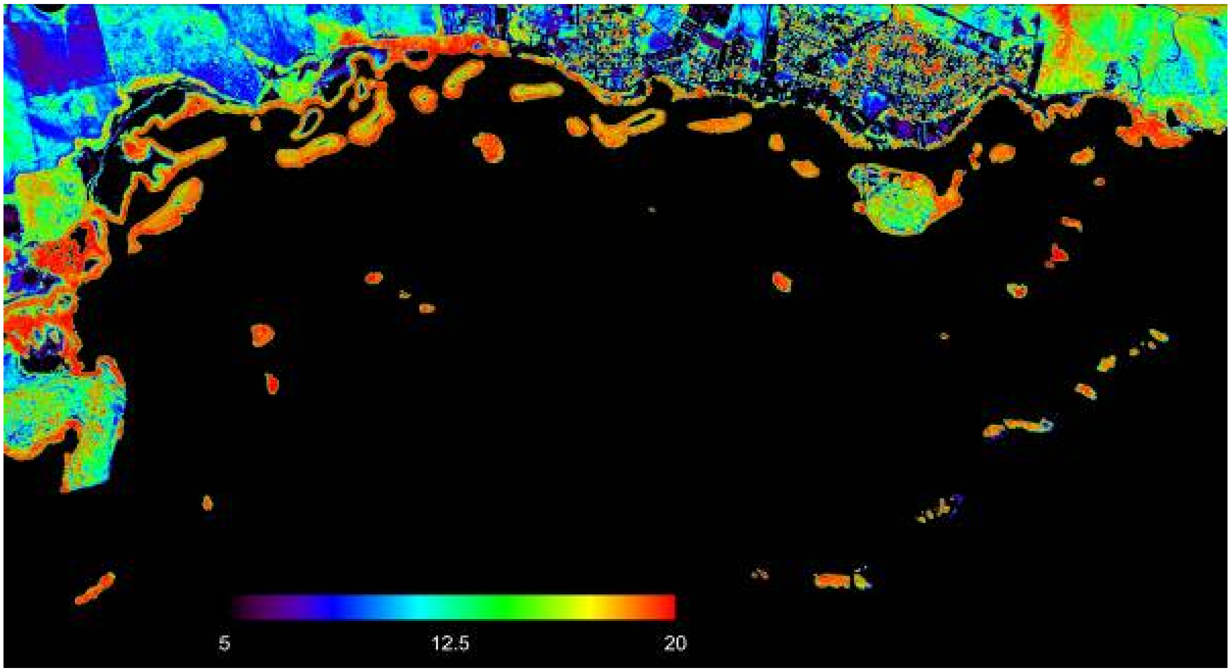


Figure 14. IKONOS estimated NPP image for La Parguera Marine Reserve

The resultant NPP image was then plotted with LAI$_{in\ situ}$ and with the leaf litter estimations acquired during the October 2006 sampling. A tendency for the NPP derived from the IKONOS imagery to increase or decrease upon specific study sites was observed. Furthermore, the spatial pattern observed for NPP was similar to the spatial LAI$_{in\ situ}$ pattern. Thus, a slight tendency for NPP to have an inverse relationship with leaf fall within spatial patterns was observed (Figures 15 and 16).

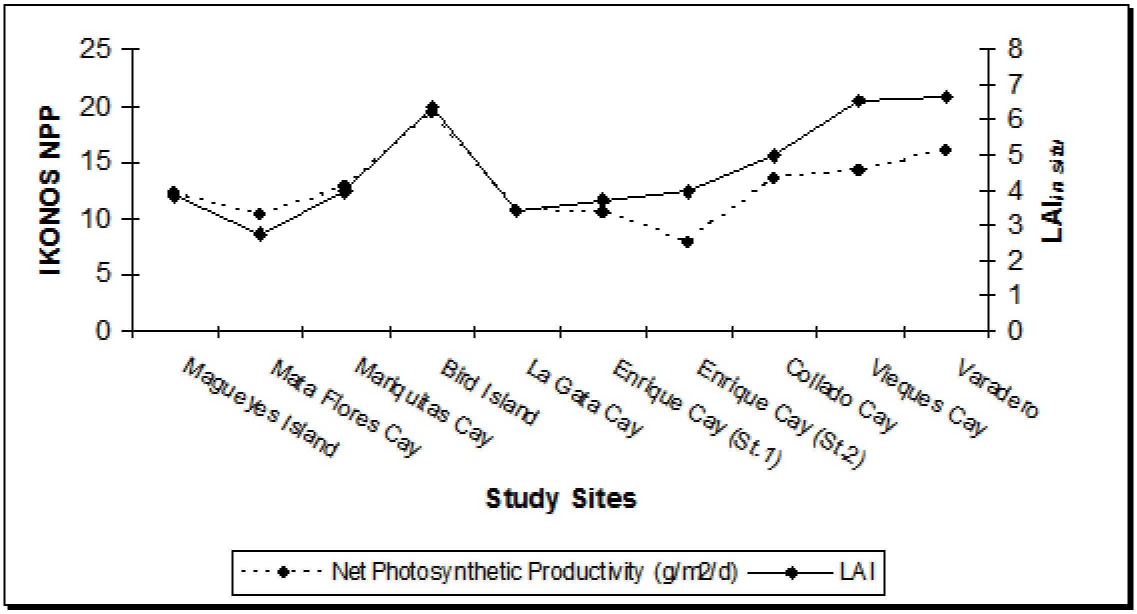


Figure 15. Spatial variations of NPP and LAI$_{in\ situ}$ with the Natural Marine Reserve.

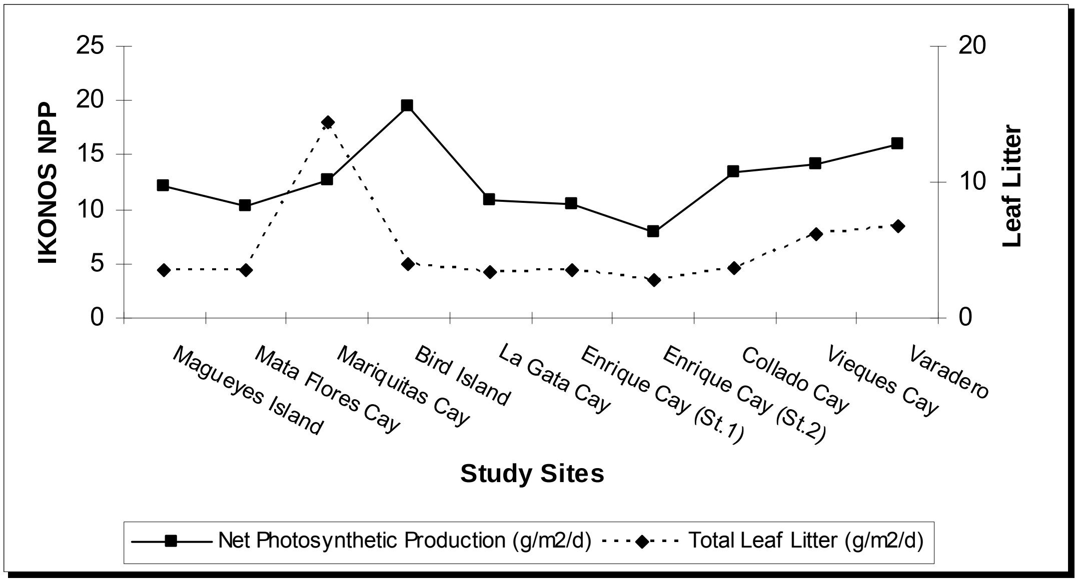


Figure 16. Spatial variations of NPP and total leaf litter within the Natural Marine Reserve.

3.5 Discussion

LAI is highly sensitive to canopy closure and VI. Lee (2004) and other investigators correlated LAI with different spectral reflectances in the visible and short-wave infrared (SWIR) wavelengths in a highly dense canopy situation. They found that near IR has a positive correlation with LAI. SWIR shows a stronger correlation than NIR and therefore it can be used to determine LAI (Lee, 2004). Vegetation spectra will be expected to range between 400-2500 nm in the electromagnetic spectra, obtaining by this means valuable information about vegetation health status (Armstrong, 1990). The present study, which uses a multispectral image with only four bands, indicates that there is a poor correlation between LAI and bands 1-2. These results were expected since absorbs more visible radiation for used during the photosynthesis process and less NIR and is mostly sensitive to red and near infrared bands. Furthermore, results confirmed that LAI has a lower but best relation with individual red and near IR bands (3-4) of the IKONOS (R^2 = 0.2, 0.32 respectively). These results validate the use of red and NIR bands within the calculation for most of the vegetation indices.

Linear regressions for vegetation indices (e.g. NDVI and SR) vs. $LAI_{in\ situ}$ indicated that there was a higher and more significant correlation between NDVI and $LAI_{in\ situ}$ measurements in comparison with SR and $LAI_{in\ situ}$ values. Moreover, the band correlation used for the NDVI estimates minimizes the influence in variation of atmospheric conditions, the NDVI models would be more appropriate for use in investigations where temporal variations are considered (Kovacs, 2004). The purpose of using spectral vegetation indices is to maximize the vegetation cover signal and at the same time minimize the response from the background (e.g. soil or understory) (Rautiainen, 2004). Limitations in the capacity to minimize background reflectance within the mangrove study sites may explain the low correlation of $LAI_{in\ situ}$ with SR values.

Furthermore, linear regressions between the derived IKONOS LAI image (based on the NDVI spectral values) and the field-based $LAI_{in\ situ}$ measurements indicated a high correlation between these parameters. This suggests that, for La Parguera Marine Reserve, the NDVI model can be used to predict LAI on multispectral satellite imagery (e.g. IKONOS) with a confidence of over 65% (APPENDEX 3). Possible errors maybe due to soil background reflectance, interference by other mangrove types (e.g. Avicennia germinans) or interference by live parts of plants other than leaves may account for the resultant 35% of variability

Overall, it is always necessary to understand the factors regulating the general high rates of aboveground net primary production, including the extent to which mangrove-derived organic matter is recycled and conserved within the forest floor (Alongi, 1998). Taking into consideration that accurate LAI (IKONOS) maps were achieved, the NPP equation was implemented to produce an NPP image of La Parguera. Values for aboveground NPP (ANPP) obtained were in the range of those previously reported for the Caribbean, Turks and Caicos and Florida above ground mangroves forests (Table 13). Hence, globally ANPP may range from 2.12 to 23.4 g/m^2/d (Sherman et al., 2003).

Table 13. Some net primary productivity values reported for the Turks and Caicos, Caribbean, and Florida red mangrove stands.

Monospecific Sites	**Net Primary Productivity (g/m^2/d)**	**References**
La Parguera, Puerto Rico	12.6 (mean)	This study
La Parguera, Puerto Rico	5.2	Golley et al., 1962
South Florida	5.6	Miller, 1970
Turks and Caicos	5.4	Edwards, 1997
Virginia Key, Florida	16.56*	Snedacker et al.,1998

* estimated value, calculated for a daily value

Subsequently, the NPP values were plotted with $\text{LAI}_{in\ situ}$ for all study sites and similar spatial patterns were observed between the parameters. Study sites with higher $\text{LAI}_{in\ situ}$ values projected higher NPP values. Herein, results may possibly indicate the relationship between the photosynthetic capacity of the mangrove canopy, the density of canopy and its closure. Since it has been reported that a model of primary production and transpiration of forest canopies predicts that the maximum photosynthesis for mangrove stands occur with a leaf-area index of about 2.5 if no acclimation to shade within the canopy occurs. A leaf area greater than about 2.5 may decrease production (Miller, 1971).

Moreover, the highest $\text{LAI}_{in\ situ}$ and NPP values were observed within the study sites that receives continual exogenous nutrient inputs (e.g. Bird Island, which has been for a long term a habitat for birds and Varadero, which receives frequent discharge from a sewage treatment plant). This may suggest that nutrients are one of the most essential parameters that drive the primary productivity of the mangrove forest in the Natural Marine Reserve of La Parguera.

Finally, the NPP model was plotted with leaf fall measurements obtained during the same month. Effects on the NPP due to the leaf fall variations were not clearly observed within the study sites. Thus, a tendency for an increase in NPP with a decrease of leaf fall was observed in some of the study sites. Correlations within NPP and leaf fall or litter production can help explain the dynamics of NPP in red mangrove ecosystems. In this direction, Bunt (1970) reported similar results correlating NPP with light attenuation and comparing his results with litter production. He measured net photosynthesis in mangrove communities using a procedure that involves measurement of light attenuation through forest canopies attributable to photosynthetic utilization and standardized against leaf pigment assays. Results showed that production estimates range between 16 to 26 kg C ha^{-1} day^{-1}. Comparison of the estimated photosynthesis production rates with the average litter production rates strongly suggested that such estimates of photosynthetic production are reasonable.

3.6 Conclusions

Although remote sensing data can be useful for monitoring vegetation changes, NPP ground-truthing is still essential for the determination of mangrove health. Leaf area index is the most important indicator of forest status because of the role of green leaves in controlling many biological and physical processes and because of its relationship with photosynthesis. The present study concludes that for multispectral images such as IKONOS:

1. Spectral data for red and NIR bands can result in high correlations with LAI$_{in\ situ}$ estimations,
2. Vegetation indices such as the NDVI can be used to produce and accurately estimate red mangrove canopy LAI. When all precautions are

taken into consideration, these derived LAI values can predict LAI with more than 65% accuracy, and

3. Spectral LAI values can be achieved and transformed to produce a highly spatial NPP resolution maps.

Overall, this research concludes that accurate high spatial resolution LAI derived products can be transformed to net primary productivity images. Spatial variations of the NPP can be derived from remotely sensed images and can possibly be used to explain ecological patterns of LAI and leaf fall. Since management and conservation is of fundamental importance for the survival of these fragile ecosystems in this new era of global climate change, this information can be beneficial for effective resource conservation and management.

4.0 General Conclusions & Recommendations for future work

This research concludes that primary productivity of mangrove forests can be estimated with direct methods (e.g. litterfall) and also by indirect methods (e.g. satellite-derived LAI data). Litterfall is an important parameter for the determination of mangrove productivity and thus it is highly influenced by other physical and chemical parameters such as LAI and nutrient availability. Leaf and seedling litter are the main components of the red mangrove litterfall. The amount of leaf litter is related to the mangrove productivity as well seedling is an account of the reproduction rate of these ecosystems. Spatial and temporal primary productivity variations within the study sites are mainly influenced by air temperature, salinity and nutrient availability.

Mangrove productivity can accurately be assessed with remote sensing techniques. This study confirms that satellite-derived LAI images can be transformed to net primary productivity maps. The spatial distribution of NPP can be clearly detected from satellite imagery.

Future work can include correlations between satellite derived NPP values and its validation with ground truthing data. Long term monitoring of red mangrove primary productivity should be a priority for research, most importantly because of the reported connectivity that exists between mangrove and other near-shore marine environments such as seagrass beds and coral reefs.

LITERATURE CITED

Agrawala, S., T. Ota, J. Risbey, M. Hagenstad, J. Smith, M. Van Aalst, K. Koshy, and B. Prasad. 2003. Development and climate change in Fiji: focus on coastal mangroves. Paris: Environment Directorate and Development Cooperation Directorate, Organisation for Economic Cooperation and Development (OECD). Report no. COM/ENV/EPOC/DCD/DAC(2003)4/FINAL.

Alberto D.J. Navarrete, Oliva - Rivera J.J. 2002. Litter Production of *Rhizophora mangle* at Bacalar Chico, Southern Quintana Roo, Mexico. Universidad y Ciencia 18 (36): 79-86.

Alongi, D. M., A. Sasekumar, F. Trendi and P.Dixon. 1998. The influence of stand age on benthic decomposition and recycling of organic matter in managed mangrove forest of Malaysia. Journal of Experimental Marine Biology and Ecology. 225: 197- 218.

Armstrong, R. 1981. Changes in Puerto Rican coral reef 1936 -1978 using aerial photoanalysis. Proceedings of the Fourth International Coral Reef Symposium, Manila. 309 – 315.

Armstrong, R. 1990. Spectral Response to Nutrient Enrichment in Mangroves. PhD thesis. University of Puerto Rico, Mayaguez Campus. 105 p.

Aschbacher, J.; Ofren R. et al. 1995. An integrated comparative approach to mangrove vegetation mapping using advanced remote sensing and GIS technologies: preliminary results. Hydrobiologia. 295. 285-294.

Bettinger, P., R. Hayashi. 2006. Estimation of above-ground biomass with remotely sensed imagery: A brief literature review. Warnell, School of Forestry and Natural Resources, The University of Georgia**.** 10. 11 p.

Bosire, J. O., F. Dahdouh-Guebas, J.G. Kairo, J. Kazungu, F. Dehairs, and N. Koedam . 2005. Litter degradation and CN dynamics in reforested mangrove plantations at Gazi Bay, Kenya. Biological Conservation. 126. 287–295.

Bouriaud, O., K. Soudani, and N. Bréda 2003. Leaf area index from litter collection: impact of specific leaf area variability within a beech stand. Canadian Journal of Remote Sensing. 29 (3). 371-380.

Breda, N. J. 2003. Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. Journal of Experimental Botany. 54 (392). 2403-2417.

Bunt, J. S. 1979. A survey method for estimating potential leaves of mangrove forest primary production. Marine Biology. 52. 123-128.

Bunt. J.S. 1995. Continental scale patterns in mangrove litterfall. Hydrobiología 239. 135-140.

Chen, J. M., J. Liu, J. Cihlar, and M.L. Goulden. 1999. Daily canopy photosynthesis model through temporal and spatial scaling for remote sensing applications. Ecological Modelling. 124. 99-119.

Chen, J. M., J. Cihlar. 1996. Retrieving Leaf Area Index from Boreal Conifer Forest using Landsat TM. Remote Sensing of Environment. 55. 153-162.

Chen, J. M., P. M. Rich, S.T. Gower, J.M. Norman, and S. Plummer. 1997. Leaf area index of boreal forests: Theory, techniques, and measurements." Journal of Geophysical Research. 102 (24). 29,429-29,443.

Chen, J. M., G. Pavlica, L. Brown, J. Cihar, S.G. Leblanc, et. al. 2002. Derivation and validation of Canada-wide coarse-resolution leaf area index maps using high-resolution satellite imagery and ground measurements. Remote Sensing of Environment. 80. 165-184.

Clough B., D. Trung Tan, D. Xuan Phuong, and D. Cong Buu. 2000. Canopy leaf area index and litter fall in stands of the mangrove Rhizophora apiculata of different age in the Mekong Delta, Vietnam. Aquatic Botany**.** 66. 311-320.

Colombo, R., D. Bellingeri. 2003. Retrieval of leaf area index in different vegetation types using high resolution satellite data. Remote Sensing of Environment. 86. 120-131.

Decagon Devices, Inc. Operator’s Manual, AccuPAR Light Interception Device. Model PAR-80. 117 p.

Duke, N. C. 2007. A World without Mangroves? Science. 317**.** 41 - 42.

Edwards, A. J. 1997. Assessing Mangrove Leaf Area Index (LAI) using CASI Airborne Imagery, 162 – 276. *In* A. J. Edwards (Eds). Applications of satellite and airborne image data to coastal Management. Coastal region and small island papers 4. UNESCO.

Emmons, L. H., P. Chatelet, L. Cournac, and N.C.A. Pitman, et. al. 2006. Seasonal changes in leaf area index at three sites along a South American latitudinal gradient. Ecotropica. 12. 87- 102.

Enriquez, S., C.M. Duarte, and K. Sand-Jensen. 1993. Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. Oecologia. 94. 457-471.

Fang, H., S. Liang, and A. Kuusk. 2003. Retrieving leaf area index using a genetic algorithm with a canopy radiative transfer model. Remote Sensing of Environment. 85. 257- 270.

FAO. 2007. The world's mangrove 1980-2005: a thematic study prepared in the framework of the Global Forest Resources Assessment 2005. F. Department, Food and Agriculture Organization of the United Nations**.** 89 p.

Fell, J.W., M. Master. 1981. Litter decomposition and nutrient enrichment, 239–251. *In* Snedaker, S.C., J.G. Snedaker (Eds.), The Mangrove Ecosystem: Research Methods. UNESCO, Bungay, UK.

Feller, I. C., M. Sitnik. 1996. Mangrove Ecology: A Manual for a Field Course. Institute**.** 135 p. Smithsonian Institute.

Feller, I. C., D. F. Whigham, J.P. O'Neill, and K.L. McLee. 1999. Effects of nutrient enrichment on with-in stand cycling in a mangrove forest. Ecology. 80 (7). 2193–2205.

Feller, I., C.E. Lovelock, and K.L. McKee. 2007. Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus Limited Mangrove Ecosystems. Ecosystems. DOI: 10.1007/s10021-007-9025-z

Fourqurean, J. W., J.E. Schrlau. 2003. Changes in nutrient content and stable isotope retaios of C and N during decomposition of seagrasses and mangrove leaves along a nutrient availability gradient in Florida Bay, USA. Chemistry and Ecology. 19 (5): 373-390.

Golley, F., H.T. Odum, and R.F. Wilson. 1962. The structure and metabolism of a Puerto Rican Red Mangrove Forest in May. Ecology. 43 (1). 9-19.

Gong, P., R. Pu, G. S. Biging, and M. R. Larrieu. 2003. Estimation of forest leaf area index using vegetation indices derived from Hyperion hyperspectral data. IEEE transactions on geoscience and remote sensing. 41 (6). 1355-1362.

Green, E. P., P.J. Mumby, A.J. Edwards, C.D. Clark. 2000. Assessing mangrove leaf area index and canopy closure. 245 – 253. *In* A.J. Edwards (Eds), Remote Sensing Handbook for Tropical Coastal Management. UNESCO.

Jin-Eong, O. 1995. The ecology of mangrove conservation and management. Hydrobiología. 239. 343-351

Johnson, L. 2003. Temporal stability of an NDVI-LAI relationship in a Napa Valley vineyard. Australian Journal of Grape and Wine Research. 9. 96-101.

Juman, R. A. 2005. Biomass, litterfall and decomposition rates for the fringed Rhizophora mangle forest lining the Bon Accord Lagoon,Tobago. Revista de Biología Tropical. 53 (1). 207-217.

Kovacs, J. M., F. Flores-Verdugo. 2004. Estimating leaf area index of a degraded mangrove forest using high spatial resolution satellite data. Aquatic Botany. 80. 13-22.

Kovacs, J. M., J. Wang and F. Flores-Verdugo. 2005. Mapping mangrove leaf area index at the species level using IKONOS and LAI-2000 sensors for the Agua Brava Lagoon, Mexican Pacific. Estuarine, Coastal and Shelf Science. 62. 377-384.

Lee,K.S.; Y. I. Park, S. H. Kim, J. H. Park, C. S. Woo, and K. C. Jang. 2004. Remote sensing estimation of forest LAI in close canopy situation. Internet.

Lee, S.Y. 1990. Primary productivity and particulate organic matter flow in an estuarine mangrove-wetland in Hong Kong. Marine Biology. 106. 453-463.

Lugo, A. E; J. A. González, B. Cintrón and K. Dugger. 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. BioTropica.10 (4). 278-291.

Lugo, A. 1989. Los manglares de Puerto Rico. Acta Científica 3 (2-3). 135-140.

Lugo, A.E. 1998. Mangrove ecosystem research with emphasis on nutrient cycling, 279 – 305. *In* Gopal, B., P.S. Pathak, K.G. Saxena (Eds.) Ecology Today: An anthology of comtemporary ecological research. International Scientific Publications, New Delhi

Lugo, A.E., S. Maurice, S.C. Snedaker. 1973. Mangrove Ecosystem Analysis. Reprint # 14479. UPR-RUM. 113-143.

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

McLoad, E., R. V. Salm. 2006. Managing mangroves for resilience to climate change. IUCN, Gland, Switzerland**.** 64 p.

Miller, P.C. 1971. Bioclimate, leaf Temperature, and primary production in red mangrove in South Florida. Ecology 53 (1). 22-45.

Musa, J.C. 1986. Influencia de los tributarios de agua dulce en la física y química del suelo, estructura, productividad, retorno y eficiencia de nutrientes (N,P,K,Ca) en el bosque de mangle de la laguna de Cabo Rojo, Puerto Rico. PhD thesis. University of Puerto Rico, Mayaguez Campus. 214 p

Murray, M., S.A. Zisman, P.A. Furley, D.M. Munro, et. al. 2003. The mangroves of Belize. Part 1. distribution, composition and classification. Forest Ecology and Management. 174. 265-279.

Navarrete, A. J. 2002. Litter production of Rhizophora mangle at Bacalar Chico, southern Quintana Roo, Mexico. Universidad y Ciencia 18 (35). 79-86.

Odum, W. E., C.C. McIvor, and T.J. Smith, III 1982. The ecology of mangroves of South Florida: a community profile., U.S. Fish and Wildlife service, Office of Biological Services, Washington, D.C. FWS/OBS-81/24. 144 p.

Onuf, C.P., J.M. Teal and I. Valiela. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology. 58. 514-526.

Pool, D.J. 1972. The role of mangrove ecosystems: mangrove leaf area indices. Bureau of Sport Fisheries & Wildlife. PB-231 745. 1-10

Pool, D.J., A. Lugo and S.C. Snedaker. 1986**.** Litter production in mangrove forests of Southern Florida and Puerto Rico. Reprint # 14462, UPR-RUM. 213-237.

Raulerson, G. A. 2004. Leaf litter processing by macrodetritivores in natural and restored neotropical mangrove forest. Agricultural and Mechanical College. Louisiana, Louisiana State University. PhD thesis. 155 p.

Robertson. A.I. 1988. Decomposition of mangrove leaf litter in tropical Australia. Journal of Experimental Marine Biology Ecology. 116. 235-247.

Rodríguez, W., I. Feller. 2004. Mangrove landscape characterization and change in Twin Cays, Belize using aerial photography and IKONOS satellite data. Atoll Research Bulletin. 513. 23 p.

Rogers, J. 1997. Nutrient dynamics and productivity in mangrove ecosystems. Literature Review-Submitted in partial fulfillment of assessment for the BSc. Honors. The University of Queensland, Australia. 71 p.

Rautiainen, M., P. Stenberg and T. Manninen. 2004. Mapping of LAI using optical satellite images. Proceedings of IUFRO Conference ‘Modeling forest production’, Vienna.

Sherman, R.E., T.J. Fahey, and P. Martínez. 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. Ecosystems. 6. 384 – 398.

Snedaker, S. C., J.G. Snedaker, Ed. 1984. The mangrove ecosystem: research methods. Monographs on oceanographic methodology, UNESCO, UK. 251 p.

Snedaker, S.C., R.J. Araújo. 1998. Stomatal conductance and gas exchange in four species of Caribbean mangroves exposed to ambient and increased CO2. Marine Freshwater Research. 49. 325 – 327.

Sonnentag, O., J. Talbot, J.M. Chen and N.T. Roulet. 2007. Using direct and indirect measurements of leaf area index to characterize the shrub canopy in an ombrotrophic peatland. Agricultural and.Forest Meteorology. doi:10.1016/j.agrformet.2007.03.001

Stenberg, P., M. Rautiainen, T. Manninen, P. Voipio, and H. Smolander**.** 2004. Reduced simple ratio better than NDVI for estimating LAI in Finnish pine and spruce stands. Silva Fennica. 38 (1). 3–14.

Stroppiana, D., M. Boschetti, R. Confalonieri, S. Bocchi, and P. A. Brivio. 2006. Evaluation of LAI-2000 for leaf area index monitoring in paddy rice. Field Crops Research. 99. 167-170.

Suárez, N. 2003. Leaf longevity, construction, and maintenance costs of three mangrove species under field conditions. Photosynthetica. 41 (3). 373-381.

Twilley, R.R., A. E. Lugo, and P. Patterson-Zucca. 1986. Litter production and turnover in basin mangroves forests in southwest Florida. Ecology. 67 (3). 670-683.

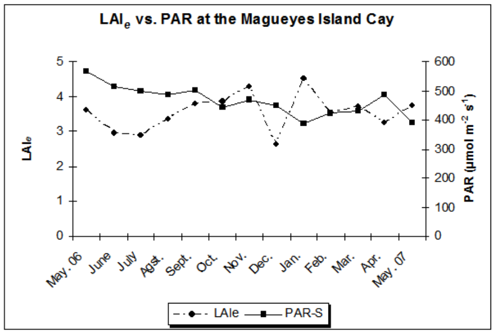
UNESCO. 1984. <u>The mangrove ecosystem: research methods</u>, UNESCO.

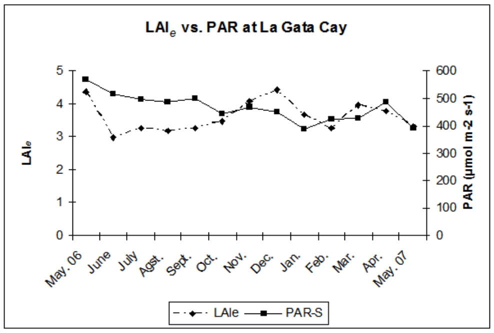
UNESCO. 1998. CARICOMP-Coral reefs, seagrass and mangrove sites. Coastal Region and small island papers 3. UNESCO. Paris. Xiv**.** 347 p.

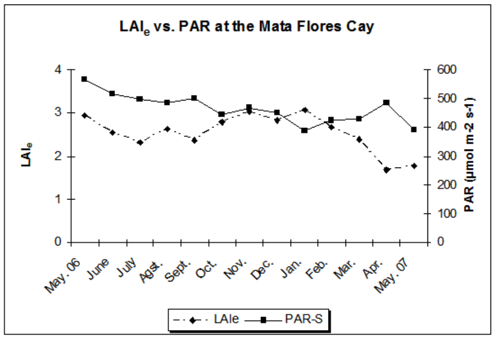
Wafar, S., A. G. Untawale, and M. Wafar. 1997. Litter Fall and Energy Flux in a Mangrove Ecosystem. Estuarine, Coastal and Shelf Science. 44. 111-124.

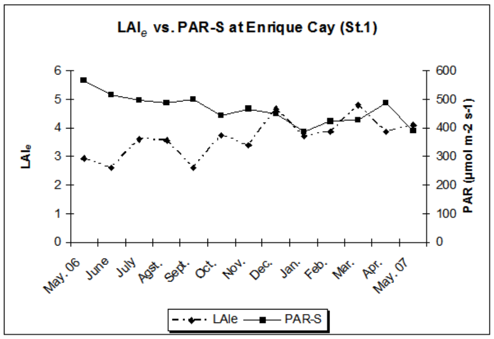
Wythers, K. R., P.B. Reich, and D.P. Turner. 2003. Predicting leaf area index from scaling principles: corroboration and consequences. Tree Physiology 23. 1171-1179.

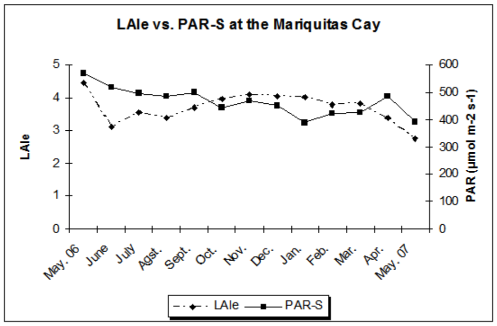
APPENDIX 1: Time series for LAIe and PAR for the study sites in La Parguera

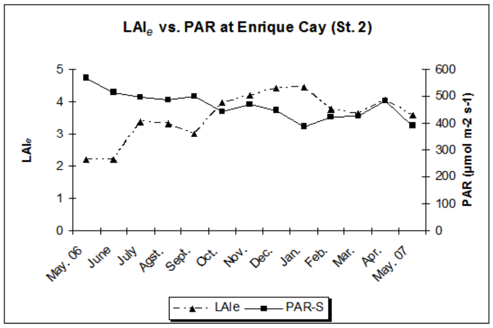

LAI$_e$ vs. PAR at the Magueyes Island Cay

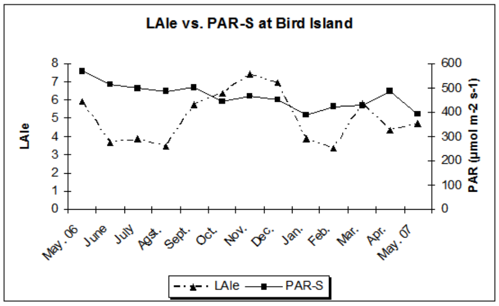

LAI$_e$ vs. PAR at La Gata Cay

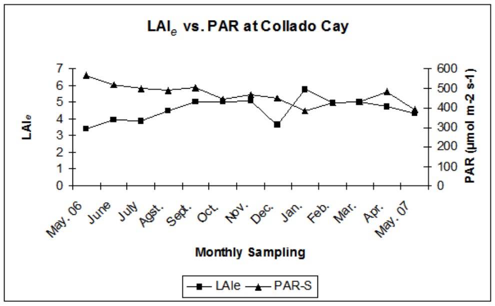

LAI$_e$ vs. PAR at the Mata Flores Cay

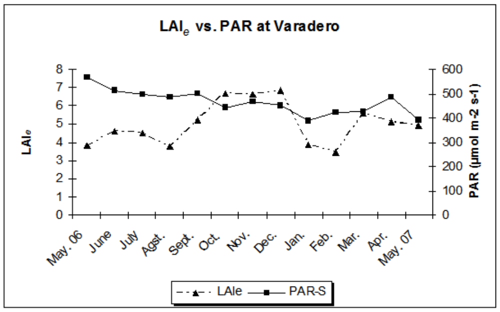

LAI$_e$ vs. PAR-S at Enrique Cay (St.1)

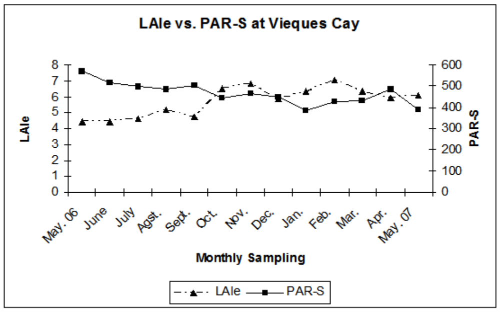

LAIe vs. PAR-S at the Mariquitas Cay


LAI$_e$ vs. PAR at Enrique Cay (St. 2)

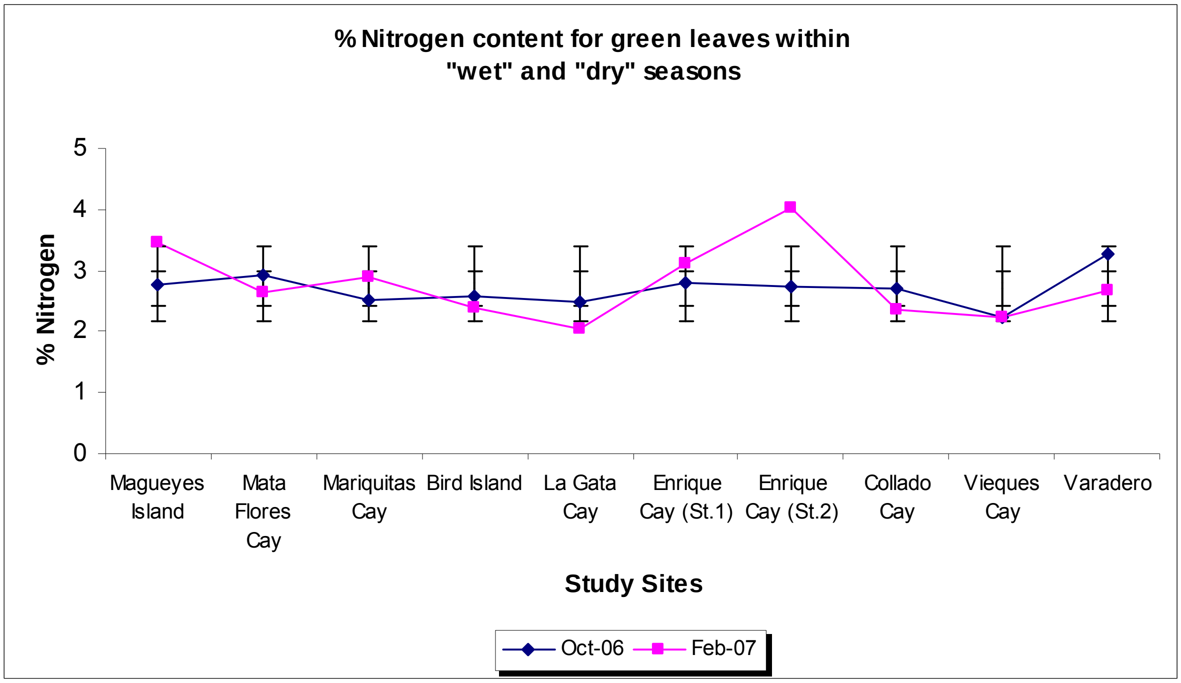

LAIe vs. PAR-S at Bird Island


LAI$_e$ vs. PAR at Collado Cay


LAI$_e$ vs. PAR at Varadero


LAIe vs. PAR-S at Vieques Cay

APPENDIX 2:
% N for green leaves within “wet” and “dry” seasons.



APPENDIX 3:
IKONOS LAI for three study sites

(LAI$_{in\ situ}$ values were significantly different between them,
Kruskall-Wallis, H = 73.99)