Ecosistemas de Manglar en América Tropical

Mangrove Ecosystem in Tropical America

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Ecosistemas de Manglar en América Tropical

Mangrove Ecosystem in Tropical America

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Presentación

El Instituto de Ecología A.C. -dentro del sistema de Centros SEP-CONACYT- es una institución de reconocido liderazgo a nivel nacional, desarrollando investigación de vanguardia y formando recursos humanos a nivel de posgrado. Al promover la publicación del libro ***Ecosistemas de Manglar en América Tropical***, este Instituto cumple con su misión de conocer, proteger, y fundamentar la utilización racional y sostenible de los ecosistemas críticos, a dos niveles. Primero, atender la urgente necesidad de presentar un libro integrado sobre los manglares, que constituyen actualmente en el mundo uno de los tópicos de mayor importancia y preocupación. Segundo, porque al disponer de un libro sobre los fundamentos para comprender ecológicamente los ecosistemas de manglar, se refleja la pertinencia de este Instituto que, en 1998 tomó la decisión de crear el Programa de Recursos Costeros, para desarrollar investigaciones de relevancia y formar recursos humanos en una eco-región que incluye las tierras bajas inundables, los humedales de la llanura costera, las planicies asociadas al litoral, las cuencas bajas de los ríos, las dunas costeras, las lagunas costeras y estuarios, la línea de costa, y desde luego los manglares.

Este libro reúne las contribuciones científicas de 34 investigadores de 27 instituciones en 10 países de América tropical. Los editores (Alejandro Yánez-Arancibia y Ana Laura Lara-Domínguez), se propusieron integrar las contribuciones científicas de especialistas de gran experiencia, cuyas opiniones autorizadas permitan avanzar en las recomendaciones de normatividad que se requieren en América tropical, para la administración integral de la zona costera. Por tal razón, el enfoque y la perspectiva de este libro son inéditos.

Los manglares constituyen un importante recurso forestal en toda la banda intertropical del planeta, con una cobertura aproximada a 240 mil kilómetros cuadrados. En América tropical incluyendo el Caribe, la cobertura se estima cerca de 60 mil kilómetros cuadrados. Son los árboles que sostienen la biodiversidad de los ecosistemas tropicales, en los humedales forestados intemareales y áreas de influencia tierra adentro. Estos ecosistemas constituyen un rasgo distintivo de gran relevancia científica y cultural. A nivel mundial los bosques de manglar constituyen un cuarto de las costas tropicales y, por lo tanto, son una gran reserva ecológica y forestal del planeta.

Este libro permitirá avanzar en resultados y bases técnicas, en busca de la Implementación de una política de gestión adecuada, en los países que poseen este importante recursos natural, a la vez que permitirá estimular un vigoroso programa de investigación sostenida para comprender, evaluar ecológicamente, valorar en términos de economía ambiental, utilizar racionalmente, y proteger estos recursos que son patrimonio de la biosfera.

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El Desafío Americano

En la cintura de América está anclada una región dinámica, bella, de gran riqueza natural, extraordinaria diversidad biológica, geográfica, y cultural, conformada por México, Guatemala, Belice, el Salvador, Honduras, Nicaragua, Costa Rica y Panamá Estrecha franja de tierra bañada por el Océano Pacifico y el Mar Caribe que sirve de puente entre dos amplias masas continentales: Norte y Suramérica. Mesoamérica es también tierra de contrastes; a pesar de su extraordinaria riqueza biológica, ésta no se ha traducido en bienestar generalizado para sus habitantes. Aunque la diversidad biológica es tema prioritario en las agendas de los gobiernos de la región; por diversas razones las políticas de conservación no siempre se basan en la relación armoniosa que debe existir entre la gente y los recursos naturales, lo que ha resultado en un alto índice de pobreza, por un lado, y en una explotación desmedida de los recursos naturales, por el otro.

En el marco de nuevos desafíos culturales, nuevas visiones políticas del mundo, nuevas posibilidades tecnológicas y un sistema económico más abierto, la lucha por la paz, la erradicación de la pobreza, la conservación de la naturaleza y el desarrollo humano sostenible y equitativo en el Planeta Tierra, requiere de esfuerzos transnacionales y estrategias novedosas que, a su vez, se concreten en acciones regionales, nacionales y locales. Conscientes de la responsabilidad que compete a cada región, y basados en las premisas del desarrollo sostenible, los miembros, las comisiones y el secretariado de la UICN en Mesoamérica, ha presentado ante la comunidad mundial reunida en Fontainebleau en Noviembre de 1998 -con ocasi6n del 50 Aniversario de la UICN-, el compromiso y propuesta general de acción para el nuevo milenio; centrado en cinco grandes renglones: Cruzada por la biodiversidad, Escenario demostrativo del desarrollo sostenible, Ciudadanía ecológica, Política con visión ambiental y Ciencia y creatividad con ética.

En Mesoamérica la Unión Mundial para la Naturaleza UICN, está trabajando desde 1988 con la *misión* de -contribuir a la consolidación de una Alianza regional para Cuidar la Tierra Mesoamericana-, Hoy se suman a esta tarea más de 50 miembros de la región -incluyendo organismos gubernamentales y ONG's-, gran cantidad de socios, más de 300 especialistas incorporados a las comisiones de la UICN y el secretariado de la Oficiné Regional de la Unión en Mesoamérica. Desde su fundación en 1988 la Oficina Regional para Mesoamérica (ORMA), coordina una serie de actividades con el propósito de poner en práctica el concepto de desarrollo sostenible, como una respuesta apropiada a las necesidades a largo plazo de esta hermosa región Mesoamericana.

En consecuencia con esta *misión,* la UICN-Mesoamérica tomó la decisión de auspiciar este libro sobre los *Ecosistemas* de *Manglar* en *América Tropical* que, en un esfuerzo sin precedentes. Integra valiosas experiencias en América, a la vez que representa una aportación más de la gran producción científica del Dr. Alejandro Yáñez-Arancibia (Miembro de la Comisión de Manejo de Ecosistemas Costeros de UICN). Nada más pertinente para la UICN-Mesoamérica que ser un co-editor de esta obra que constituye otro instrumento valioso para el desafío Mesoamericano.

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Foreword

An international ecological monograph with the participation of 34 researches from 27 different institutions from 10 countries of Topical America.

The main purpose of this book is to produce an up-to-date, authoritative, peer-reviewed, multi-authored volume on significant processes in mangrove ecosystems. The scientific contributions are focused on resource management and policy decisions that are required fort management of mangroves ecosystems in Tropical America. The book has the support of the International Union for Conservation of Nature and Natural Resources (UICN). The National Marine Fisheries Service (NMFS). National Oceanic and Atmospheric Administration (NOAA), US Department of Commerce also has provided funding support for this publication.

Presently, coastal management is a prominent topic of concern to the world. It is urgent to produce a complete book to serve as a basis for understanding the ecological processes in mangrove ecosystems. These ecosystems are a distinctive feature in the tropical and subtropical coastlines of the Americas and the Caribbean Sea, with great scientific, economic and cultural value. At the worldwide level, mangrove forests constitute one-fourth of the tropical coast and thus constitute expansive ecological and forest reserves.

At the same time, mangrove forests are very important to humanity for the following reasons: a) they export organic matter which becomes a nutritious food source for a variety of fish resources, with an accompanying stimulatory effect on primary productivity of the adjacent aquatic ecosystem; and b) they support important tropical fisheries; because they constitute a refuge with high food availability for the early critical stage of life for many species of shellfish and fishes. These species use the mangrove ecosystem as reproductive and/or nursery areas.

Mangrove forests also provide several goods and service for human populations such as tannins, timber, firewood and charcoal. They constitute an important genetic pool for flora and fauna biodiversity and are very important regionally as an ecological heritage. These attributes increase their scientific, economic and cultural value. Mangroves are also noted for their ability to stabilize coastal shorelines that otherwise might be subject to erosion and loss.

On October 11, 1966, the United States Congress signed into law the Sustainable Fisheries Act Amendments to the Magnuson-Stevens Fisheries Conservation and Management Act. Within this Act were provisions required to establish of Fisheries Management Council in the United States to amend existing Fishery Management Plans to include a description of Essential Fish Habitat, which is defined as those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity. This publication on the structure, function and management of mangrove systems provides a major contribution to the establishment of mangrove ecosystems as Essential Fish Habitat. Three US Fishery Management Councils, because of the major distribution of mangroves within their spheres of fishery management responsibility, will particularly benefit from this publication: the Caribbean Fishery Management Council. The Gulf of Mexico Fishery Management Council and the South Atlantic Fishery Management Council.

The monograph can help promote research and provide a technical basis related to the search for suitable management policies in developing countries that possess this natural resource. This book can also support sustainable research program to understand, evaluate, exploit and conserve mangrove ecosystems.

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Después de un largo proceso, este libro Ecosistemas de Manglar en América Trópical, fue finalmente publicado gracias al esfuerzo, entusiasmo, amistad y aporte institucional, de las siguientes personas: Dr. Gordon W.Thayer de la NOAA/NMFS; Dr. John W. Day, Jr. de Louisiana State University; Dr. Enrique Lahmann de U/CN/ORMA; Dr. Sergio Guevara Sada del Instituto de Ecología, A. C. ya Eduardo Sáinz-Hernández del Centro EPOMEX-UAC. Los Editores les dedicamos un especial reconocimiento.

Dedicatoria

Alejandro Yáñez - Arancibia dedica este libro -con el cariño de toda una vida- a Paula, Rodrigo, Alexander, Paty, Daniela y Tania

Ana Laura Lara - Domínguez dedica este libro a Eduardo, Antón y Rodrigo

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1

Charter for Mangroves *

Colin D. Field

City Polytechnic of Hong Kong

The General Assembly of the United Nations adopted and solemnly proclaimed on 28th October 1982 a World Charter for Nature, affirming that nature shall be respected, genetic viability on earth shall not be compromised, conservation shall be practiced, sustainable management shall be utilized by man and nature, shall be secured against degradation.

The General Assembly now being aware that:

a) Mangrove forests are unique intertidal ecosystems that occur primarily in tropical regions of the world;

b) The total world-wide mangrove area is estimated at not less than 170,000 km and that there are some sixty species of trees and shrubs that are exclusive to the mangrove habitat;

c) Mangroves support genetically diverse communities of terrestrial and aquatic fauna and flora that are of direct and Indirect environmental, economic and social value to human societies throughout the world 41

d) Sustainable development of mangrove ecosystems implies the maintenance and rational use of the natural resource to ensure ecological resilience and economic opportunities for present and future generations,

e) Mangroves must be conserved in various parts of the world to prevent the occurrence degraded coastal lands.

Convinced that:

a) Destruction and degradation of mangrove forests are world-wide phenomena, as a result of activities related to the non-sustainable use and over-exploitation;

b) The value of mangrove lands is consistently underestimated when the areas are converted for non-sustainable purposes;

c) The sustainable use of mangrove ecosystems would provide a better use of the resource;

d) There is en urgent need to restore degraded mangrove ecosystems for economic, social and conservation reasons;

Persuaded that:

a) Mangroves are a valuable natural resource with distinctive genetic diversity, high intrinsic natural productivity and unique habitat value;

b) Mangroves sustain important economic and ecological values in adjacent terrestrial and marine systems;

c) Mangroves play en important role in the economic and social resources available to subsistence coastal dwellers in the tropics;

d) Mangroves play en important role In coastal protection and in the reduction of coastal erosion;

e) Mangroves buffer coastal waters from undesirable land-based Influences, such as sediment, contaminant or nutrient runoff;

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Reaffirming that people must acquire the knowledge lo use natural resources in a manner which ensures the protection and enhancement of species and ecosystems for their intrinsic values and for the benefit of present and future generations.

Convinced of the need for appropriate measures el Individual, collective and national levels lo manage, conserve and promote understanding of the mangrove ecosystem.

Convinced also of the need to foster the sharing of Information and understanding at an international level, and co-operation In all aspects of management and study of mangrove ecosystems.

Adopts, to these ends, a Charter which proclaims the following principles for the utilization of mangrove ecosystem by which all human conduct affecting mangrove ecosystems is lo be judged.

General Principles

1) Mangrove ecosystems shall be respected and their intrinsic characteristics shall be preserved wherever possible.

2) The genetic diversity inherent In mangrove ecosystems shall be safeguarded; lo this end the necessary habitats must os preserved.

3) Mangrove ecosystems that are utilized by people shall be managed lo achieve and maintain sustainable productivity without degrading the integrity of other ecosystems with which they coexist.

4) Mangrove ecosystems shall be secured against: indiscriminate destruction, natural ha hazards pollution and damage resulting from disturbance of surrounding areas

5) The sustainable utilization of mangrove ecosystems by traditional users shall be recognized and provided for to improve the welfare of the indigenous people.

6) The acquisition and dissemination of knowledge with respect lo structure, function and management of pristine and disturbed mangrove ecosystems shall be encouraged by all possible means, Including international research and technical cooperation.

Functions

7) The decisions affecting the management of mangrove ecosystems shall be made only in the light of best existing knowledge and an understanding of the specific location.

8) Decisions on how to manage a mangrove ecosystem shall be informed by definition of the following parameters:

(i) the biological components and the physical characteristics of the area under consideration, by means of inventories, maps and the collection of physical and biological data;

(ii) the needs of people In relation lo sustainable uses of the resource while ensuring adequate reserves for preservation purposes;

(iii) the national and international significance of the resource as habitat and as a genetic reservoir;

(iv) the national and international significance of the site for coastal stability and fisheries production;

(v) the local requirements for education, recreation and aesthetic values;

(vi) the requirements that must be satisfied for non-sustainable usos of the resource;

(vii) the extent to which rehabilitation and compensation mechanisms can be used lo mitigate the impact of non-sustainable use.

9) The information collected In (8) shall be used lo define the areas necessary for preservation, lo define strategies for the management, restoration and preservation of the resource, or lo define areas necessary for sustainable use.

10) Decisions on the use of mangrove ecosystems shall include consideration of the need:

(i) to utilize the mangrove resources so that their natural productivity la preserved;

(ii) to avoid degradation of the mangrove ecosystems;

(iii) lo rehabilitate degraded mangrove areas;

(iv) to avoid over exploitation of the natural resources produced by the mangrove ecosystems;

(V) to avoid negative impact on neighboring ecosystems;

(vi) to recognize the social and economic welfare of indigenous mangrove dwellers;

(vii) to control and restrict non-sustainable uses so that long term productivity and benefits of the mangrove ecosystems are not lost;

(viii) to Introduce regulatory measures for the wise use of mangrove ecosystems.

11) Activities which might impact on mangrove ecosystems shall be controlled by appropriate national, regional and international laws and agreements.

12) Activities which are likely lo pose a risk to a mangrove ecosystem shall be subjected lo en exhaustive examination prior lo decisions being made. Only after it has been publicity demonstrated that the potential advantages outweigh the potential damage should the activity be allowed to commence.

13) Mangrove ecosystems degraded by human activities shall be rehabilitated for purposes In accord with their natural potential and compatible with the well-being of the affected people.

Implementation

14) The principles set forth In the present Charter shall be reflected In the law and practice of each state, as well as at the international level.

15) Knowledge of the structure, function and importance of mangrove ecosystems shall be communicated by all possible means at local, national and international levels.

16) Knowledge of the structure, function and management of pristine and disturbed mangrove ecosystems shall be enhanced.

17) Educational programmes and regional centres shall be provided lo train scientist, planners, managers and the general public and lo encourage en awareness of the importance of mangrove ecosystems.

18) All planning shall include the establishment of biological, physical and socioeconomic inventories of the mangrove ecosystems under consideration and assessments of the effects on the systems and their surrounds of the proposed activities. All such considerations shall be open lo public scrutiny and comment prior lo any decision.

19) Resources, programmes and administrative structures necessary lo achieve the sustainable use of mangrove ecosystems shall be provided.

20) The status of mangrove ecosystems shall be monitored nationally and internationally to ensure evaluation of current practices and to enable early detection of adverse effects.

21) States shall establish specific statutory provisions or regulations for the protection and management of mangroves and mangrove ecosystems.

22) States, other public authorities, international organizations, non-government organizations, individuals, groups and corporations, to the extent that they are able, shall:

(i) co-operate in the task of managing mangrove ecosystems for sustainable purposes

(ii) establish procedures and methodologies for assessing the status of mangrove ecosystems and for managing them;

(iii) ensure that activities within their jurisdiction do not cause unnecessary damage lo mangrove ecosystem within or beyond their jurisdiction;

(iv) implement national and international legal provisions for the protection and conservation of mangrove ecosystems.

23) Each state shall give effect to the provisions of the present Charter through its competent organs and In cooperation with other states.

24) All persons, In accordance with their national legislation shall have the opportunity to participate, individually or collectively, In the formation of decisions of direct concern lo the conservation and sustainable use of mangrove ecosystems.

25) Affected people shall have means of redress when their mangrove ecosystems have suffered damage.

26) Each person has the duty lo act in accordance with the provisions of the present Charter, acting individually, In association with others, or through participation In a political process. Each person shall strive lo ensure that the objectives and requirements of the Charter are met.

Lacerda, L. D. and Y. Schaeffer-Novelli, 1999. Mangroves of Latin America: The need for conservation and sustainable utilization, p. 5-8. *In*: A. Yáñez-Arancibla y A. L. Lara-Domínquez (eds.). Ecosistemas de Manglar en América Tropical. Instituto de Ecología A.C. México, UICN/ORMA, Costa Rica, NOAA/NMFS Silver Spring MD USA. 380 p.

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Mangroves of Latin America: The Need for Conservation and Sustainable Utilization *

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Twenty years after the Stockholm Conference, when the Charter of the Environment was first adopted by the United Nations, a second Conference on the Environment and Development (UNCED.91, will be sponsored by UN in Rio de Janeiro, Brazil. The key topics of the UNCED will be Biodiversity and Sustainable Development. Since Stockholm, the world has witnessed an accelerated destruction of Its; natural resources, in particular in developing nations, most of them located In tropics. The process has been so destructive that most forest cover In the tropics may disappear, together with its large biological diversity, by the beginning of the next century.

Latin America has been one of the most affected regions by this rush for wealth al the expenses of Nature. The social-economic crisis of the 80's has driven nearly half of its population (c.a. 200 million people) Into complete poverty, creating heavy pressure upon the environment to achieve better living conditions at any cost. In this scenario, tropical ecosystems have been destroyed at unprecedented rates, either for their timber, charcoal, mineral resources, and the land itself. Among these ecosystems, mangrove forests, due to the exponential growth of coastal, urban, and industrial areas, have been most affected by diverse unsustainable uses, to a point that in certain Latin America countries up to 40% of the original mangrove cover have been eliminated.

Mangroves are the dominant vegetation for over 70% of tropical and sub-tropical coastlines of the world. They form complex forests with high wood biomass and structural complexity. Mangroves have developed morphological, physiological and reproductive adaptations which have allowed the colonization of salty, waterlogged and frequently reducing soils, with rapid growth in areas subject to geomorphic changes. These forests present high rates of primary production and are a key step in the transfer of nutrients, in particular of Carbon, from the continents to the sea and may play an important role, either as sources or sinks in the global cycle of such substances.

In Latin America, mangroves occur in all maritime countries except the three Southernmost nations of the continent. Although only scarce information of total mangrove area in Latin America exists, these forests may cover from 40,000 to 60,000 km^2 in the entire continent, en area equivalent to the mangrove forests of Southeast Asia and nearly twice the areas occupied by mangroves In Africa The forests are unevenly distributed along the continent's coastline, with the Atlantic and Caribbean coasts harboring nearly 70% of the total mangrove area in Latin America; The Pacific coast has a more restricted distribution due to climatic constrains generated by peculiar oceanographic conditions along the Peruvian coasts. The upwelling of the cold Humboldt

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Current waters suppresses convective activity and results in very arid climates, high soil salinity and nearly no freshwater inputs, restricting the extension of mangrove forests along the Pacific coast of South America to only $3^0$30' S, at the Tumbes River estuary. In the Atlantic coast mangroves extends Northward up to Bermuda (lat. 32 ^{0}N) and Southward to Paranagua; In Brazil (28^0 30´S).

Mangrove forest In Latin America are best developed along equatorial coasts influenced by the intense convective activity within the Intertropical convergence zone, which generates annual rainfall higher than 2,000 mm, and subjected to mesotidal or macrotidal regimes. These conditions era roughly restricted to within 10° of the equator and occur in the Northwestern part of South Ameríca from Northern Equator, Pacific coast of Colombia to Panama and South Costa Rica. On the Eastern coast, the optimal conditions occur South of Gulf of Paria (Venezuela) to Sao Luiz, in Brazil. In this dynamic and humid regions, mangrove forests attain their maximum growth. Red mangrove forests 40 lo 50 m In height and more than 1.0 m in diameter have been reported In Ecuador end Colombia. At the Southern coast of Costa Pica and several areas of the Panamanian coast, where seasonality is less pronounced and annual rainfall range from 2,100 lo 6.400 mm, mangrove trees exceed 35 m in height and a biomass of 280 ton/ha. Well developed black mangrove forests, with trees up lo 30 m in height and 0.7 m in diameter, occur on the coasts of Suriname, French Guyana and Northern Brazil, frequently with biomass over 200 ton/ha. Contrary to Southeastern Asia, Latin America mangrove forests are very poor In number of trees species. Although further systematic Investigation is needed due to high population variability among species of a given genus, Latin America mangroves include only 11 species. These are dominated by the genus *Rhizophora* (4 species) and *Avicennia* (4 species). Other important genus are *Laguncularia, Conocarpus* and *Pelliciera*, all with only one species. However, over 140 species of birds end 220 species of fish and hundreds species of Invertebrates species and a complex flora of mangrove associates, create high biodiversity environments along otherwise low biodiversity mudflats. Many mangrove areas, duo lo the accelerated destruction of inland forests in some Latin American countries, have become important sanctuaries and migratory routes of various species, which otherwise would be threatened lo extinction.

Mangrove play an important role in tropical coastal ecology including many goods and services for the human population. These include: coastline protection and stabilization, nursery for a variety of economically Important shellfish, and a source of Important products to coastal human populations in the form of timber, firewood and charcoal, although some of these benefits are presently little understood or unrecognized among many Latin American countries. Examples of the importance of such amenities provided by mangrove are many in Latino America.

Waterways protection using mangroves are common in Ecuador and Colombia. In Brazil, mangroves have recently been included in the management plans of marinas and coastal condominiums. In Panama, up to 60% of total shrimp fisheries is based on 5 species which depend on mangroves for completing their development Along the Maranhao coast, North Brazil, huge shrimp production Includes two species of shrimp which develop inside the local mangroves. Apart from these indirect amenities, mangrove products themselves are particularly important for many coastal populations. Firewood and charcoal seem lo be the major uses of mangroves in Latin America. In countries like Nicaragua, where nearly 80% of households use wood for cooking, mangroves provide a significant percentage of firewood.

In this country annual firewood extraction reaches up to 9.000 m^3. In Honduras the use of firewood may range from 80,000 to 120,000 m^3, and in El Salvador, with only 350 km^2 of mangroves, up lo 30,000 m^3 of firewood are extracted annually. In Brazil, mangroves are a regular source of firewood for bakeries and potteries, even along the most: developed areas of the Southeastern coast.

Charcoal production lo another major use of mangrove wood, although only a fraction of the total possible yield to collected due to inefficient extraction techniques. In Costa Rica up to 1,300 m^3 of mangrove charcoal is produced annually in the Terraba-Sierpe forests and, in Panama this may reach up lo 7,400 m^3. Mangrove bark is still an important source of tannins in most Latin America countries. Bark yields range from 1,840 lo 4,490 kg/ha in Costa Rica, while bark production in Panama may reach over 400 ton/yr.

Despite its enormous importance for most coastal tropical countries in Latin America, mangrove ecosystems have been witnessing en accelerated rush for their resources, most of the time without the necessary care to maintain their integrity and threatening their sustainable utilization. Estimates of deforestation in mangrove areas of Latin America are scarce. Central America has annual cover losses estimated for Nicaragua (385 ha); for Guatemala

(560 ha) and for Costa Rica (45 ha), mostly for conversion into rice fields, salt ponds and mariculture. In Ecuador nearly half of its mangrove area (*circa*. 80,000 ha) has been deforested for various purposes, particularly for shrimp ponds, during the last two decades. In the Ilha Grande Bay, Southeastern Brazil, almost 80% of the 600 ha of mangrove forest in existence in the early 80's has been reclaimed to build condominiums and marinas.

Apart from deforestation itself, degradation of large mangrove areas is taking place In many Latin America countries due to the misuse of coastal resources. Diversion of freshwater for irrigation and land reclamation purposes has been one of the major actions leading to mangrove degradation. Guanabara Bay mangroves, Rio de Janeiro, occurred an area of 50 km^2 in the beginning of the century, is presently nearly totally degraded with less than 15 km^2 of pristine forests, mostly due to clear cutting of creeks and river banks, oil spills, solid waste dumping and decreased freshwater Inputs.

Worldwide, mangrove forests have received special attention by decision makers in Southeast Asia countries, where these forests have traditionally been incorporated in the local economy, and many forms of sustainable uses are presently taking place. However in other parts of the world, particularly in Latin America, sustainable uses of mangrove forests are virtually nonexistent, resulting in deforestation and degradation of mangrove forest, many cases exposing the coastal zone to destructive ocean forces.

Although much damage has been done, extensive areas of pristine forests still exist in many countries of Latin America. These areas should be preserved and managed for sustainable utilization. Others, which have suffered varying degrees of human impact, may be rehabilitated through replanting, for non-destructive aquaculture, shoreline protection and enrichment of coastal waters. Lessons from past positive and negative experiences should be recorded and analyzed. Taking this Into consideration, the International Tropical Timber Organization (ITTo) and the International Society for Mangrove Ecosystems (ISME) started an International project on “Conservation and Sustainable Utilization of Mangroves in Latin America and Africa Regions”. Within the framework of this project, workshops on both continents will be organized, starting with a meeting in Rio de Janeiro, prior to the UNCED meeting In May'92. Briefly the objectives of these workshops are the following:

- To review the present status of mangrove forests in Latin America and Africa, including an evaluation of the data available on their total area, distribution, biodiversity, biogeochemistry and anthropogenic interactions.

- To assess mangrove forests utilization and their social economic Importance for the region, as well as en overview of the major environmental impacts upon these forests due to anthropogenic activities.

- To identify and propose management strategies and methods, future research needs and policies to be introduced in the region, to provide sustainable utilization and rational management of mangrove forests.

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Los Manglares de América Latina En la Encrucijada*

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Resumen

Los ecosistemas de manglar constituyen el tipo de vegetación dominante de las costas en la banda tropical y subtropical. Representan un enorme valor científico, económico y cultural para América Latina y el Caribe. Existen manglares en toda América Latina, exceptuando las tres naciones más al sur del continente. Su Importancia ecológica es bien reconocida, su valor económico está menospreciado, su protección legal es débil y su. deterioro ambiental es severo.

Abstract

Mangrove ecosystems are the dominant type of vegetation In the tropical and subtropical band. They bear en important economic, scientific, and cultural value for Latin America and the Caribbean. They are found throughout most part of the coastal countries of the region, except for the three southernmost countries of the continent. Although their ecological importance la well recognized, their economic significance is undervalued, their legal protection Is weak, and their environmental degradation is severe.

Distribución

Considerando las estimaciones recientes sobre el área total de manglar que existe en América Latina, estos bosques tienen una cobertura de mas de 40,000 km^2 en todo el continente, distribuidos uniformemente a lo largo de la línea costera (Tabla l). Más del 70% del área total de manglares está ubicada en las costas del Atlántico y Caribe. En el Pacífico, éstos tienen una distribución más restringida debido el clima generado por las peculiares condiciones oceanográficas a lo largo de las costas del Perú, donde las surgencias de las aguas frías de la corriente de Humboldt suprimen la actividad convectiva resultando en climas muy áridos, suelos muy salados y casi sin suministros dulceacuicolas. Esto restringe la extensión de los manglares en las costas de¡ Pacífico de Sur América hasta sólo 3^{0}30'S, en el Estuario del Río Tumbes en Perú (Fig. 1). Su distribución al norte está definida por la frecuencia, duración y/o intensidad de las temperaturas frías de invierno y precipitaciones. El límite Norte de los manglares de América Latina es la costa Oeste del Golfo de California en la Bahía de los Ángeles en Baja California (28° 54' N, 113° 31'W); sin embargo, existen va-

* Este capitulo contiene información previamente publicada en: Faro, 1: 3,7 (Septiembre, 1994) Santiago de Chile. Revista para Administración de Zonas Costeras en América Latina. Reproducido con permiso de ICSED

Tabla 1 . Estimaciones recientes de cobertura de los manglares y porcentajes respectivos con relación a áreas totales y longitud de los litorales de los países del continente americano

	Área (ha)	% superficie del País	Área/litoral manglares	Autor
Países Continentales				
EUA	190.00	0.02	10	Odum *et al*. (1982)
México	524.600	0.27	56	Yáñez-Arancibia *et al*. (1993)
Belice	73.000	3.10	189	Seenger *et al*. (1983)
Guatemala	16.040	0.15	40	Jiménez (1992)
Nicaragua	60.000	0.50	66	Seenger *et al*. (1983)
Honduras	121.340	1.08	148	Jiménez (1992)
costa Rica	41.330	0.08	32	Jiménez (1992)
El Salvador	35.235	1.65	45	Jiménez (1992)
Panamá	171.000	2.22	69	D'Croz (1993)
Colombia	358.000	0.31	148	Álvarez León. (1993)
Ecuador	161,770	0.60	72	MAG (1991)
Perú	4,791	<0.01	2	Echevarría y Sarabie (1993)
Venezuela	250.000	0.27	76	MARNR (1986)
Guayana Francesa	5.500	0.06	15	Seenger *et al*. (1983)
Guayana	150.000	0.70	326	Seenger *et al*. (1983)
Surinam	115.000	0.70	298	Seenger *et al*. (1983)
Brasil	1'012.376	0,12	134	Hertz (1991)
Países Insulares				
Trinidad y Tobago	7.150	1,40	20	Bacon (1993)
Jamaica	10.624	1.02	7	Bacon (1993)
Cuba	529.700	4.80	142	Padrón (1992).
Haití	18.000	0.65	10	Seenger *et al*. (1983)
Rep. Dominicana	9.000	0.20	7	Seenger *et al*. (1983)
Puerto Rico	6.500	0.71	-	Seenger *et al*. (1983)
Bahamas	141.957	10.18	40	Bacon (1993)
Bermuda	20	<0.01	< 1	Ellison (1993)
Guadalupe	8.000	4.49	20	Seenger *et al*. (1983)
Martinica	1.900	1.73	7	Seenger *et al*. (1983)
Islas Caimán	7.268	27.60	45	Bacon (1993)
Antillas*	24.571	--	--	Bacon (1993)

*Incluye sólo las islas donde hay registros de Inspecciones confiables (Anguila, Barbados, Barbuda, Bonaire, Curacao, Dominica, Granada y Grenadinas, Montserrat, Nevis, St. Kitts, St. Lucia, St. Vicent, Turks y Caicos

FIgura 1. Temperatura a 100 m de profundidad, Ilustra el hundimiento hacia el Oeste de la termoclina en cada océano. Isotermas de l0, 15, 20 y -sombreado en negro- >25 ^{0}C (en Longhurst: y Pauly, 1987). Esto se correlaciona con la extensión latitudinal de los manglares en América Tropical.

rias áreas pequeñas de comunidades de *Rhizophora mangle*, *Laguncularia recemosa* y *Avícennia germinans* de menos de 5 m de altura, como en las costas Este de Isla Tiburón, Punta Peñas (29° 2'N, 113° 36' W), y próximo a la costa Este de¡ continente del Golfo de California (Tabla 2) en un canal de marea denominado Estero del Soldado (29°17'N, 112°19' W). En la costa del Pacífico de Baja California los límites son similares. Además del clima, la fisiografía litoral es otro aspecto que restringe la extensión latitudinal de los manglares en el Pacífico. En la costa Atlántica, los manglares se extienden hacia el Norte hasta las Bermudas (latitud 32° N) y hacia el Sur hasta la región de Laguna en Brasil latitud 28° 30' S).

Tabla 2. Cobertura de bosques de manglar en las costas Atlántica y Pacífica de América Latina, Incluyendo las islas del Caribe, comparado con las áreas de bosques de manglar del mundo

	Área manglárica (ha)	% del Total	Autor
Costa Atlántica	2'143,356	52.8	Lacerda *et al*., 1993
Costa Pacífica	1'154,289	28.5	Lacerda *et al*., 1993
Islas del Caribe	764,690	18.7	Lacerda *et al*., 1993
TOTAL	4'062,335	28.6(100)	Lacerda *et al*., 1993
África	3'257,799	22.9	Diop, 1993
Suroeste Asiático	6'877,600	48.5	Seenger *et al*., 1983
TOTAL MUNDIAL	14'197,635	100	Lacerda *et a*l., 1993

Desarrollo

Los manglares en América Latina están bien desarrollados a lo largo de las costas ecuatoriales. Están influidos por la Intensa actividad convectiva dentro de la zona de convergencia intertropical, la cual genera precipitaciones anuales superiores a los 2,000 mm, y regímenes variables de mareas. Estas condiciones, óptimas en la parte Noroeste de Sur América, restringen severamente a los manglares dentro de los 10^{0} del Ecuador y los mejor desarrollados se presentan desde el Norte de Ecuador, en la costa Pacífica de Colombia, Panamá y el sur de Costa Rica. Asimismo, en la costa Este del continente, las condiciones tropicales óptimas se presentan desde el Sur del Golfo de Perla (Venezuela) hasta Sao Luiz en Brasil. En estas regiones dinámicas y húmedas, los manglares alcanzan su máximo crecimiento. En Ecuador y Colombia se han reportado bosques de manglar rojo *(Rhízophora mangle*) de 40 a 50 m de altura y más de 1 m de diámetro. Al sur del litoral de Costa Rica y diversos regiones de la costa Panameña, donde la estacionalidad es menos pronunciada y los rangos anuales de precipitación ven desde 2,100 a 6,400 mm, los árboles de manglar exceden los 35 m de altura y biomasa de 280 ton/ha. En la costa de Surinam, Guyana Francesa al Norte de Brasil, se presentan bosques de manglar negro *(Avicennia germinans) bien* desarrollados, con árboles por arriba de los 30 m de altura y 0.7 m de diámetro, con una biomasa frecuentemente mayor a las 200 ton/ha De manera excepcional, hacia el norte de dichas condiciones ambientales, en la Región de la Laguna de Términos en México (91° 00', 92°20' W y 18°20', 19°00' W), existen bosques de manglar negro (*Avicennia germinans*) con una altura máxima de 31 m y diámetro promedio aproximado de 0.4 m, y biomasa estimado de 760 ton/ha, indicando que el bosque es maduro, de elevada estabilidad ecológica y sin impacto ambiental. En éste localidad algunos árboles presentan diámetro de más de 1 m.

Un aspecto Importante de la estructura de los manglares es la variabilidad de los principales parámetros de acuerdo con el gradiente latitudinal. La Tabla 3 muestra esta variabilidad en todo el continente americano donde se presentan manglares (Lacerda *et al*., 1993).

Contrario a lo que se presenta en el Sureste de Asia, los manglares en América Latina son muy pobres en número de especies de árboles, donde tan sólo existen 11 especies. Estos son dominados por el género *Rh1zophora (4* especies), y *Avícennia* (4 especies). Otros géneros importantes son *Laguncularia, Conocarpus* y *Pelliceria*, con sólo una especie cada uno. Por lo tanto, la influencia de la temperatura en la distribución de los manglares es evidente al comparar la restringida banda de manglares a lo largo de la costa Pacífica de América del Sur, con una de las mayores áreas de manglar de la de Sudamérica debido al flujo de aguas cálidas región localizada a lo largo de la costa Atlántica hacia el sur (Tomilson, 1986; Fig. 2).

Figura 2. Distribución de las áreas de manglar (latitudes norte y sur) en las regiones tropicales y subtropicales del mundo (en Twilley *et al*., 1983)

Importancia

Estos ecosistemas tienen una flora y fauna compleja asociada con los manglares creando ambientes altamente diversos. Los manglares juegan un importante papel en la ecología de las costas tropicales y proporcionan muchos bienes y servicios para las poblaciones humanas. Estos Incluyen: protección y estabilización de la línea de costa, criaderos para numerosos recursos pesqueros económicamente importantes, y una variada fuente de productos a las poblaciones humanas costeras en forma de madera, leño y carbón.

Al mismo tiempo, los manglares son muy importantes para el hombre por las siguientes razones: exportan materia orgánica que es el alimento directo de diversos recursos pesqueros o estimulante de la producción primaria en el ecosistema acuático adyacente. Sustentan importantes pesquerías tropicales porque ofrecen refugio y alimento en las etapas críticas de los ciclos de vida de muchos peces, crustáceos y moluscos, que utilizan los manglares como áreas de reproducción y crianza. Del manglar se pueden extraer taninos, madera aserrable, postes, durmientes, leña y carbón., constituyen en acervo genético fundamental para una comunidad diversa de plantas y animales que son importantes como patrimonio de la región, lo cual incremente su valor científico, turístico y educativo. En la zona costera los manglares reducen la erosión atenuando los efectos de olas y corrientes, ofrecen protección a los cambios climático-meteorológicos e hidrodinámicos, y son refugio de los depredadores a la variada fauna y flora que coexiste en el ecosistema.

Deterioro e Impacto Ambiental

No obstante, su enorme Importancia para la mayoría de los países costeros tropicales en América latina, los ecosistemas de manglar han presenciado una acelerada embestida por la explotación de sus recursos, la mayoría de las veces, sin el cuidado necesario para mantener mayoría de los países costeros tropicales en su integridad, la cual amenaza su utilización sustentable (Fig. 3). Por ejemplo, agricultura de la llanura costera, expansión urbana, desarrollo de industrias asociadas al petróleo, construcción de carreteras y puentes y reconversión para granjas de camarón.

Figura 3. Diagrama que muestra cómo las funciones ecológicas de los ecosistemas de manglar son un puente entre el "valor" y el "beneficio neto" económico. El equilibrio entro la utilización del sistema por el hombre y preservar la calidad ambiental, determina un balance entro "deterioro" y "conservación"

Las estimaciones de deforestación de las áreas de manglar en América Latina son deficientes. Sin embargo, se reconoce que en muchos países entre 25 y 100 % de la cobertura de manglar ya ha sido destruida en los últimos 25 años. Algunos datos muestran valores dramáticos. Por ejemplo, en México, de¡ millón y medio de hectáreas originales, más del 60% de la superficie total nacional de manglares ha sido deforestada por la presión de obras de infraestructura Industrial. De igual manera en algunas zonas de Ecuador, donde más del 70% de la superficie original de los manglares ha sido destruida para reconversión en acuacultura y agricultura. En las Antillas menores, el efecto del turismo ha determinado una deforestación que sobrepasa el 35% de la cobertura original.

Además de la deforestación, grandes áreas de mangles están siendo degradadas debido al mal uso de los recursos costeros. Por ejemplo acuacultura (Fig. 4). El reemplazo, deteriorado la calidad del agua y del hábitat y eliminando el efecto natural de)as mareas por la construcción de bordos destruyendo los manglares, desemboca en un proceso que se va encareciendo y colapso ecológica y económicamente. (R. Twilley com. per). Por otra parte, la desviación del agua dulce para irrigación y fines de recuperación de tierras son una de las principales causas de la degradación de los manglares.

En términos generales, el deterioro global de los manglares se debe a:

a) Inapropiado legislación de la propiedad de recursos naturales así como la de los sistemas para su acceso y uso.

b) Inadecuado funcionamiento del mercado, que no reflejo el valor de los servicios ambientales de los manglares ni su real precio.

c) Conversión no controlada del sistema de manglar por cambios en la organización del tipo de vida de las comunidades costeras; cambios temporales en la actividad económica alternando entra pescador, campesino y artesano

d) Incremento en el consumo de energía *per capita*

e) Centralización de las decisiones políticas sobre las áreas de manglar en los acuerdos económicos Internacionales

f) Manejo descoordinado y fragmentado o ausencia de un plan de manejo

g) ausencia de planes integrales de desarrollo costero

h) Depreciación del valor ecológico con presi6n sobre uso y abuso a corto plazo; expíotaci6n no sostenible

i) Poco impacto de los resultados científicos y su disponibilidad en términos prácticos, para los usuarios del sector oficial; carencia de términos de referencia, de vocación y aptitud de la región, evaluación de recursos, viabilidades ecológicas para desarrollos productivos; reconversión de áreas de manglar en agricultura y acuacultura que se colapso en pocos años

j) Desconocimiento de los posibles impactos dinámicos resultantes de las diversas estrategias de uso y manejo de los manglares.

Figura 4. Diagrama que muestra el desarrollo de granjas camaronícolas en la zona costera sin manejo Integral y los Impactos (positivo o negativo) probables en términos ecológicos-económicos, en relación con una zona costera con manejo Integral (ver Cap. 14, Twilley *et al*. este volumen)

Soluciones Frente a la Encrucijada

La solución al problema debe ser integral y requiere:

a) Conocer la estructura y funcionamiento natural de¡ ecosistema, su vulnerabilidad, capacidad de carga y de reacción a cambios como la variación climática y nivel medio de¡ mar.

b) Establecer condiciones locales (a nivel Municipal) sobre aspectos económicos, sociales y ecológicos en áreas pilotos demostrativas, considerando las características ambientales de¡ ecosistema, en el marco de un plan integral de manejo.

c) Resolver y tomar decisiones sobre la base de la estructura y funcionamiento del ecosistema a través de caracterizaciones ecológicas, y su vínculo con la comunidad inserta en el ecosistema.

d) Mitigar la vulnerabilidad de los manglares por los estrés que induce el hombre

e) Demostrar la función amortiguadora de carga orgánica de los manglares, de estabilización de la erosión litoral, del papel ecológico como hábitat crítico, su valor para las pesquerías artesanales, y el ecoturismo.

f) Mejorar el conocimiento por parte de la sociedad de los atributos, bienes y servicios que proporcionan los manglares, que frecuentemente es subvalorada.

A pesar del daño realizado, todavía existen extensas áreas de bosques prístinos en muchos países de América Latina. Estas áreas deben ser conservadas para un uso y manejo sostenible. Otras que presentan diversos grados de impactos humanos, pueden ser rehabilitadas a través de replantación, para acuacultura no destructiva, para protección de la línea de costa y enriquecimiento de las aguas costeras.

A nivel mundial, la preocupación sobre los manglares se evidencia en la redacción de La Carta Mundial para la Naturaleza, generada por la Asamblea General de las Naciones

Unidas proclamada el 28 de octubre de 1982. Dentro de este marco, el Comité Ejecutivo de la Sociedad Internacional para los Ecosistemas de Manglar (ISME), decidió preparar la Carta para los Manglares y ponerla a consideración en la Conferencia de Naciones Unidas sobre Medio Ambiente y Desarrollo realizada en Brasil en Junio de 1992, con el propósito de anexada a la Carta de la Tierra. en este documento, se establece que la Asamblea General está consiente de que: a) los bosques de manglar son los únicos ecosistemas de intermareas que se presentan principalmente en las regiones tropicales del mundo; b) el área total de manglares alrededor del *2* mundo se estima en no menos de 170,000 km y existen 60 especies de árboles y arbustos que son exclusivos de los hábitat de manglar; c) los manglares soportan diversos comunidades de flora y fauna acuática y terrestre que están directa o indirectamente en el ambiente; d) el desarrollo sustentable de los ecosistemas de manglar implica el mantenimiento y uso racional de los recursos naturales para asegurar su capacidad ecológica y oportunidades económicas para las generaciones presentes y futuras; y e) los manglares deben ser conservados en diversas partes del mundo para prevenir la presencia de tierras costaras degradadas.

Ante este panorama, se publica el presente libro con la participación de 34 investigadores de 10 países de América Latina El principal propósito de este proyecto fue reunir las contribuciones científicas de los especialistas de mayor prestigio y experiencia, para avanzar en recomendaciones de normatividad ecológica que es requiere en América tropical, para la administración integral de la zona costera tropical. Asimismo, estimular programas de investigación para entender, evaluar manejar y proteger estos recursos.

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4

Mangrove Ecosystem Research with Emphasis On Nutrient Cycling

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Abstract

Mangroves are the subject of a struggle between those who want to maximize economic benefit through intensive uses of the system (sometimes at the cost of eliminating the biota in favor of urban or other developments) and those who advocate complete preservation of the ecosystem even at the exclusion of people. As tropical countries continue to develop economically, their governments must balance the various uses of mangroves and other coastal areas to assure sustainability of development. However, this will not be possible without a constant flux of scientific information on these ecosystems. Scientists must provide accurate information upon which resource managers and policy makers can base their decisions.

Resumen

Los manglares son los sujetos de lucha entre aquellos quienes quieren maximizar el beneficio económico a través de intensos usos del sistema (a veces por el costo de eliminar la biota en favor de los desarrollos urbanos u de otro tipo) y aquellos quienes se abocan a la preservación completa del ecosistema aún por la exclusión de la población. Como en los países tropicales continúan desarrollándose económicamente, sus gobiernos deben equilibrar los diversos usos del manglar y otras áreas costeras para asegurar un desarrollo sustentable. Sin embargo, esto no ser posible sin un flujo constante de información científica de estos ecosistemas. Los científicos deben proporcionar información precisa sobre la cual puedan basar sus decisiones el administrador de recursos y el diseñador de gestiones. Este Capítulo sugiere tópicos que ofrecen las mejores oportunidades de investigación en el contexto del actual conocimiento de los manglares en cualquier parte del mundo.

Distribución

Not all the desired uses of mangroves are compatible with the sustainability of the mangrove ecosystem. However, mangrove ecosystems are resilient within a range of environmental conditions (Lugo, 1980). Thus, the values that humans can derive from mangroves can be optimized if proper management techniques are used. Such management techniques must be based on information gathered continuously by active research programs. Because mangroves are open systems and closely coupled to marine, terrestrial, and freshwater ecosystems, mangrove research must be holistic and focused at the same spatial scales as those in which management actions interact with the system.

For example, some management options require understanding of life histories of individual species and stand dynamics (e.g., for silvicultural reasons), but others require understanding of complex regional hydrological systems (e.g., for fisheries management) or of regional land use patterns (e.g., for assessments of water quality and floodwater storage functions). Yet, any mangrove research program must rest on a sound analysis of the individual mangrove ecosystem. An example of an integrated and multidisciplinary program of mangrove research is that described for the Ranong mangrove ecosystem in Thailand (Macintosh, 1991).

I recommend research that will advance current understanding of mangrove ecosystems and that will also be useful to the management of mangroves. Such research focuses on maximum benefit to people while conserving the integrity and biological diversity of mangrove forests. This report suggests topics that offer the best research opportunities in the context of current understanding of mangroves elsewhere in the world.

Methods

To prepare this review, I examined recent literature on mangroves to identify the areas of research that are receiving the greatest attention by scientists (Lugo, 1987, 1990a). I then grouped those areas that have shown the greatest progress since 1962 when functional studies of mangroves began (Table 1). The objective was to identify gaps in knowledge. Such gaps are, in fact, research needs in the region. These were then grouped into the following categories: 1) diversity of mangroves habitats, 2) primary productivity, 3) nutrient cycling, 4) food chains, 5) birds, fisheries, and other wildlife, 6) silviculture, 7) responses to stressors, 8) restoration, 9) basic biology, 10) values, and 11) change in sea level. In discussing these topics, I support my statements with references to recent works that illustrate the point being made or which represent an example of the type of study being recommended. I avoided references to older literature which has been reviewed elsewhere (e.g., Chapman, 1976; Lugo and Snedaker, 1974; Macnae, 1968; Walsh, 1974). The list of research needs is not given in order of priorities, because the determination of priorities is best done by scientists at the local level.

Table 1. Topics of mangrove research that have received the greatest scientific attention (Lugo, 1987)

Research Area	Key Sources
Species richness community structure and physiognomy	Chapman, 1975; 1976; Fosberg, 1975; Pool *et al*., 1977
Anatomy, morphology and taxonomy	Tomlinson, 1986; Seager, 1982
Mangrove habitats classification	Cintrón *et al*., 1986; Lugo and Snedaker, 1974; Thom, 1975; 1982; 1984
Zonation and succession	Chapman, 1976; Lugo, 1980; Macnae, 1968; Snedaker, 1982
Ecosystem function including ecophysiology	Chapman, 1975; 1976; Clough, 1982; Lugo and Snedaker, 1974; Walsh, 1974
Regional importance of mangroves	*Carter et al*., 1973; Odum, 1970; Snedaker and Lugo, 1973; Turner, 1977
Leaf dynamics production, turnover and detritus dynamics	Twilley, 1985; Twilley *et al*., 1986
Mangrove stressors	Lugo, 1978; Lugo *et al*., 1981
Management and conservation	Hamilton and Snedaker, 1984; Watson, 1928

The data base available to evaluate the nutrient dynamics of mangroves is scarce (Table 2). Here I report only leaf chemistry data for different species. The few numbers available constrains the breath of analysis that can be made. Large gaps of information, use of different methods for studying the same phenomena, and inconsistency in the reporting of data are typical problems encountered in any global review.

However, filling those gaps and inconsistencies, and developing consistent methodology become critical research priorities for investigators of the mangrove biome. For example, site description in mangrove reports is poor and inconsistent (Table 3). Also, most studies are short-term and of limited scope. Comprehensive long-term ecological research in mangroves is critically needed.

Table 2. Description of data on chemical composition of mangrove tissue and soil. Brackets contain the number of individuals sites. • Six regions (Australia[4], Asia[5], Puerto Rico[4], Cantral America[1], Florida[10], and South America[6]. • Thirty individual sites. • Twenty two species (listing in Fig. 1). • Eleven compartments (live leaves, live stems, live branches, live roots, seedlings, miscellaneous live, leaf fall, miscellaneous litter fall, leaf litter, miscellaneous litter, and soil). • Twenty six elements. • Distribution of analyses

	LIVE						FALLING		LITTER		
Element	**Leaves**	**Stems**	**Branches**	**Roots**	**Seedlings**	**Misc.**	**Leaves**	**Misc.**	**Leaves**	**Misc.**	**Soil**
N	38	12	5	3	7		23	5	9	4	37
P	44	7	6	1	3		10		7	1	41
K	53	15	5	2	6	4	12		5	1	3
Ca	50	15	5	3	5	4	12		4		3
Mg	48	15	5	3	3	4	8	5	1		3
S	2		1								
C	6	3	3		2		10		5	5	25
H	3	3	3		1						
Al	6	5	4	1	1						
B	7	2		1							
Ba	2	2		1							
Cl	6		1								
Co	8	8		3	1	3			1		1
Cr	5	3	2						2		29
Cs	2	2		1					1		1
Cu	15	10	3	3	2	4	8		3		30
Fe	25	14	5	3	2	5	8		3		30
Mn	24	12	5	3	2	6	8		3		30
Mo	2	2		1							
Na	49	12	2	3	2	4	8		1		22
Ni	3	1	3		1		8				
Pb	8	2	1	1			8		1		27
Si	14		1								
Sr	7	5	3	1	1				1		1
Ti	1	2		1							
Zn	22	14	4	3	2	5	8		3		30

Table 3. Identification and characteristics of sites used for describing the chemical properties of mangrove ecosystems

Site	Type of Mangrove	Location	Latitude	Longitude	Tidal ampl (m)	Annual Rainfall (mm)	Mean annual Temp (°C)	Source
A1	Many including fringe and basin	Hinchinbrook Island, Missionary Bay, Australia	18°13'S	146°10'E	2-3	2000-3000		Bunt, 1982
A2	Fringe-basin transect, 9 sites	Hinchinbrook Island, Missionary Bay, Australia	18°13'S	146°11'E	>1.2			Boto and Wellington, 1983, 1984
A3	Fringe	Western Port Bay, Victoria, Australia			2.8			Clough and Attiwill, 1975
A4		Barker Inlet, Gulf of St. Vincent, South Australia	34°S	138°W	2.5			
B1	Managed stands	Matang Mangrove Reserve, Port Weld Perak, Malaysia	4°50'N	100°35'E	<2			Ong *et al*., 1982a,b
B2	Riverine	Sungai Merbok Estuary, Kedah, Malaysia						Ong *et al*., 1980b, 1981
B3		China						Rodin and Bazilevich, 1967
B4	Fringe	Matang Mangrove Reserve, Pulau Kecil, Malaysia	4°48'N	100°35'E				Putz and Chan, 1986
B5		India						Walsh, 1974
C1	Many in 7 sites and 9 stations	Puerto Rico (north, south and east coast)	18°-18°13'N	65°15'-67°W				Snedaker and Brown, 1981
C2	Fringe	Joyuda Lagoon, Puerto Rico	18°8'N	67°14'W				Levine, 1981; Musa, 1986
C3	Basin	Joyuda Lagoon, Puerto Rico	18°8'N	67°14'W				Musa, 1986
C4	Fringe	Jabos Bay, Puerto Rico	18°N	66°15'W	0.4	884	26.4	Lugo *et al*., 1987
D1	Riverine	Darien, Santa Fe, Panama				2000	25	Golley *et al*., 1975

Table 3. Cont.

Site	Type of Mangrove	Location	Latitude	Longitude	Tidal ampl (m)	Annual Rainfall (mm)	Mean annual Temp (^oC)	Source
E1	Basin	Rookery Bay, Florida	25° 22' N	81° 34' W	0.55	1,346	23.6	Lugo and Snedaker, 1975; Twilley, 1985; Twilley *et al*., 1986
E2	Dwarf	Turkey Point, Southeast Florida	25° 20' N	80° 60' W	0.23	1,488	24	Sanford, 1976; Snedaker and Brown, 1981
E3	Hammock	Turkey Point, Southeast Florida	25° 20' N	80° 60' W	0.23	1,488	24	Sanford, 1976; Snedaker and Brown, 1981
E4	Many in 11 stations	Turkey Point, Southeast Florida	25° 20' N	80° 60' W	0.23	1,488	24	Sanford, 1976; Snedaker and Brown, 1981
E5		Mostly from Florida						Walsh, 1974
E6	Basin	Estero Bay, Fort Myers, Florida	26° 02' N	81° 45' W	0.55	1,346	23.6	Twilley *et al,* 1986
E7	Fringe	Indian River, Ft. Pierce, Florida	27° 27' N	80° 20' W				Onuf *et al*., 1977
E8								Heald, 1969
E9	Riverine	Gordon River at Naples, Florida			0.6-1.2			Sell, 1977
E10	Riverine	Everglades City, Florida			0.6-1.2			Sell, 1977
F1	Riverine	Itanhaém, Sao Paulo, Brazil	24° 11' N	46° 47' W		1,717	21.9	Lamberti, 1969
F2	Many in 18 sites	Southeast Coast of Brazil	10° 25' S 23° 15' S					Lacerda *et al*., 1985
F3	Fringe	Baia de Sepetiba, Rio de Janeiro, Brazil	23°S	44° W				Lacerda *et al*., 1986b
F4		Brazil						Rodin and Bazilevich, 1967
F5		Catalaô Island, Guanabara Bay, Brazil	22° 46' S	44° 47' N				Aragon *et al*., 1986
F6		Baia de Sepetiba, Rio de Janeiro, Brazil	23°S	44° W				

Mangrove Habitats

Quantitative descriptions of stands, if repeated periodically, are the cornerstone for planning further mangrove research and for establishing long-term observation plots for the assessment of stand dynamics (growth, mortality, regeneration, ingrowth, primary productivity, etc.). However, to make maximum use of this information, it is necessary to also assess the variability of mangrove habitats, their distribution, and areal coverage. Examples of mangrove inventories, including the use of satellite images are those of Khan et al. (1990) and Petteys *et al*. (1986).

Research in Australia has led the world in showing the geomorphological basis for mangrove stand classification (Semeniuk, 1985a, b; Thom, 1975; 1982; 1984). These scientists have carefully documented how growth conditions in mangroves are a function of the geomorphology of their physical habitats.

One of the critical problems of management-oriented research is the extrapolation of results from small-scale measurements to the whole landscape in which human activities take place. In the past, values from stand-level measurements were multiplied by the area of ecosystem to estimate the magnitude of regional processes. In plantation forestry the site index is used for weighing such extrapolations of research results. For mangroves this can be accomplished from a sound understanding of the number and area of each type of mangrove habitat in the region of interest. Classification of mangrove habitats, rather than species, is the recommended approach, because the number of species is few and they are very plastic in their response to growth conditions (Tomlinson, 1986). Thus, the same species may have different growth rates and physiognomy in different habitats.

Much of the work in Florida and Puerto Rico has been based on a geomorphological classification of mangrove stands (*sensu* Lugo and Snedaker, 1974). Many attributes of mangroves can be inferred from the type of stand (Cintrón and Schaeffer-Novelli, 1984; 1985). Recently, I suggested a hierarchical approach to mangrove research and selection of research areas (Lugo 1987, Lugo and Brown, 1991). The first scale in the hierarchy is the landscape level for which the classification system proposed by Thom (1982;1984) [and modified for the Pacific islands by Woodroffe, 1987] provides the context in which mangroves will function. This level of mangrove habitats is also addressed by Semeniuk (1985a, b). Semeniuk elaborated a finer set of mangrove environments based on stratigraphic and lithological criteria. This scheme is useful for intermediate geographical scales. The second scale in the hierarchy is the individual ecosystem scale. The classification of Lugo and Snedaker (1974) is recommended because it incorporates hydrological and geomorphological criteria that influence ecosystem function. Finally, the third and smallest scale in the hierarchy is the individual stand which may be grouped according to dominant tree species, the targets of management actions. Semeniuk (1985b) applied a hierarchical system of mangrove habitat classification to the mangroves of north and northwestern Australia.

These different levels of mangrove classification provide a means for extrapolating research results from stand level to the landscape and vice versa. They can also be adapted to Geographical Information Systems and use in conjunction with Global Positioning Systems for rapid and accurate interpolation to other regions or islands. Research priority should be given to those types of mangroves most likely to be impacted by human management. Furthermore, a comprehensive program should address contrasting types of mangroves so that wide ranges of ecosystem responses to environmental conditions can be safely established for the region.

Primary Productivity

Litter production in mangroves is fairly well understood (Bunt, 1982; Lugo and Snedaker, 1974; Twilley *et al*., 1986). However, litter production is a fraction of the system's primary productivity, and for management purposes it is necessary to understand the complete process. For example, although the mangrove forests of Vaitupu in Micronesia produced litter at the same rate as those of Malaysia (Woodroffe and Moss, 1984), it is unlikely that they would match Malaysian mangroves in the production of wood or roots. However, any mangrove forest growing in environments more favorable than the one described by Woodroffe and Moss (1984) could be expected to be as productive as mangroves in Malaysia. The same principle applies to comparisons of mangrove ecosystems anywhere in the world.

Studies of primary productivity of mangroves should be conducted in conjunction with the establishment of permanent plots for long-term observation of stand dynamics. In Malaysia, plots such as these have proven useful in the evaluation of the impact of long-term (since early this century) silvicultural treatments of stands (Ong *et al*., 1982a, b; Manan and Khan, 1984; Putz and Chan, 1986). In wet areas, crown epiphytes as well as epiphytes on roots may play an important role in the primary productivity of mangroves. This aspect also deserves study.

Nutrient Cycling

The movement of nutrients through mangrove ecosystems is one of the least understood aspects of the function of these ecosystems. In my literature review I found only 30 sites in the world for which at least one chemical analysis of a vegetation or soil sample was reported (Table 3). None were from the Pacific islands. Moreover, there is no mangrove forest in the world for which a complete nutrient budget has been estimated. This is an astounding fact given the importance of nutrient cycling to several of the vital functions of mangroves. Boto (1982) addresses the subject of nutrient cycling for Australian mangroves.

Understanding of nutrient cycling in mangroves is required to understand their potential role in regulating water quality, for assessing causal relations for the presumed loss in productivity after the second or third harvest rotation, in the understanding of the coupling of the forest ecosystem with upland and marine ecosystems, and for learning how the mangroves maintain nutritional homeostasis while being subjected to high rates of water turnover (ocean and freshwater) that certainly must leach large amounts of nutrients. Work on the nutrient cycles of mangroves has fundamental importance to understanding the function of wetlands and ecosystems while also providing valuable practical information for managing them. A useful model of the many nutrient fluxes in wetlands is given by Lugo (1982). Models such as this one can be used to plan research in these ecosystems.

Nutrient cycles in mangrove ecosystems are open and can be subjected to either reduced or oxidized states. Harbison (1986) concluded that three major influences of trace metals (i.e., fine particulates, organic matter, and sulphide production) are inherent characteristics of mangrove muds and confer them an enhanced capacity for metal accumulation. Biotic processes in mangrove muds can alter the source-sink function of mangroves by altering the pH and Eh of muds. This has vital implications to their role in absorbing nutrients and pollutants or allowing pollutants to enter coastal waters.

Mangroves also accumulate organic matter and nutrients in highly organic soils and biomass. Their role as carbon and nutrient sinks is well recognized (Lugo, 1982). What is less understood are the nutrient conservation mechanisms of mangroves? Are there any? Is mangrove function so dependent on external inputs that nutrient use-efficiency is low? Lugo et al. (1990) proposed a nutrient cycling model for wetlands and described seven biotically-controlled and three abiotically-controlled nutrient use-efficiency ratios that could be used to evaluate nutrient use-efficiency in these ecosystems. Each of the indices evaluates a different sector of the ecosystem and thus, it is incorrect to use any one index to evaluate the ecosystem as a whole. The scarcity of data, however, limits the breath of evaluations to a few indices that focus on leaves and litter i.e., the accumulation of nutrients per unit biomass or tissue nutrient concentration, the rate of nutrient retranslocation before leaf fall, and the amount of nutrient return per unit biomass in litterfall.

Nutrient Concentrations

Nutrient concentrations of mangrove tissues are within the range reported by Rodin and Bazilevich (1967) for upland tree species. However, there is much variation in the concentration of macronutrients in mangrove leaves (Fig. 1). Variations in nutrient concentrations could be used as indices of nutrient use-efficiency i.e., nutrients stored per unit biomass. Accordingly, high concentrations reflect greater nutrient demand (storage) per unit mass. Ideally, this calculation is best done at the ecosystem level, i.e., estimating total mass and nutrient storage by compartment and obtaining their ratio. Such a calculation would cancel out short term variations due to physiological state of tissue. Here I only compare leaf tissue concentration to illustrate potential variability among mangrove species (Fig. 1). Moreover, I highlight the comparison between species of the genus *Rhizophora* and those from the genus *Avicennia*, because they usually grow in contrasting environments (Lugo, 1990b). He suggested that *Rhizophora* is more common in environments with water in motion and therefore more open conditions from a nutrient point of view, while *Avicennia* predominates in still waters where the opportunity for recycling is greater. Outliers are identified in the figures to call attention to these examples.

Figure 1. Concentration of nitrogen (a), phosphorus (b), potassium (c), calcium (d), and magnesium (e) of live leaf tissue of mangrove species from sites identified in Table 3. Standard error of the mean is shown if more than one analysis is available. The original data set is available from the author. Species identification with the abbreviation code in parenthesis is as follow: 1. *Acanthus ilicifolius* (Ai), 2, *Acrostichum aereum* (Aa), 3. *Aegiceras corniculatum* (Ac), 4. *Avicnenia alba* (Ava), 5. *Avicennia germinans* (Avg), 6. *Avicennia marina* (Avm), 7. *Avicennia officialis* (Avo), 8. *Avicennia schaueriana* (Avs), 9. mean for all *Avicennia* spp (Av), 10. *Bruguiera caryophilloides* (Bc), 11. *Ceriops candolleana* (Cc), 12. *Conocarpus erectus* (CE), 13, *Derris ulginosa* (Du), 14. *Exocaria agallocha* (Ea), 15. *Hibiscus tiliaceus* (Ht), 16. *Laguncularia racemosa* (Lr), 17. *Lumnitizera racemosa* (Lur), 18. *Rhizophora apiculata* (Ra), 19, *Rhizophora brevistyla* (Tb), 20. *Rhizophora mangle* (Rm), 21. *Rhizophora mucronata* (Rmu), 22. *Rhizophora* sp from Australia (Rsp), 23. mean for all *Rhizophora* spp, 24. *Sonneratia apetala* (Sa).

Leaves of species in the genus *Rhizophora* tend to have lower concentrations of most nutrients (Fig. 1, a, b, c, and e) except Ca (Fig. 1d). However, the differences are not consistent with the possible exception of N and Ca. The data for *Rhizophora mucronata* and Avicennia germinans are highly variable and stand out. Relative to *Rhizophora* and *Avicennia*, *Laguncularia racemosa* leaves have intermediate concentrations of N, K, and Ca, and low concentrations of P and Mg. Results in progress along a salinity gradient in a Puerto Rican mangrove (E. Medina and A.E. Lugo, personal communication) show that leaf nutrient concentrations change for the same species along the gradient, are different among individuals of different species but found in the same location, and change with the age of the leaf. These ecophysiological dynamics are responding to environmental conditions and greatly complicate the interpretation of data such as those in Fig. 1.

Nutrient Return by Litterfall

The ratio of mass fall to nutrients in mass was used by Vitousek (1984) as a measure of within stand nutrient use-efficiency. The higher the ratio, the higher the efficiency of nutrient use by litter fall because more carbon is circulated in that pathway per unit of nutrient. Data on this parameter was reviewed by Lugo *et al*. (1990) and I offer a summary of their findings.

Nitrogen use efficiency in mangroves was a function of species and habitat conditions. Most values are higher than the 130 used by Vitousek to delimit N-efficient upland sites. The most N use efficient species was *L. racemosa*, followed by a group of mangrove species from Australia. *Rhizophora mangle*, growing in southeastern Florida, exhibited high N-use efficiency but those from Puerto Rico and *A. germinans* did not.

(b)
Phosphorus Concentration (%)
Species
Ai
Aa
Ac
Ava
Avm
Avg
Avo
Avs
Av
Bc
Cc
Du
Ea
Ht
Lur
Lr
Ra
Rb
Rm
Rmu
Rsp
R
Sa

(c)
Potassium Concentration (%)
Species
Ai
Aa
Ac
Ava
Avg
Avm
Avo
Avs
Av
Bc
Cc
Ce
Du
Ea
Ht
Lur
Lr
Ra
Rb
Rm
Rmu
R
Sa

(d)
Calcium Concentration (%)
Species
Ai
Aa
Ac
Ava
Avg
Avm
Avo
Avs
Av
Bc
Cc
Ce
Du
Ea
Ht
Lr
Lur
Ra
Rb
Rm
Rmu
R
Sa

(e)
Magnessium Concentration (%
Species
Ai
Aa
Ac
Ava
Avg
Avm
Avo
Avs
Av
Bc
Cc
Du
Ea
Ht
Lr
Lur
Ra
Rb
Rm
Rmu
R
Sa

Species differences were not as important as habitat conditions in determining P use efficiency. All species in a Florida hammock forest were equally efficient in recycling P even though they had different leaf nutrient concentrations when growing in less rigorous conditions. The lowest values for P use efficiency were for mangroves in moist and wet areas in Joyuda Lagoon, Puerto Rico and Malaysian forests. The highest values corresponded to dwarfed *R. mangle* forests in Florida.

Retranslocation

Another measure of nutrient use-efficiency is the amount of re-absorbed nutrients before leaf fall, expressed as quantity per unit leaf weight or area or as a percent of nutrient content. The higher the retranslocation, the more use-efficiency is the plant because it recirculates more nutrients and reduces dependency on absorption by roots.

Table 4 shows data for three mangrove species and two contrasting environments (a salina with soil salinity in excess of 70 parts per thousand, and a fringe with soil salinity of about 40 parts per thousand). There are differences in the amount of nutrient reabsorbed, differences between N and P retranslocation, and among species. More N is retranslocated than P, but the retranslocation of P is a larger proportion of the total P in leaves than it is for N. This is because there is less P than N in leaves and because P is probably more limiting to these trees. *Rhizophora mangle* had a higher amount and proportion of retranslocation in the salina than it did in the fringe. *Avicennia germinans* retranslocated more N and P than the other two species. There was not as much difference in the proportion of N retranslocated by the three species (62-65%) as there was for P retranslocation (78-84%).

Mangroves are Efficient in the Use of Nutrients

The general applicability of available data lie in illustrating how complex the process of nutrient use can be in a forested wetland. Each nutrient and each species represents a wide array of possibilities that defy generalization at this moment. However, the results reviewed here and those of Twilley *et al*. (1986), Twilley (1988) and Lugo et al. (1990) are consistently showing that when the mangroves are exposed to high water exchange, the within-stand nutrient use-efficiency of Vitousek increases, suggesting a more conservative use of nutrients by trees. Moreover, using the Vitousek index, mangroves appear to be more nutrient use-efficiency than freshwater wetlands and upland forest (Lugo *et al*., 1990). Our studies in progress in Puerto Rico (E. Medina and A. E. Lugo, personal comm.) suggest a similar behavior when mangroves are exposed to high salinity stress. Steyer (1988) found increased N retranslocation in mangroves exposed to low N fertility. It would appear then that in spite of the open nature of mangroves (and perhaps because of this) and in spite of the opportunity of continuous replenishment of upland- or marine-derived nutrients, mangroves are efficient users of nutrients and this property coincides with their function as sinks of carbon and minerals.

Table 4. Retranslocation of nitrogen and phosphorus in mangrove forests at Jobos Bay, Puerto Rico. Retranslocation is the difference in nutrients content between mature and senescent leaves. The percentage of the nutrients content of mature leaves that is retranslocated is also given. Data are formLugo *et al*., 1987.

Species and location		N		P	
		mg/cm^2	%	mg/cm^2	%
Salina	*Laguncularia racemosa*	0.112	65	0.012	80
	Avicennia germinans	0.204	62	0.017	84
	Rhizophora mangle	0.165	65	0.009	78
Fringe	*Rhizophora mangle*	0.082	59	0.005	73

Food Chains

The food chains of mangroves have always attracted the attention of zoologists and ecologists. Macnae (1968) wrote the most detailed account of the animals in the Indo-west Pacific mangroves including those of the Pacific islands. Macnae's account did not include a comprehensive discussion of the detrital food chains. In fact, because of their ecotonal nature, mangroves support a diversity of food chains including marine, estuarine, freshwater, and terrestrial. These in turn can be further subdivided by the source food, e.g., grazing food chains originating in leaves, seedlings, wood, fruits, etc., and detrital food chains. The detrital food chains can be extremely complex, because they originate from many kinds of litter, particulate detritus, dissolved organic materials, etc. The complexity and diversity of food chains in mangroves is one reason why diversity of animal species is so high in these ecosystems.

The first modern synthesis of the detrital food chains of mangroves was completed by Odum (1970) who highlighted the importance of detritus to commercial marine fisheries. Since that study, numerous other studies from all parts of the world have addressed the linkage between mangrove detritus and various animal groups (Carter *et al*., 1973, Lewis et al., 1985, Mun, 1984, Turner, 1977). A recent article from Australia focuses on crabs that bury large amounts of leaves and cautions against assuming that the food chains proposed for Florida apply equally well to Australia and the Pacific (Robertson, 1986). Crab activity alone could cause a 22 percent overestimation of leaf export in mangroves in which crabs are numerous.

As one travels throughout the tropics it becomes obvious that fish exports are increasing from coastal zones with large mangrove areas. To what extent do these exports depend on mangroves? Clearly many fish species use mangroves as reproductive, nursery, or habitat areas at some point in their life cycle. These uses can be documented through autecological research on commercially important species. A more difficult question to address is the degree of dependence of commercial fisheries on mangrove detritus. I recommend the application of High Performance Liquid Chromatography to address this question. This technique identifies chloropigments in organic matter, fecal pellets, and sediments, and helps trace them to producers (Bianchi *et al*., 1988). The technique may be faster and more reliable than the controversial one based on carbon isotope ratios.

Because the nature of the food chains is critical to the flow of energy and materials through mangrove systems, it is important to at least understand the natural history of food chains in mangroves. As a minimum, this information will indicate which food chain model (if any) of those available applies to the region of interest.

Birds, Fisheries, and Other Wildlife

Mangroves harbor a large diversity of wildlife species. For example, the mangroves of Bangladesh harbor some 400 animal species including eight amphibian, 50 reptilian, 261 bird, and 49 mammal species (Khan, 1986, Ismail 1990). Studies in French Guiana demonstrate that mangroves are rich in bird fauna and that these animals follow the same patterns of zonation and succession described for trees (Tostain 1986). The same is true of African mangroves (Cawkell, 1964). A critical determinant of bird use of mangroves is the architecture of the forest, particularly its tree density, height, foliage diversity, and canopy structure (Bismark, 1986, Tostain, 1986). This type of information is relevant to timber management practices and for evaluating their impacts on wildlife resources. To what extent do these results apply to tropical America?

In terms of fishery values, mangroves have always been known to be nurseries for a great abundance of fish species (Macnae, 1968) and to support economically important fisheries (Chakrabarti, 1986 b). Recent research in this area is beginning to identify environmental factors that influence migration and abundance of fish. Most studies show seasonal patterns of migration (e.g., Louis et al., 1985), but they differ in the causal factors. Although some studies report that salinity and rainfall are important to fish movements (Wright, 1986), others do not find such correlations (Louis *et al*., 1985). It is possible that in mangrove environments with strong seasonality of rainfall and runoff, changes in salinity caused by these events do induce movement of organisms. But, in relatively stable conditions, such environmental cues may be masked by genetic factors. Clearly, the resolu-

tion of this phenomenon may be complex because of the diversity of mangrove habitats. Each mangrove habitat has different environmental signals to which organisms cue in. What are the most important factors that regulate the behavior of fisheries in tropical America? Some of these factors were identified in an early attempt to culture fish in the waters of mangroves in coral atolls (Gopalakrishnan, 1978).

Wildlife management in mangroves is further complicated by the presence of commercially important shellfish, mollusks, and crustaceans. Moreover, there are important groups of organisms, such as insects and mesofauna, which have been poorly studied and greatly contribute to sustaining energy flow in these ecosystems (Murphy *et al*., 1990). It is paradoxical that a botanically simple ecosystem should support a zoologically complex wildlife community. This paradox was documented for the Sunderbans mangroves by Chakrabarti (1986a) who found greater richness in animal species below tidal level where plant species richness was at its lowest. The causes of this complexity were discussed above in the section on food chains. Studies of crustaceans and shellfish show that natural conditions, as opposed to artificial cultivation, are required for optimal production of larvae of these organisms (Ramos *et al.*, 1986; Twilley, 1987).

Wildlife influence the function of mangrove ecosystems in a variety of ways. For example, bird rookeries enrich mangrove soils with phosphorus (Onuf *et al*., 1977). Crabs consume wood (Lacerda, 1981) and change the topography of the mangrove floor (Warren and Underwood 1986). Seed predator influence the distribution of tree species (Smith, 1987a, b). Another focus is ecophysiological i.e., trying to understand how animals respond to the strong environmental gradients in mangroves. An example is the work of Paphavasit *et al*. (1990) on crabs.

Wildlife management in mangrove forests requires a holistic understanding of the system. Wildlife research must be integrated into other types of mangrove research, which include information on ecosystem physiognomy and primary productivity, forest hydrology, and on the movement of organisms and materials inside and outside of the system.

Silviculture

The oldest silvicultural systems for mangrove forests were developed in Malaysia and described by Watson (1928). These systems are still in practice today and have recently been evaluated from a silvicultural (Hassan, 1981, Liew *et al*. 1975), nutrient cycling (Wongh *et al*., 1982), and primary productivity point of view (Ong *et al*., 1982a, b; Putz and Chan, 1986). Silvicultural systems for mangroves have also been proposed for and implemented in the mangroves of Guarapiche in Venezuela (Taninos y Madera Venezolanas C.A., 1971) and for those in Fiji (Marshall, undated; Baines, 1979). Plantation research focusing on mangrove species is underway in Bangladesh (Siddiqui *et al*., 1990) and elsewhere in Asia (Macintosh *et al*., 1991).

How widely applicable are the available mangrove management systems? How much of a given mangrove area and which stands are suitable for intensive silvicultural practices? What is the minimal area of swamp that can treated with a positive economic return? What alternative silvicultural systems can be developed for small mangrove areas so that environmental impacts of harvest are minimized? What silvicultural practices are most compatible with the diverse wildlife of mangroves? Will there be regeneration problems in mangroves of the American tropics as in those of Malaysia where cutover site are dominated by the fern *Acrostichum* (Hassan, 1981)?

The evidence is conflictive regarding the effect of *Acrostichum* on mangrove regeneration. Chan *et al*. (1987) report adequate regeneration of *R. mucronata* in spite of a high density of Acrostichum. However, Sukardjo (1987) found poor regeneration of *R. apiculata* and *B. gymnorrhiza* in the presence Acrostichum. Species and site conditions may explain the conflicting reports, but research is clearly needed to identify causal mechanisms. Unanswered questions about the adequacy of mangrove regeneration under different conditions underscore the need to closely couple silvicultural activities with research. Silvicultural practices must also be closely coordinated with the management of other forest resources such as fish and wildlife. Such integrated focus has been described in various countries Liew (1970), Srivastava (1980) and Yao (1986), Tang *et al*. (1981).

Responses to Stressors

Recently, Gordon (1987) completed a comprehensive assessment of human-induced changes in the environmental conditions of mangrove habitats in Western Australia. A major effect of human activity on mangrove ecosystems is the change in hydrological conditions either through alteration of regional hydrology or modification of the geomorphology of the mangrove basin. These factors are so important to mangrove function that trees die very quickly even if the environmental change is slight (Jimenez *et al*.. 1986). The mechanisms of action are very complex and include changes in water quality (either salinity, nutrients, or toxic materials), unusual flooding and subsequent asphyxiation of trees, extreme drought, reduction in aeration, burial by sediments, erosion, siltation, over exploitation, etc. Examples of these stressors and mangrove responses to them are given in Gordon (1987), Lugo *et al.* (1981), Cintrón *et al*. (1978), and Mukherjee (1984). However, human stressors of mangroves are many, and each region has a suite of mangrove stressors that managers must be prepared to deal with. Each region requires an assessment of these stressors with a focus on their intensity, duration, and return time. For each of these aspects it is necessary to understand the response of mangrove ecosystems as well as the response of species. Comparisons with other parts of the world are useful because it appears that the pattern of response of mangroves to stressors is fairly universal (Lugo *et al*., 1981). What varies regionally (other than the type of stressors), is the susceptibility of the stressed mangroves. Response to stressors depends on the previous history of stress, the maturity of the vegetation, the species involved, and the type of mangrove habitat. It is necessary to again emphasize that research priority should be given to the most common or extensive mangrove habitats and to extreme habitats so that a wide range of mangrove responses can be determined.

Restoration

If the conditions of a mangrove habitat are maintained intact and trees and wildlife are managed properly, it is unlikely that irreversible change will occur in the system or that restoration procedures will be required. But where damage to the mangrove ecosystem has been extensive, restoration practices that go well beyond the planting of trees may be required. There is little information on the restoration ecology of mangroves. Most of the restoration efforts focus on tree plantings (Banerjee and Choudhury, 1986). I suggest two approaches to reduce the current ignorance in this topic.

First, there is the need to study damaged mangrove ecosystems. Damaged stands have been ignored in mangrove research. Study of damaged ecosystems will be useful in determining attributes of ecosystems that are resilient and those that are not. Management guidelines for ecosystem restoration will emerge from such studies.

Second, better understanding of the critical stages in the life cycles of mangrove plants and animals would facilitate restoration efforts. Ecological life histories of mangrove species have received little scientific attention (Jiménez, 1985 a, b; Jimenez and Lugo, 1985). Considerable information can be collected immediately from observations of indigenous peoples and their systems for culturing key mangrove species (Christensen, 1983).

Basic Biology

A comprehensive research program in mangrove ecosystems must include basic research in the biology and natural history of the mangroves. Recent literature focuses on several critical problems that both help advance mangrove science but could also be of practical value to management and conservation of mangroves. For example, much can be learned about species tolerance to environmental conditions from an understanding of the natural distribution of mangrove species in the region (Clusener and Breckle, 1987). Similar insights for management can be derived from ecologically oriented studies of plant morphology and physiological adaptations to natural conditions (Mukherjee, 1986). Recent emphasis on biodiversity issues has implications for the conservation of mangrove species. For example, Naskar and Bakshi (1986) have argued that changes in the landscape due to human intervention in the Sunderbans may lead to the extinction of several mangrove species. Also, accurate estimates of the gene pools of the mangrove flora require clarification of the many taxonomic problems associated with the mangroves of the region (Dagar and Basu, 1985).

Values

Many sectors of society are in conflict over how best to use the land and resources in mangrove environments. Some of the uses are incompatible with the conservation of mangrove ecosystems. However, the ultimate determinant of use is value. A fundamental problem of resource management is assigning value to products and services provided by ecosystems.

With mangroves, the problem is less complex than with other tropical ecosystems because so many of the services of mangroves can be assigned a value in dollars. For example, yields of fish, shrimp, tannins, chips, wood, charcoal, fuelwood, or honey; and damages caused by floods or storm waves can all easily be estimated in dollars. These dollar values are then divided by the area of mangrove believed to be contributing to the service in order to estimate a value per area of ecosystem. This value is then compared against real estate value. As an example, Snedaker (1988) estimated that an acre of mangroves (0.4 ha) in Florida had a value of $40,000 based only on the production of food for marine organisms. He considered this an underestimate of value because it did not include services such as shoreline erosion control, protection from waves, water quality improvement, and others.

The calculations described above have additional limitations that underestimate value (Lugo and Brinson, 1979). For example, values from mangroves are delivered continuously, whereas a real estate value may be short-term and eventually be converted to a cost. Also, values are usually assigned to those commodities that enter the market, but, what about non-market values? Furthermore, how can one estimate the value or contribution of those ecosystem processes that make possible the ones we believe are useful? For example, what is the value of litterfall without which there would be no detritus to feed the fish that enters the market economy?

Research is urgently needed to address the problem of valuation of mangrove resources. Without adequate methods for estimating real value equitably, short-term economics will always prevail over technical arguments that help conserve the resource. Unfortunately, the net result of a continuous reliance on short-term market economics will be a steady loss of mangroves. Examples of new and innovative approaches to the calculation of value of wetlands and resources are summarized in Costanza and Daly (1987), Farber and Costanza (1987), Hannon *et al*. (1986), Lugo and Brinson (1979) and Odum *et* al. (1987).

Change in Sea Level

The review by Woodroffe (1987) concluded that oscillations in sea level during the quaternary disrupted mangrove distribution in the Pacific. Present mangrove swamps in this region developed and extended during the late Holocene. Aging of mangrove peats through the whole region yielded peat younger than 6,500 yr. Today, there is public concerns that change in sea level as a result of human impact on global climates may affect coastal locations all over the world. The mangroves of Pacific islands would be affected by a change in sea level, particularly those in low islands. The same is true of mangrove forests throughout the rest of the world.

Although there is no evidence of significant change in the "normal" rise in sea level of 15 cm/century (Barnett, 1982), research today should address questions pertaining to potential responses of mangroves to changes in sea level as well as the use of mangroves to mitigate increased marine intrusions into lowland areas.

Proposed Focus for Research

A research program for mangroves should:

- Have a holistic focus and use ecosystem analysis techniques for research planning, data gathering, and interpretation.
- Use a hierarchical system of habitat classification for selecting study sites. Site selection should focus on the most common type of mangrove ecosystem (in terms of area) and include types with sufficient contrast of ecological characteristics so that, together, all selected sites provide an envelope of mangrove function "vis-a-vis" site conditions.
- Have individual studies that address scales that are consistent with the scale at which management actions take place. For wildlife and timber management research, the scale at which research is conducted may range from autecological to regional. This means that studies must be formulated carefully so that the questions addressed have relevance to the management problems.

- Assure that all research is geographically referenced to specific mangrove habitats. This way, extrapolation and interpolation to larger or smaller scales will be possible using geographic information systems. This option should be maintained in any research program design.

- Establish a network of permanent plots (at least 1 ha in area) for studies at the local ecosystem scale. All trees in these plots should be tagged, measured, and remeasured periodically. Studies of stand dynamics, biological diversity, primary productivity, and carbon and nutrient cycling can all be conducted using these permanent plots.

- Include extensive measurements of environmental conditions. Usually, interpretation of biological data is limited by poor environmental information or poor match between the scale at which environmental and biological data are collected. Measurements should include a complete suite of climatic data, edaphic factors (chemical, physical, and textural), and hydrologic conditions.

- Orient all research to the long-term understanding of the function of mangrove ecosystems. The coastal environment is extremely variable in temporal and spatial scales, and long-term research is needed to attain adequate understanding of cause-effect phenomena. Currently, few places in the world have long-term research programs in mangrove forests.

- Give attention to native cultures and indigenous management practices in mangrove environments. These uses of the resources by natives may open important areas of research inquiry and provide shortcuts in the development of sustainable recommendations.

- Encourage team research, particularly research by multidisciplinary teams working in the same area with a general ecosystem model as a tool to integrate and focus the team in its data-gathering and problem-solving effort.

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Mangrove Swamp Communities: An Approach in Belize *

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Abstract

Belize has the longest barrier reef of the northern hemisphere, extending 220 kilometers from Mexican border in the north to the Gulf of Honduras in the south. Behind this barrier lies an enormous lagoon system averaging 25 kilometers between the mainland and open ocean. Mangroves border most the coastline, extend upstream of the countless river mouth and fringe or cover most lagoon cays. Twin Cayss has become our study site and experimental laboratory. The purpose of this chapter is document the biology, geology, ecological balance, economic importance, and aesthetic value of a prominent coastal ecosystem.

The inventory of species has yet to be completed, but the most phyla are represented by species of which 10 to 25 percent, and in some microscopic-sized groups up to 60 percent, are undescribed. The red mangrove fringe, the specialized vegetation, the physical environment, and the associated fauna and flora form a complex and diverse island community above water as well as below. The mangrove community itself can be through of as being composed of three components: the above-water "forest", the intertidal swamp and the underwater system. The mangrove produce fine sediment and organic detritus and stabilize them by modifying the wave and current regime of the open lagoon. Furthermore, the mangrove swamp is rich in recycled nutrients and high production rates but its occupants are severely stressed by factors such as salinity and temperature fluctuations, desiccation potential, and size grain sediment.

Resumen

Belice posee la barrera arrecifal mas grande del hemisferio norte, extendiéndose 220 km desde el borde mexicano al norte, hasta el Golfo de Honduras al sur. Detrás de esta barrera se sitúa un enorme sistema lagunar promediando 25km entre el continente y el mar abierto. Los manglares que bordean la mayor parte de la línea de costa, se extienden río arriba por las innumerables bocas del río y cubren la mayoría de los cayos lagunares. La localidad de los estudios y laboratorio experimental se encuentra en los *Twin Cayss* (Cayos Gemelos). El propósito de este capítulo es documentar la biología, geología, balance ecológico, importancia económica y valor estético de este notable ecosistema costero.

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El inventario de especies aun esta siendo integrado y la mayor parte de los *phyla* están representados por especies de las cuales entre 10 y 25 % no están descritas y algunos son grupos crípticos de tamaños microscópicos. Dentro del ecosistema, el manglar rojo de franja, la vegetación especializada, el ambiente físico y la fauna y flora asociada conforman una comunidad insular compleja y diversa, tanto por arriba del agua como por debajo. La comunidad de manglar por si misma puede considerarse que esta constituida por tres componentes: el bosque por debajo del agua, los pantanos de intermarea y el sistema por arriba del agua. Los manglares producen sedimentos finos y detritus orgánico, estabilizándolos por la modificación del oleaje y el régimen de la laguna abierta. Además, el pantano del manglar es rico en nutrientes reciclados y altas tasas de producción, pero sus habitantes están severamente estresados por factores tales como las fluctuaciones de salinidad y temperatura, la desecación potencial y la granulometría del sedimento.

Introduction

"The roots gave off clicking sounds, and the odor was disgusting. We felt that we were watching something horrible. No one likes the mangroves." That is how John Steinbeck and E.F. Ricketts depicted the mangroves in 1941 in the "Sea of Cortez." Many people will agree with them. So why have two dozen scientists from the Smithsonian Institution, primarily the National Museum of Natural History, and twice as many colleagues from American and European universities and museums devoted a decade of exploration to one square kilometer of "black mud,... flies and insects in great numbers..., impenetrable... mangrove roots..., and... stalking, quiet murder"?

The study started in the early 1980s and focuses on an intertidal mangrove island known as Twin Cays, just inside the Tobacco Reef section of the barrier reef of Belize, a tiny Central American nation on the Caribbean coast. The principal purpose of this research is to document the biology, geology, ecological balance, economic importance, and aesthetic value of a prominent coastal ecosystem using the example of a diverse and undisturbed swamp community.

Properties of Mangrove Swamps

Mangrove swamp communities dominate the world's tropical and subtropical coasts, paralleling the geographical distribution of coral reefs.

Mangroves on the Atlantic side of the American coasts occur between Bermuda and the mouth of the Rio de la Plata and throughout the West Indies. Like reefs, mangrove swamps are environments formed by organisms, but unlike most coral communities, they thrive in the intertidal zone and endure a wide range of salinities.

"Mangrove" refers to an assemblage of plants from at least five families with common ecological, morphological, and physiological characteristics that allow them to live in tidal swamps. Worldwide, at least 34 species in nine genera are considered to be true mangroves. P.B. Tomlinson's recent book *Botany of Mangroves* defines this group of plants by five features: 1) they are ecologically restricted to tidal swamps, 2) the major element of the community frequently forms pure stands, 3) the plants are morphologically adapted with aerial roots and vivipary (producing new plants instead of seeds), 4) they are physiologically adapted for salt exclusion or salt excretion, 5) they are taxonomically isolated from terrestrial relatives, at least at the generic level. "Mangrove swamp" or "mangal" refers to communities characterized by mangrove plants.

Mangrove trees are used for water-resistant timber, charcoal, tannins, dyes, and medicines. They resist coastal erosion during storms and have the reputation of promoting land-building processes by trapping sediment and producing peat. The protective subtidal root system of red mangrove is quoted as serving as nursery ground for many commercially valuable species of fishes, shrimps, lobsters, crabs, mussels, and oysters. An attractive fauna of birds, reptiles, and mammals is also at home in the mangrove thickets and tidal channels.

Human disturbances have made a heavy impact on many mangroves near populated areas as a result of dredging and filling, overcutting, insect control, and garbage and sewage dumping. The intertidal environment of mangroves is endangered by pollutants in water, air, as well as in the soil. Accidental oil spills appear to be particularly damaging. Oil and tars not only smother algae and invertebrates, but also disrupt the oxygen supply to the root system of the mangrove trees by coating the respiratory pores of the intertidal prop and air roots.

Figure 1. Map of study area, Twin Cays, Belize. The National Museum of Natural History's coral reef field station is located on Carrie Cay, about four kilometers southeast. (from Rützler and Macintyre, 1982, Smithsonian Contributions to the Marine Sciences 12)

A Mangrove Laboratory in Belize

Belize (formerly British Honduras), boasts the longest barrier reef of the northern hemisphere, extending 220 kilometers from the Mexican border in the north to the Gulf of Honduras in the south. Behind this barrier lies an enormous lagoon system averaging 25 kilometers between the mainland and open ocean. Mangroves border most of the coastline, extend upstream of the countless river mouths, and fringe or cover most lagoon cays.

One of these is Twin Cays (Fig. 1) -an island divided into two by an S-shaped channel. Twin Cays has become our study site and experimental field laboratory. Although we usually spend the nights and conduct lab bench work on nearby Carrie Bow Cay—site of the National Museum's coral reef field station for 20 years (founded in 1972)- most days and many nights are spent in the mangrove channels, lakes, ponds, mudflats, and even the trees. Many important climatic parameters are monitored by a self-contained weather station on Carrie Bow Cay. Selected oceanographic measurements, such as tides, temperature, turbidity, salinity, are recorded at substations in the swamp. The bibliographies on mangroves show that during the last 200 years

more than 6,000 papers have been published describing biological and geological details from almost as many different swamps over the world. Our ongoing study aims to analyze as many components as possible of a single mangrove swamp and, ultimately, assemble them to a mosaic reflecting structure as well as function of this unique ecosystem.

Geological History of Twin Cays

A popular theory holds that mangroves are builders of land because they trap and hold fine sediments. Early on in our study we discovered that this is not necessarily true. We tried to reclaim nearby Curlew Cay, which had been lost to a hurricane (it is now known as Curlew Bank), by planting an assortment of young red mangroves, but were unsuccessful. So the question arose, if islands are not built by mangroves, how do they get started?

To learn more about the Holocene (recent time—back to 18,000 years before present) stratigraphy under the present island, Ian G. Macintyre of the Smithsonian Department of Paleobiology, along with Robin G. Lighty and Ann Raymond of Texas A & M University, drove pipes 8 meters into the sediment down to the Pleistocene level (marks the beginning of the Holocene), and retrieved sediment cores which date back seven thousand years, the maximum sediment accumulation in this particular area. They also collected rock cores below this level. What they found below the mangroves was a carbonate substrate consisting of a dense limestone formed mostly by finger corals (*Porites*) with abundant mollusk fragments, indicating an environment of deposition similar to today's calm-water patch reefs. The sequence of peat, algal-produced sand, and mangrove oysters in the sediment cores indicate that this mangrove was apparently established on a topographic high formed by a fossil patch reef and kept pace with the rising sea level. However, there is also evidence that the island repeatedly changed its size and shifted position, generally transgressing lagoon sediments on the windward coasts, while eroding at the leeward edge, which is characterized by shallow-water bottoms formed by stranded peat deposits.

The mangrove community itself can be thought of as being composed of three components: the above-water "forest", the intertidal swamp, and the underwater system. In our descriptions, we will start from the bottom and work up.

Environments Below the Tides

The bottom of the mangrove (Fig. 2), from the intertidal to three meters, the greatest depth of the main channel, is composed of what most people would call muck. To us it displays many varieties, such as carbonate silt, mud, and sand with varying amounts of mucus, organic detritus (products of plant and animal decay), peat, and silicious skeletons derived from diatom algae and sponges. Many fine-grained limestone sediments are produced by physical and biological erosion on the nearby reef and carried into the mangrove by water currents. Sands, on the other hand, are primarily produced within the community by digestion or decay of calcareous green algae (*Halimeda*). The most abundant and ecologically important plant on the submerged mangrove bottoms is the turtle grass (*Thalassia*). It stabilizes the muddy bottom, offers substrate for egg cases and many small sessile organisms, and provides food and shelter to animal groups ranging from microbes to 2-meter manatees. Jörg A. Ott, a seagrass ecologist from the University of Vienna, determined that turtle grass in the Twin Cay mangrove is more dense and grows three times faster than *Thalassia* in the nearby open lagoon, resulting in an almost 10-fold net leaf production.

Red mangrove stilt roots line all channels, creeks, and ponds and, below tide level, support spectacularly colored clusters of algae, sponges, tunicates (sea squirts), anemones, and many associates. They also provide hiding places for many mobile animals, such as crabs, lobsters, sea urchins, and fishes.

Algae without the ability to root in mud bottoms abound on the stilt roots. Mark Littler, from the Smithsonian Department of Botany, and coworkers Diane Littler and Philipp Taylor found that, curiously, fleshy algae seem to prefer roots that had penetrated the water surface but had not yet reached the bottom of the channel or lake. Calcifying algae (such as the sand-producing *Halimeda*), on the other hand, are common on the submerged parts of anchored roots and along the channel banks. Experiments demonstrated that the hanging roots offer palatable plants protection from benthic herbivores such as sea urchins and many fishes, whereas *Halimeda* has its own skeletal protection.

Figure 2. Channel fringed by red mangrove. Sponges and other sessile organisms are attached to prop roots and to the underwashed peat bank to the right; turtle grass and algae cover the mud bottom. A black mangrove with short intertidal air roots protruding from the bottom is seen on the left. (After Rützler, 1969, *Proceedings of a Coastal Lagoon Symposium*, Mexico City; redrawn by Molly K. Ryan)

Certain algae and many sessile invertebrates on the subtidal mangrove roots are protected from predators by toxic substances stored in their tissues and produced by their own metabolism. Sponges are particularly well known for their antibiotic and feeding-deterrent properties and are used by many smaller organisms, such as anemones, polychaete worms, shrimps, crabs, amphipod crustaceans, gastropod mollusks, and brittle stars as an effective physical and chemical shelter. Collaborating with our Smithsonian colleagues Kristian Fauchald, Gordon Hendler (now at the Los Angeles County Museum), and Brian Kensley, we extracted up to 40 species and 400 specimens of endozoans larger than 2.5 millimeters from, as an example, a 1-liter fire sponge (*Tedania*), a species that causes burning, itching, and even severe dermatitis in humans.

Sponges are among the most common, massive, and colorful invertebrates in the submerged mangrove. To settle and metamorphose, their larvae need solid substrate with low exposure to sedimentation, although we observed grown specimens surviving for months buried in light mud after they had fallen from their place of original attachment. Only two kinds of firm substrate are available to such settlers, red mangrove stilt roots, and vertical or overhanging banks composed of a peat and live mangrove rootlets and flushed by tidal currents.

In both locations, the competition for space is fierce, not only among sponges but also between sponges and other sessile organisms, such as algae, hydroids (the polyp-generation of many medusae), corals, anemones, bryozoans (moss animals), and tunicates (sea squirts). With our colleagues Dale Calder, Royal Ontario Museum, Ivan Goodbody, University of the West Indies, and Jan Kohlmeyer, University of North Carolina, we are analyzing the sequence of settlement of species at different seasons, following their growth and subsequently the methods and hierarchies of competition.

We have found that within days new substrates (wood, plastics) are colonized by ubiquitous bacteria, fungi, and lower algae. The next to arrive are coralline algal crusts, sponges, hydroids, scyphozoan polys (the polyp stage of the upside-down jellyfish

Cassiopea), anemones, serpulid and sabellid worms, bryozoans, and ascidians. After 3 to 6 months, substrates are fully covered by a spectrum of organisms. The spectrum varies greatly and depends on the season in which the experiment was started, the habitat position of the substrate, and the environmental endurance of the settlers.

Not all subtidal mangrove life is restricted to the bottoms and roots. Fishes of all size and age classes hide or feed in the water column around the red mangrove roots and along the banks. Many of these depend on plankton, such as copepod and mysid crustaceans, for food. Members of both groups form characteristic swarms during the day. Smithsonian's Frank Ferrari teamed up with Julie Ambler, Texas A & M University, Ann Bucklin, University of Delaware, and Richard Modlin, University of Alabama, to study the systematic, ecology, and genetics of the swarms and found population densities much greater than expected. They counted more than two thousand copepods per cubic meter of water in a small bay at night, and estimated 100 million individuals congregated during the day in a band of swarms along a 1000-meter stretch of channel bank.

The Intertidal Mangrove Swamp

Although the tidal range in the Caribbean is small, in shallow coastal areas it can strongly influence current flow and distribution of organisms. At Twin Cays, the mean tidal range is only 15 centimeters, yet a combination of astronomic, geomorphologic, and meteorological factors can cause a range of more than a half meter.

Red mangrove (*Rhizophora*) prop roots, black mangrove (*Avicennia*) pneumatophores (aerial roots), peat banks, and mudflats are the typical substrates of the intertidal zone supporting distinctive communities. Barnacles (*Chthamalus*), wood-boring isopods (*Limnoria*), oysters (*Crassostrea*), and "mangrove oysters" (*Isognomon*, not a true oyster) are the best known indicators of intertidal hard substrates, while fiddler crabs (*Uca*) are typical for the mud flats. Green algal mats (*Caulerpa*, *Halimeda*) are found exposed on peat-mud banks during low tide. The most abundant and characteristic intertidal mangrove community, however, is called the bostrychietum, named after the principal components of an association of red algae (*Bostrychia*, with *Catanella* and *Caloglossa*).

The bostrychietum (Fig. 3) has a remarkable water-holding capacity, which allows the plants and their associated animals to survive extended dry periods. We measured water loss rates in two of the substrate species and found evidence of two different methods of water retention. *Bostrychia* is a delicate, tufted plant that holds water primarily interstitially (between the branches). *Catenella* is more fleshy and less elaborately branched and holds water intracellularly (within the cells) in its tissues.

Loren Coen, Dauphin Island Marine Laboratory, examined the animal associates of the bostrychietum, particularly in respect to grazing. He found that amphipods (*Parhyale*) become concentrated in the algal mats in high numbers during receding tides, and that their grazing on *Bostrychia* can match or exceed the algal growth. The mangrove tree crab *Aratus*, and other crabs from low tide level were also found with large quantities of *Bostrychia* in their guts.

Desiccation and related problems of increased temperature and salinity in organisms subjected to exposure at low tide became particularly apparent during an extreme low tide in June, 1983. A 20-centimeter zone below mean low tide level became exposed during noon hours under a clear sky. Large communities of low intertidal (rarely exposed) and subtidal (never exposed) organisms, such as occupants of seagrass meadows (including the turtle grass itself), and mangrove mud banks and stilt roots, were killed during the long exposure to desiccation. Estimates indicate that more species of algae and invertebrates, and much more living matter (biomass), were destroyed during those days of June than during two hurricanes combined (Fifi, 1974; Greta, 1978).

Collaborating eco-physiologist Joan Ferraris, National Institutes of Health, is experimentally examining a number of organisms (sponges, sipunculan worms, shrimps, crabs) that are exposed to strong salinity-temperature stress in their natural environment. Results so far show a fine correlation between experimental tolerances in the animals and range of variability of stress factors in their natural habitat. In the case of sponges, regulatory mechanisms controlling water-ion balances are still unknown, but in the absence of organs they must take place inside individual cells.

Unfortunately, the intertidal swamp is not only an exciting biological study zone but also a gallery of pollutants. Even in this remote location every imaginable piece of floating debris discarded by man can be found, washed in by currents among the mangrove roots and deposited by the receding tides.

Figure 3. The bostrychietum community, based on an intertidal association of red algae. Oysters are located at mid-tide and upper-tide levels, while the mangrove tree crab and periwinkle stay above the water line. (Illustration: Candy Feller)

Mangrove Forest Above the Tide

Unlike the adjacent marine systems, the supratidal flora and fauna of the mangrove-covered islands appear less complex and diverse. From the water, an unbroken, monotonous barrier of red mangrove trees confronts, and frequently intimidates, the casual explorer.

The species composition of the above-water plant community around Twin Cays is relatively simple. Three halophytic tree species, known collectively as mangroves, dominate the natural vegetation on most of the islands: red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and white mangrove (*Laguncularia racemosa*). On cays with slightly higher ground, additional woody and herbaceous halophytes are associated with the mangrove, such as buttonwood (*Conocarpus*), saltwort (*Batis*), and sea purslane (*Sesuvium*).

In general, mangrove forests have well-defined horizontal zonation. On these mangrove islands, the seaward and channel margins typically are fringed by dense, 4 to 10-meter tall stands of red mangrove. Behind this fringe, the red mangrove is usually more open and shorter, with black and white mangroves intermixed. The zonation is easily recognized: dull gray-green spires of black mangrove, and flattened, yellow-green crowns of white mangrove stand slightly above and behind the dark green dome of the fringing red mangrove.

The interiors of some of the larger islands off Belize, like Twin Cays, have several extensive, unvegetated mudflats and shallow ponds. Numerous stumps throughout the mudflats are evidence that the trees that once grew there fell victim to some environmental stress. The red mangrove trees growing around the margins of the mudflats and in the ponds are severely stunted and widely spaced. Over the years, these natural bonsai have been distorted and pruned by their environment into fantastic forms, seldom over 1.5 meters tall. A. Lugo and S. Snedaker, in their 1974 review of mangrove ecology, estimated the age of comparable dwarf trees in south Florida and the Florida Keys to be 40 years old. Our collaborators Irving A. Mendelssohn, Karen McKee, and Colin D. Woodroffe (Wetland Biogeochemestry Institute, Louisiana State University) suggest that abiotic factors, such as high sulfide levels in the soils, may be responsible for the die-back and reduced tree vigor.

The supratidal fauna on the cays is considered by most investigators to be introduced from the Belizean mainland. Even on the largest mangrove islands, most of the “land” is intertidal; therefore, the only environments available to terrestrial animals are arboreal. The fauna is limited to birds, lizards, snakes, snails, and arthropods, such as land crabs, spiders, and insects. These animals probably reached the cays from the mainland by flying, or rafting on or in pieces of wood and other floating debris.

A few land birds species have established permanent breeding populations on the mangrove islands. James F. Lynch (Smithsonian Environmental Research Center) reports that the mangrove yellow warbler is the most characteristic land bird throughout the cays, but the Yucatan vireo is also a well-established resident on most of the cays. Both of these species are insectivorous. The hummingbird, *Anthracocorax*, has been observed nesting in red mangrove on Twin Cays but not on smaller islands. Mangrove cuckoos, grackles, and white-crowned pigeons, common on the large mangrove islands, are also thought to be permanent residents. Several of the islands also provide nesting sites for ospreys. These birds frequently build their nests atop tall snags of black mangrove.

At Twin Cays, the clapper rail with its loud, rather sudden clattering is more often heard than seen, although occasionally one can catch a glimpse of it walking under the prop roots of red mangrove where it feeds on crabs. The green-back heron is the most commonly observed wading bird at Twin Cays. It breeds on the island and builds its twig nest in the red mangrove fringe along the channels. It is frequently seen diving for small fish in the shallow, interior ponds. The most conspicuous birds of the area are the brown pelican and frigate bird, which can always be seen flying overhead or perched in mangrove trees.

Only four or five reptile species are known from the Belizean mangrove cays. James F. Lynch has found one species of lizard (*Anolis sagrei*) to be ubiquitous on the islands. It is commonly seen in red mangrove trees, feeding on ants, termites, and other insects. Less common is the boa constrictor (*Boa*) which populates most of the larger islands. The ground iguana (*Ctenosaura*) and a couple of gecko species are present only on a few of the islands.

Two common land crab species occur on the islands. The mangrove tree crab (*Aratus pisonii*, currently under study by Kim Wilson, Central Connecticut State University) moves up and down the bole and aerial roots of red mangrove. *Ucides*, the largest land crab on the islands, lives on the ground under the dense mangrove canopy where it builds large, extensive burrows near the upper limits of the high tide. Belizean fishermen consider the burrows of *Ucides* to be the primary breeding sites for sandflies and mosquitoes. William P. Davis (Environmental Protection Agency, Gulfbreeze, Florida) and D. Scott Taylor (Vero Beach, Florida) have found *Ucides* burrows to be havens for the mangrove *Rivulus*, a hermaphroditic fish.

The periwinkle (*Littoraria angulifera*) is widespread on all the mangrove islands. These arboreal snails migrate slowly between the mean high water level and the tops of red mangrove trees; they are the subject of thesis research conducted by Laurie Sullivan, University of Alabama. Brad Bebout and Jan Kohlmeyer, University of North Carolina determined that these snails feed on a fungus that is restricted to a very narrow zone on the prop roots, just above the mean high-water level.

Insects are, by far, the most Species-rich and abundant group of supratidal animals inhabiting the Belizean mangrove cays. Ants, in 28 or so species, are clearly the most abundant. Termites, because of their huge nests and extensive covered walkways, are the most conspicuous. Some major groups of insects, such as bees, are poorly represented in the mangrove fauna. As in other tropical ecosystems, a large percentage of the insect species that we have found associated with mangroves is undescribed.

The surface of the salt water, the interior ponds, and the mudflats provide habitats for aquatic and semiaquatic insects, including members of five families of true bugs (Hemiptera) and three families of beetles

Figure 4. Red mangrove twig terminal with associated organisms (Illustration: Candy Feller)

(Coleoptera). Paul J. Spangler and Robin Faitoute (Department of Entomology, Smithsonian Institution) studied this group alongside similar fauna on the mainland. The cays have fewer kinds of aquatic habitats, and a corresponding lower species diversity in this part of the insect fauna.

Wayne N. Mathis (Department of Entomology, Smithsonian Institution) found an astounding 51 species of shore flies (Ephydridae) along the margins of these mangrove islands although none of these species is endemic. Most of these species are detritivores, living on the peat-based muck or in decaying seagrass and algae that wash ashore.

The mangrove trees and mangrove associates provide numerous supratidal habitats for primary and secondary phytophagous insects as well as their parasites and predators. Because most of these species have cryptic behavior, the

diversity of insects in mangroves can easily be underestimated. The foliage of each species of mangrove supports a unique suite of leaf-eating insects, although the damage to the leaves is much more apparent than the insects themselves.

Leaves and twig terminals of red mangrove, in particular, serve as an important habitat for a diverse assemblage of insects (Fig. 4). Because vegetative growth in the canopy is derived almost exclusively from apical buds in twig terminals, herbivore damage here is particularly important to the tree. The apical bud is commonly attacked by a moth larva (*Ecdytolopha* sp) that causes the enveloping stipules to turn black. A larva usually eats only a portion of the young, folded leaves in a bud, leaving the meristematic tissue intact. However, sometimes the entire apical bud is destroyed as a result of this form of herbivore and any potential for further growth by the damaged twig is lost. A number of other moth larvae feed on red mangrove leaves, but because insect taxonomy is based primarily on adult specimens, identifications of these larvae are almost impossible without rearing them. Moth larvae that feed on leaf surfaces encase themselves in a variety of protective coverings, such as frass tubes or portable cases built of mangrove twigs and bark. Serpentine galleries of a leaf, twig, and propagule mining moth larvae (Microlepidoptera, Gracillariidae) are also common on red mangrove, although both larval and adult specimens are rare. Adult insects that feed on these leaves are primarily nocturnal. A guild of at least six species of wood-boring insects is primary herbivores on the twigs of red mangrove. Ordinarily, each twig hosts only one individual. As it feeds, the larva hollows the twig. When the adult wood-borer emerges via an exit hole, access is provided to the hollow twig. These spaces are critical to many small arthropods, including ants, other insects, and spiders, that are not wood-eating and are dependent on finding suitable spaces in which to build nests or to take refuge. So far, we have found more than 70 species associated with hollow red mangrove twigs.

At least 35 species of xylophagus (wood eating) beetles and moths have been extracted from the three mangrove species. More than half of these are wood-borers in the Long-Horned Beetle family (Cerambycidae). Although some of the species are generalists, feeding on any available dead wood, a few specialist species appear adapted to a single mangrove species. Our research indicates that these arboreal wood-borers play significant roles in the mangrove ecosystem. The larval stages of these insects are the primary herbivores. They modify the trees by constructing galleries and pupal chambers in the living and dead woody tissue. These spaces are used as habitats by numerous invading arthropods, such as ants, termites, other beetles, spiders, isopods, scorpions, pseudoscorpions, scale insects, centipedes, crickets, katydids, and roaches. The infestation by wood-borers is extensive on the islands; all species of mangroves and almost every tree sampled have hosted at least one and usually several species. Wood-borers girdle, as well as hollow, mangrove stems and boles. In red mangrove, these activities frequently result in death, weakening, and subsequent pruning of all branches beyond the point of attack.

Conclusions

The red mangrove fringe, the specialized vegetation, the physical environment, and the associated fauna and flora form a complex and diverse island community above water as well as below. We have learned that mangroves produce fine sediments and organic detritus and stabilize them by modifying the wave and current regime of the open lagoon. The inventory of species has yet to be completed, but already we have shown that most phyla are represented by species of which 10 to 25 percent, and in some cryptic microscopic-sized groups up to 60 percent, are undescribed. The mangrove swamp is rich in recycled nutrients and high in production rates but its occupants are severely stressed by factors such as salinity and temperature fluctuations, desiccation potential, abundance of fine sediments, and shortage of firm substrates. Space, from the sea bottom to the tree tops, is distinctly partitioned by the animals that exploit this specialized plant community. These intertidal islands, because of their isolation from the Belizean mainland, provide us with ideal locations to study pure mangrove communities in the Caribbean.

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Ambiente, Distribución y Características Estructurales en los Manglares del Pacífico de Centro América: Contrastes Climáticos

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Resumen

Centro América se consolidó como istmo, hace aproximadamente 3.5 millones de años. Las especies de manglar (*Rhizophora*, *Avicennia*, *Laguncularia* y *Pellicera*) se encontraban ampliamente distribuidas en el Caribe y el Pacífico. Las diferencias en la composición florística entre estas dos costas se manifiestan después de este periodo, siendo la causa más probable, los procesos climáticos a principios del Mioceno cuando ocurre un cambio progresivo hacia climas secos estacionales y culmina con las glaciaciones ocurridas en el Pleistoceno. Asimismo, se originan dos grupos florísticos de manglares **1)** especies restringidas a climas secos estacionales (e.g. *Avicennia bicolor*, *Clerodendrum pittieri*) y **2)** especies limitadas a climas lluviosos (e.g. *Pelliciera rhizophorae*, *Mora oleifera*). Estos grupos restringidos climáticamente, están acompañados por un núcleo de especies que trascienden estas fronteras (e.g. *Rhizophora mangle*, *Avicennia germinans*).

Los manglares de la costa Pacífica de Centro América cubren un área aproximada de 320,000 ha. De acuerdo a la geomorfología de la costa, los manglares se clasifican en dos grupos: **1)** ambientes con fuerte oleaje y barrera arenosa y **2)** ambientes de bajo oleaje y amplio rango de mareas. La vegetación de estos ecosistemas esta compuesta por una mezcla de árboles, hierbas, lianas y epifitas. Se registran tres especies de *Rhizophora* (*R. mangle, R. racemosa, R. harrisonii*), de *Avicennia* dos especies *A. germinans* y *A. bicolor*, también están presentes *Laguncularia racemosa*, y *Conocarpus erecta*. En cuanto a la fauna asociada a los manglares es muy variada. El dosel esta ocupado por una gran diversidad de insectos, aves y reptiles. Dentro de estas comunidades, destacan las aves que comprenden más de 160 especies, de las cuales más del 25% son migratorias. Los moluscos son otro componente importante, cuya distribución dentro del manglar muestra patrones espaciales claramente diferenciados. Estos ecosistemas proveen a las comunidades de peces un importante hábitat, principalmente en fase larval o juvenil. Las diferencias en la estructura y función de las comunidades de manglar se manifiestan de acuerdo a su ubicación, como resultado a la interacción de un gran número de factores y procesos ambientales.

Abstract

Central America consolidates as isthmus, approximately 3.5 million years ago. The mangroves species (*Rhizophora, Avicennia, Laguncularia* and *Pellicera*) were widely distributed on the Caribbean and the Pacific coast. The differences in floristic composition among these two coasts shows after this period, being the most probable reason, the climatic processes at the beginning of the Mioceno when a progressive shift toward dry seasonal climates occurs and culminates by the glatiations occurred at the Pleistoceno. Also, they originate two floristic groups for mangroves: **1)** species restricted to dry seasonal climates (e.g. *Avicennia bicolor*, *Clerodendrum pittieri*) and **2)** species confined to rainy climates (e.g. *Pelliciera rhizophorae*, *Mora oleifera*). These groups climatic restricted, is accompanied by a nucleus of species which they transcend these boundaries (e.g. *Rhizophora mangle*, *Avicennia germinans*).

The mangroves of the Pacific coast of America Center cover an area approached of 320,000 km^2. According to the geomorphology of the coast, the mangroves are classified in two groups: **1)** environments with strong surf and sandy barrier and **2)** environments of low surf and wide range of tides. The vegetation of these ecosystems are compounded for a mix of trees, herbs, lianas and epiphyts. There are reported three species of *Rhizophora* (*R. mangle*, *R. racemosa, R. harrisonii*), for *Avicennia* genus is reported two species *A. germinans* and *A. bicolor*. Likewise *Laguncularia racemosa* and *Conocarpus erecta* are present. The fauna associated with the mangroves are very varied. The canopy is busy for a great diversity of insects, birds and reptiles. The birds are a component important of the community which include more than 160 species, 25% of them are migratory. The mollusks are another component important, whose distribution inside the mangrove exhibits space patterns clearly differed. These ecosystems provide the communities of fish an important habitat, mainly in larval or juvenile phase. The difference at the structure and function on the mangrove communities shown according to their location, as result of the interaction of a great number of factors and environmental processes.

Antecedentes Biogeográficos

Hace aproximadamente 3.5 millones de años, Centro América terminó de consolidarse como istmo (Gómez, 1986). Anteriormente el istmo estaba representado por una cadena de islas volcánicas a través de las cuales existía una comunicación entre el Atlántico y el Pacífico.

Las especies de manglar, presumiblemente derivadas de una flora pantethyana, se encontraban ampliamente distribuidas en el Caribe y el Pacífico. Estudios palinológicos han demostrado que polen de *Rhizophora, Avicennia, Laguncularia* y *Pelliciera* estuvieron presentes a través de la cuenca del Caribe desde el Oligoceno (Jiménez, 1984).

Las diferencias en la composición florística de los manglares del Caribe y el Pacífico se manifestaron, por lo tanto, hasta después del Oligoceno. La causa más probable de estas diferencias parece estar relacionada con los procesos climáticos que se iniciaron a principios del Mioceno.

Durante esta época parece que ocurrió un cambio progresivo hacia climas secos estacionales, evidenciado por un aumento del polen de pastizales en el área del Caribe (Germeraad *et al*., 1968). Un considerable número de elementos florísticos y faunísticos desaparecieron de la cuenca del Caribe durante el Mioceno (Flenley, 1979; Pregill y Olson, 1981). Este cambio hacia climas secos estacionales culminó con las glaciaciones ocurridas en el Pleistoceno.

En los manglares, estos cambios resultaron en la desaparición de aquellos elementos florísticos asociados con ambientes de baja salinidad (e.g. *Pelliciera rhizophorae, Nypa fruticans*; Moore, 1973; Jiménez, 1984).

La aridez glacial del Plioceno debió afectar tanto los manglares del Pacífico como los del Caribe. Sin embargo, la región del Chocó, en la costa Pacífica de Colombia, parece haber mantenido altas precipitaciones. Por consiguiente se lograron conservar ambientes salobres que funcionaron como refugio para algunas especies de manglar (Gentry, 1982) restringidas a suelos con salinidades menores a las 35 ‰ (Jiménez, 1984).

Además de permitir la supervivencia de estas especies, esta región promovió el surgimiento de nuevas especies a partir de ancestros encontrados tanto en el Pacífico como en el Caribe. El surgimiento y consolidación del istmo centroamericano separó definitivamente la flora del pacífico, impidiendo que estas nuevas especies colonizaran el Caribe Centroamericano. Estas nuevas especies, dieron su característica identidad y mayor diversidad a la flora de los manglares del Pacífico (e.g. *Phryganocidia phellosperma, Mora oleifera, Pavonia rhizophorae*, Gentry, 1982).

Con el advenimiento de climas más húmedos, después del Pleistoceno, las especies de esta región fueron colonizando aquellas secciones del litoral Pacífico influenciadas por climas húmedos (Costa Rica, Panamá, Colombia y Ecuador).

Los sucesos climáticos asociados al periodo glacial del Pleistoceno diferenciaron, florísticamente, los manglares del Caribe y del Pacífico; pero al mismo tiempo originaron, en la ya consolidada costa Pacífica de Centro América, dos grupos florísticos de manglares: un grupo de especies restringidas a climas secos estacionales (*Avicennia bicolor, Clerodendrum pittieri*) y otro grupo de especies limitadas a climas lluviosos (*Pelliciera rhizophorae, Mora oleifera*). Estos dos grupos, climáticamente restringidos, están acompañados, sin embargo, por un núcleo de especies que trascienden fronteras climáticas (e.g. *Rhizophora mangle, Avicennia germinans*). Estas especies son encontradas tanto en climas lluviosos como secos.

Condiciones Climáticas Actuales

La costa Pacífica de Centro América se extiende a lo largo de más de 4,000 km, en una posición general noroeste-sureste. Comparada con la costa Caribe, la costa Pacífica es más seca. Las precipitaciones en la zona norte de la costa Pacífica centroamericana raramente exceden los 1,600 mm anuales.

Los elementos climáticos dominantes en esta zona son la Zona de Convergencia Intertropical (ZCI), los frentes fríos del hemisferio norte, las ondas del este, los huracanes y los fenómenos climáticos locales (Herrera, 1986).

Los movimientos latitudinales de la ZCI son el factor determinante de la estacionalidad climática que domina la costa Pacífica de Centro América. A inicios de mayo la ZCI migra hacia el norte ubicándose cerca del los 6° N, y generando lluvias entre los 14° N y los 2° S. Debido a este comportamiento, la costa Pacífica centro-americana recibe una fuerte precipitación entre los meses de mayo y noviembre. Durante esta época, especialmente entre junio y octubre ocurren las ondas del este, zonas de baja presión que generan cumulo nimbus y tormentas eléctricas importantes, producto de los ciclones ocurridos en el Caribe.

En Diciembre, con el inicio del invierno en el hemisferio norte, se activan los frentes fríos que traen bajas temperaturas y que, conjuntamente con la migración de la ZCI hacia el hemisferio Sur, provocan periodos secos entre Diciembre y Abril en la mayor parte de la costa.

La precipitación a lo largo de la costa Pacífica muestra un claro patrón espacial. En la parte norte del istmo la precipitación promedio anual varía entre los 1400 y los 1600 mm. La precipitación aumenta en un patrón ascendente hacia al sur superando los 2,000 mm/año al sur de la Península de Nicoya, Costa Rica (Fig. 1). La parte interna del Golfo de Nicoya, es sin embargo más seca (1500 mm/año). En la sección sur de la costa Pacífica de Costa Rica la existencia de la importante Cordillera de Talamanca reduce el efecto desecante de los alisios del Caribe. Como resultado de esta reducción la estación seca se limita a los meses de enero y febrero y la precipitación promedio anual sigue aumentando (3,000-4,000 mm/año). En áreas como la península de Osa, Costa Rica, la precipitación anual sobrepasa los 5,000 mm/año. Al disminuir la altura y extensión de los macizos montañosos, condiciones secas estacionales reaparecen en la costa Pacífica de Panamá (alrededor de la Península de Azuero) tornándose, otra vez más húmedas, cerca del Golfo de San Miguel donde la precipitación anual supera otra vez los 2,000 mm/año.

Rasgos geomorfológicos de las Comunidades de Manglar

La costa Pacífica de Centro América tiene una amplia representación de ambientes redimentarios. La existencia de una cordillera transístmica, relieves abruptos, climas tropicales y lluviosos favorecen la erosión y el consecuente suministro de abundantes sedimentos terrígenos a la zona costera. No es de extrañar, entonces, que en aquellos sitios con amplia escorrentía terrestre, los bosques de manglar alcanzan extensiones importantes como las encontradas en el Estero Jaltepeque, el Golfo de Fonseca, el Golfo de Nicoya, el delta Térraba-Sierpe, el Golfo de Chiriquí y el Golfo de San Miguel.

La existencia de amplios ambientes sedimentarios asociada con la presencia de regímenes meso y macromareales (amplitudes mareales de 2.5-5.1 m) permite que las extensiones de manglar asociadas a estos sitios alcancen miles de hectáreas.

Los rasgos geomorfológicos de la costa Pacífica centroamericana permiten clasificar los manglares en dos grupos principales:

Figura 1. Localización de las áreas geográficas de la costa pacífica de Centro América, que presentan las mayores extensiones de manglar

Ambientes con Fuerte Oleaje y Barrera Arenosa

En áreas sometidas a fuerte oleaje y corrientes de deriva litoral el material es reacomodado en cordones arenosos detrás de los cuales se encuentran extensiones considerables de manglar comunicadas con el océano, a través de una o varias bocas (Fig. 2). Estos ambientes, dominados por el oleaje, en donde el elemento geomorfológico principal es el cordón o barrera litoral, son los más comunes a lo largo de la costa Pacífica de Centro América. Áreas como Barra de Santiago en El Salvador, el delta de Térraba-Sierpe en Costa Rica, y el Estero Padre Ramos en Nicaragua son ejemplos típicos de estos ambientes.

Ambientes de Bajo Oleaje y Amplio Rango de Mareas

En las secciones internas de Golfos y Bahías donde el efecto del oleaje ha sido considerablemente reducido, los manglares ocupan bancos de lodo y limo. En estos casos, no se encuentra una barrera física entre el bosque y la masa de agua principal. Sin embargo, durante la marea baja es posible observar en algunos sitios extensos bajos limo-arcillosos frente al bosque (Fig. 3). Los manglares que ocupan el frente de estas formaciones, están generalmente dominados por rodales de *Rhizophora mangle* con escaso desarrollo estructural. En las partes internas, donde la influencia directa de los ríos reduce la salinidad, se encuentra un mayor desarrollo y diversidad del bosque. Las partes internas del Golfo de Fonseca y el Golfo de Nicoya son ejemplos típicos de estos ambientes.

Composición Florística

La vegetación de los manglares del Pacífico de Centro América esta compuesta por una mezcla de árboles, hierbas, lianas y epífitas. Esta vegetación muestra diversos grados de adaptación al ambiente salino e inundado. Se han encontrado variaciones importantes en la composición florística a lo largo de la costa Pacífica, de acuerdo a las condiciones climáticas e hidrológicas en cada sitio. El núcleo principal del bosque, tanto en climas secos o lluviosos, está compuesto por especies de los géneros *Rhizophora* y *Avicennia*.

Figura 2. Ambientes geomorfológicos dominados por el oleaje. La existencia de una barrera arenosa permite el establecimiento de considerables extensiones de manglar asociadas a la desembocadura de uno o varios ríos.

Tres especies de *Rhizophora* son encontradas en estos bosques; *R. racemosa* G.F.W. Meyer, *R. mangle L*. y *R. harrisonii* Leech. (Jiménez, 1987; Fig. 4).

R. mangle se caracteriza por sus hojas anchas ovaladas y su inflorescencia pequeña con sólo dos o tres flores. En la mayor parte de los sitios esta especie forma densos rodales con fustes poco desarrollados, donde las raíces aéreas se confunden con los troncos. Este tipo de rodal recibe el nombre de mangle casilar o ñangal. Generalmente son encontrados en suelos poco consolidados en la sección convexa de los meandros.

R. racemosa es una especie de hojas peque as y alongadas con una inflorescencia corta y apretada con numerosas flores. La especie es encontrada en suelos consolidados donde forma extensos rodales monoespecíficos. Debido a su desarrollo estructural, esta especie posee una gran importancia comercial dentro de los manglares centroamericanos.

Figura 3. Ambientes geomorfológicos protegidos del oleaje donde no existe una barrera física entre la masa de agua y el bosque de manglar. Las partes internas de varios golfos y bahías muestran este tipo de ambiente.

R. hariisonii muestra características intermedias en la forma y tamaño de las hojas sugiriendo que pueda ser un híbrido entre *R. mangle* y *R. racemosa* (Breteler, 1977). La inflorescencia es considerablemente más larga y laxa que la de *R. racemosa*. Los botones florales son más puntiagudos y las brácteolas en las bifurcaciones de la inflorescencia y en los botones florales son significativamente más

Figura 4. Diferencias anatómicas entre las inflorescencias de las tres especies de *Rhizophora* reportadas para la costa pacífica de Centro América. Las inflorescencias de *R. mangle* (a) son de pocas flores (2-4), y los botones florales muestran formas cuadradas. Las inflorescencias de *R. harrisonii* (b) y *R. racemosa* (c) son multifloreadas con número variable de flores por inflorescencia

largas (x= 0.31 cm) que en *R. racemosa* (x= 0.37 cm). No existen registros suficientes para determinar la actual distribución de estas dos últimas especies a lo largo del litoral Pacífico de Centro América, ni existen estudios que determinen el grado de aislamiento reproductivo entre ellas. Un alto grado de hibridización parece, sin embargo, evidente, lo que hace difícil la identificación de todos los especimenes en el campo.

El género *Avicennia*, está representado por dos especies *A. germinans* (L.) *L*. y *A. bicolor* Stand. Las diferencias anatómicas son evidentes entre estas dos especies. *A. germinans* muestra una corteza fragmentada en placas siendo la de *A. bicolor* lisa. A nivel de hojas *A. bicolor* muestra una hoja ovalada con un evidente contraste de colores entre el haz y envés, la flor muestra una corola de color blanco. *A. germinans* muestra una hoja lanceolada donde el contraste no es tan marcado, la parte interna de la corola posee una coloración amarilla. La distribución de las dos especies responde a variaciones ambientales determinadas por el clima. *A. germinans* es encontrada a lo largo de toda la costa pacífica de Centro América, mientras que *A. bicolor* está restringida a áreas con clima seco estacional (Jiménez, 1990). Rodales importantes de esta última especie sólo se encuentran en sitios con escorrentía superficial.

Otras especies de árboles como *Laguncularia racemosa* Gaertn y *Conocarpus erecta* L, están también presentes en la mayoría de los sitios, bajo climas secos y lluviosos, aunque su abundancia es muy limitada. Estas dos especies no forman rodales extensos a lo largo del litoral pacífico. Existen otros elementos comunes a manglares de climas secos y climas húmedos como son el arbusto *Hibiscus tiliaceus* L., el helecho *Acrostichum aureum*, la enredadera *Dalbergia brownei* (Jacq.) Urban y la hierba *Fimbristylis spadicea* (L.) Vahl.

Entre los componentes florísticos de manglares con climas lluviosos, destaca el árbol *Pelliciera rhizophorae* Tr. y Planch., quien es fácilmente diferenciable por sus raíces aéreas que semejan gambas. La flor pentámera es muy llamativa y es aparentemente la única polinizada por vertebrados (el colibrí *Amazilia* sp) en los manglares centroamericanos. Sus hojas lanceoladas y asimétricas son fácilmente identificables por una hilera de glándulas en uno de los márgenes. *P. rhizophorae* es abundante al sur de la Península de Nicoya, Costa Rica, pero está ausente al norte de esta localidad donde los climas se vuelven secos y estacionales (Jiménez, 1984). Su distribución fue muy amplia durante el Terciario, encontrándose en sedimentos del Oligoceno-Mioceno en Chiapas, México, en sedimentos del Eoceno en Jamaica y Panamá, y en sedimentos del Eoceno-Mioceno en Venezuela y Brasil. Dentro de los bosques esta especie parece estar limitada a zonas de moderada elevación formando extensos rodales en las áreas entre canales alejadas de los márgenes.

Otro componente de sitios lluviosos o con abundante escorrentía es el árbol *Mora oleifera* (Triana) Duke. Este forma pequeños rodales, puros o entremezclados con *A. germinans*, en ambientes de muy baja salinidad crecen mezclados con el árbol *Anona glabra* L. En áreas lluviosas, se encuentran además, un conjunto de lianas [e.g. *Phryganocidia phellosperma* (Hemsl.) Sandw., *Rhabdadenia biflora* (Jacq) Mull.], arbustos [*Pavonia spicata* Killip, *Pavonia rhizophorae* Killip, *Tabebuia palustris* Hemsl.], lirios (*Hymenocalis littoralis* Salisb., *Hymmenocalis pedalis* Herb. y *Crinum erubescens* Soland.) y helechos (A*crostichum danaefolium* Langsd y Fish.)) que forman parte importante de la vegetación en sitios donde las salinidades del suelo son inferiores a las del agua de mar.

En climas secos, donde la escorrentía terrestre no es significativa, la vegetación asociada a manglares es menos diversa. Destacan en este grupo el arbusto *Clerodendrum pittierii*, que forma cordones extensos en áreas elevadas del bosque, donde las salinidades son altas pero la inundación es reducida. En el borde interno del bosque, las hierbas *Heliotropium curassavicum* L. y *Sesuvium portulacastrum* L. crecen en suelos con altas salinidades.

Un gran número de otras especies aparecen ocasionalmente en los manglares aunque pertenecen a otro tipo de ambientes (Jiménez y Soto, 1985).

Fauna Asociada

La fauna asociada a estos manglares es muy variada y sorprendentemente poco estudiada. El dosel del bosque está ocupado por una gran variedad de insectos, aves y reptiles que practican la vida arbórea. Destacan entre las aves la reinilla de manglar *Dendroica petechia-eritacorides* y el gavilán cangrejero *Buteogallus antracinus*. En bosques de *P. rhizophorae* es muy abundante el colibrí *Amazilia boucardi*, quien parece ser el agente polinizador de ese árbol en Costa Rica.

En troncos huecos, especialmente en bosques de *A. bicolor*, anidan importantes poblaciones de la lora nuca amarilla *Amazona auropalliata*. La avifauna de estos bosques incluye más de 160 especies, de las cuales más del 25% de ellas son migratorias (Tabla 1). En la distribución de las aves dentro del manglar, es posible determinar patrones espaciales. Especies como *Chirophixia linearis* son encontrados en las zonas de *Avicennia* en el margen interno del bosque, otras especies como *Himantopus mexicanus* están restringidas a los bancos y áreas de canales en la sección externa de los manglares.

En las ramas y troncos de los árboles es frecuente encontrar poblaciones de termites (*Nasusitermes corniger, N. nigriceps* y *Termes panamaensis*) que forman nidos de grandes dimensiones. Los mamíferos arbóreos más frecuentemente observados en estos manglares incluyen los osos hormigueros *Tamandua mexicana* y *Cyclopes didactylus*. Los monos congo (*Allouta palliata*) forrajean ocasionalmente en ramas tiernas de *Rhizophora*. El mono carablanca (*Cebus capucinus*) destruye una gran cantidad de frutos de *P. rhizophorae* de los cuales lame una secreción azucarada que se produce entre los cotiledones y roba huevos de los nidos de muchas especies de aves, especialmente de zanates (*Quiscalus mexicanus*). Los mapaches (*Procyon lotor* y *P. cancrivorus*), son observados en el dosel de los árboles, aún cuando es más común encontrarlos en el suelo, consumiendo cangrejos y moluscos. En bosques de *A. bicolor* y *L. racemosa* es posible encontrar venados (*Odocoileus virginianus*) que se alimentan del rico follaje de estas especies. Las ramas del dosel también albergan reptiles como la *Boa constrictor*, la *Iguana iguana* y el garrobo *Cthenosaura similis*.

Tabla 1. Avifauna asociada a los manglares de la costa Pacífica de Centro América. La abundancia es clasificada en orden ascendente como rara, escasa, ocasional, frecuente, común y abundante. Se indica además el tipo de alimentación más frecuente en cada especie.

FAMILIA/ESPECIE	ABUNDANCIA	ESTATUS	ALIMENTACION
PELECANIDAE			
Pelecanus occidentalis	común	local	peces
PHALACROCORACIDAE			
Phalacrocorax olivaceus	común	local	peces
FREGATIDAE			
Fregata magnificens	común	local	peces
ANHINGIDAE			
Anhinga anhinga	común	local	peces
ARDEIDAE			
Nycticorax nycticorax	común	local	peces
Nyctanassa violacea	común	local	peces
Bubulcus ibis	común	local	invertebrados
Butorides virescens	común	local	invertebrados
Egretta caerulea	común	local/migratorio	invertebrados
Egretta tricolor	frecuente	local/migratorio	invertebrados
Egretta rufescens	escaso	migratorio	invertebrados
Egretta thula	común	local/migratorio	vertebrados
Casmerodius albus	común	local/migratorio	invertebrados
Ardea herodias	frecuente	migratorio	invertebrados
COCHLEARIDAE			
Cochlearius cochlearius			
CICONIIDAE			
Mycteria americana	común	local	peces/invertebrados
THRESKIORNITHIDAE			
Eudocimus albus	común	local	invertebrados
Plegadis falcinelus	escaso	local	invertebrados
Ajaia ajaja	común	local	invertebrados
ANATIDAE			
Cairina moschata	ocasional	local	vegetales
Dendrocygna autumnalis	ocasional	local	vegetales
CATHARTIDAE			
Coragips atratus	ocasional	local	carroña
Cathartes aura	ocasional	local	carroña
PANDIONIDAE			
Pandion haliaetus	ocasional	migratorio	peces
ACCIPITRIDAE			
Buteogallus anthracinus	común	local	vertebrados/invertebrados
Buteo nitidus	ocasional	local	vertebrados/invertebrados
Buteo platyperus	ocasional	migratorio	vertebrados/invertebrados
Buteo magnirostris	ocasional	local	vertebrados/invertebrados
Buteo magnirostris	ocasional	local	vertebrados/invertebrados
Elanus leucurus	ocasional	local	vertebrados/invertebrados
Harpagus bidentatus	ocasional	local	vertebrados/invertebrados
FALCONIDAE			
Poliborus plancus	ocasional	local	vertebrados/carroña
Falco peregrinus	ocasional	migratorio	aves
Herpetopteres cachinnas	ocasional	local	reptiles
PHASIANIDAE			
Colinus leucopogon	ocasional	local	granos/invertebrados
RALLIDAE			
Aramides cajanea	escaso	local	invertebrados
Aramides axillaris	raro	local	invertebrados
HAEMATOPODIDAE			
Haematopus palliatus	ocasional	migratorio	invertebrados
RECURVIROSTRIDAE			
Himantopus mexicanus	común	local/migratorio	invertebrados

Tabla 1 (Continuación)

CHARADRIIDAE			
Pluvialis squatorola	escaso	migratorio	invertebrados
Charadrius semipalmatus	común	mogratorio	invertebrados
Charadrius wilsonia	común	migratorio	invertebrados
SCOLOPACIDAE			
Catoptrophorus semipalmatus	abundante	migratorio	invertebrados
Calidris minutilla	común	migratorio	invertebrados
Calidris pusilla	común	migratorio	invertebrados
Calidris mauri	abundante	migratorio	invertebrados
Calidris canutus	común	migratorio	invertebrados
Limosa fedoa	común	migratorio	invertebrados
Numenius phaeopus	común	migratorio	invertebrados
Tringa melanoleuca	escaso	migratorio	invertebrados
Arenaria interpres	abundante	migratorio	invertebrados
Limnodromus griseus	común	migratorio	invertebrados
Actitis maculaia	común	local/migratorio	invertebrados
LARIDAE			
Larus pipixcan	común	migratorio	peces
Larus atricilla	común	migratorio	peces
Sterna hirundo	común	migratorio	peces
Sterna sandvicensis	común	migratorio	peces
Sterna elegans	ocasional	migratorio	peces
RHYNCOPIDAE			
Rhyncops niger	común	migratorio	peces
COLUMBIDAE			
Columba leucocephala	rara	local	granos
Columbina talpacoti	abundante	local	granos
Columbina passerina	común	local	granos
Columbina inca	abundante	local	granos
Columbina minuta	rara	local	granos
Leptotila verrreauxi	rara	local	granos
Clavaris pretiosa	ocasional	local	granos
Columba cayennensis	ocasional	local	granos
Columba flavirostris	común	local	granos
Zenaida asiatica	abundante	migratoria	granos
Zenaida macroura	común	local	granos
PSITTACIDAE			vegetal
Brotogeris jugularis	común	local	frutos
Aratinga finshi	ocasional	local	frutos
Aratiga caniculares	común	local	frutos
Amazona autumnalis	ocasional	local	frutos
Amazona auropalliata	común	local	frutos
Ara macao	escasa	local	frutos
CUCULIDAE			
Coccyzus americanus	escaso	migratorio	invertebrados
Coccyzus minor	ocasional	local/migratorio	invertebrados
Crotophaga sulcirostris	común	local	invertebrados
TITONIDAE			
Tito alba	común	local	invertebrados/vertebrados
STRIGIDAE			
Otus cooperi	escaso	local	invertebrados/vertebrados
Ciccaba nigrolineata	raro	local	vertebrados
CAPRIMULGIDAE			
Chordeiles acutipennis	común	local	invertebrados
Chordeiles minor	común	local	invertebrados
Nyctidromus albicolis	común	local	invertebrados
APODIDAE			
Streptoprogne zonaris	ocasional	local	invertebrados
Chaetura vauxi	ocasional	local	invertebrados
TROCHILIDAE			
Phaeochroa cuvierii	ocasional	local	nectar/insectos
Anthracothorax prestii	ocasional	local	nectar/insectos
Florisuga mellivora	ocasional	local	nectar/insectos
Eugenes fulgens	ocasional	local	nectar/insectos
Hiloclaris eliciae	ocasional	local	nectar/insectos
Glaucis aenea	ocasional	local	nectar/insectos
Amazilia boucardi	común	endémico	nectar/insectos
Amazilia tzacatl	ocasional	local	nectar/insectos
Amazilia rutila	escaso	local	nectar/insectos
Amazilia saucerottei	ocasional	local	nectar/insectos

Tabla 1. (Continuación)

TROGONIDAE			
Trogon violaceus	ocasional	local	frutos-insectos
Trogon melanocephalus	ocasional	local	frutos-insectos
Trogon massena	ocasional	local	frutos-insectos
ALCENIDAE			
Chloroceryle amazona			
Chloroceryle americana			
Chloroceryle aenea	escaso	local	peces
Ceryle torquata	común	local	peces
Ceryle alcyon	abundante	local	peces
Chloroceryle amazona	común	local	peces
Chloroceryle americana	escaso	migratorio	peces
Chloroceryle aenea			
MOMOTIDAE			
Eumomota superciliosa	común	local	invertebrados/vertebrados
PICIDAE			
Melanerpes hoffmanni	común	local	invertebrados
Melanerpes rubricapillus	escaso	local	invertebrados
Campehphilus guatemalensis	escaso	local	invertebrados
DENDROCOLAPTIDAE			
Dendrocincla anabatina	común	local	invertebrados
Xiphorhynchus guttatus	común	local	invertebrados
Lepidocolaptes souleyetti	abundante	local	invertebrados
FORMICARIIDAE			
Tamnophilus bridgesi	escaso	local	invertebrados
Tamnophilus doliatus	ocasional	local	invertebrados
Tamnophilus puntatus	ocasional	local	invertebrados
TITYRIDAE			
Pachyramphus cinnamomeus	escaso	local	invertebrados
Pachyramphus polychopterus	escaso	local	invertebrados
Tityra semifasciata	escaso	local	invertebrados
COTINGIDAE			
Carpodectes antoniae			
Carpodectes nitidus	raro	local	invertebrados
PIPRIDAE			
Chiroxiphia linearis	común	local	invertebrados
TYRANNIDAE			
Tyranus melancholicus	común	local	invertebrados
Megarhyncus pitangua	común	local	invertebrados
Camptostoma imberbe	ocasional	local	invertebrados
Myiodynastes maculatus	ocasional	local	invertebrados
Myiodynastes granadensis	ocasional	local	invertebrados
Myiozetetes similis	común	local	invertebrados
Pitangus sulphuratus	común	local	invertebrados
Myiarchus panamensis	común	local	invertebrados
Myiarchus tyrannulus	ocasional	migratorio	invertebrados
Myiarchus tuberculifer	abundante	local	invertebrados
Myiarchus crinitus	ocasional	migratorio	invertebrados
Myiobius atricaudus	común	local	invertebrados
Todirostrum cinereum	común	local	invertebrados
Sublegatus modestus	escaso	local	invertebrados
Sublegatus arenarum	ocasional	local	invertebrados
Tolmomias sulphurescens	escaso	local	invertebrados
Pachyramphus sulphurescens	escaso	local	invertebrados
Pachyramphus aglaiae	escaso	local	invertebrados
Pachyramphus cinnamomeus	escaso	local	invertebrados
HIRUNDINIDAE			
Tachycineta albilinea	común	local	invertebrados
Tachycineta thalassina	escasa	migratoria	invertebrados
Notiochelidon cyanoleuca	común	local	invertebrados
CORVIDAE			
Calocyta formosa	escasa	local	invertebrados/vertebrados
Psilorinus morie	común	local	invertebrados/vertebrados
TROGLODITIDAE			
Thryothorus rufalbus	Escaso	local	invertebrados
Thryothorus pleurostictus	escaso	local	invertebrados
Troglodites aedon	común	local	invertebrados
Campilorhynchus rufinucha	común	local	invertebrados

Tabla 1. (Continuación)

TURDIDAE			
Catharus ustulatus	ocasional	migratorio	invertebrados
Catharus minimus	ocasional	migratorio	invertebrados
Hylocichla mustelina	ocasional	migratorio	invertebrados
VIREONIDAE			
Cyclarhis gujanensis	común	local	invertebrados
Vireo pallens	común	local	invertebrados
Vireo olivaceus flaroviridis	común	local	invertebrados
Vireo flavifrons	escaso	migratorio	invertebrados
Hylophilus decurtatus	escaso	local	invertebrados
PARULIDAE			
Protonataria citrea	abundante	migratoria	invertebrados
Dendroica petechia-petechia	abundante	local	invertebrados
Dendroica petechia erithachorides	abundante	local	invertebrados
Vermivora pinus	escasa	migratoria	invertebrados
Vermivora peregrina	escasa	migratoria	invertebrados
Setophaga ruticilla	común	migratoria	invertebrados
Mniotilla varia	común	migratoria	invertebrados
Helminteros vermivorus	escasa	migratoria	invertebrados
Seiurus noveboracensis	abundante	migratoria	invertebrados
Seirus aurocapillus	escasa	migratoria	invertebrados
Oporornis philadelphia	escasa	migratoria	invertebrados
ICTERIDAE			
Quiscalus mexicanus	común	local	invertebrados/vertebrados
Icterus galbula	escasa	migratoria	invertebrados/nectar
FHRAUPIDAE			
Euphonia minuta	escasa	local	invertebrados/frutos
Piranga bidentata	escasa	local	invertebrados/frutos
FRINGILIDAE			
Sporophila torqueola			
Volatinia jacarina			
Aimophila ruficauda			
Passerina ciris			
Passerina cyanea			

Tabla 2. Principales moluscos encontrados en los manglares del Pacífico de Centro América.

Familia	Especie	Familia	Especie
BIVALVIA		**GASTROPODA**	
Arcidae	*Anadara tuberculosa* *Anadara similis* *Anadara grandis*	Melongenidae	*Melongena patula*
Corbiculidae	*Polymesoda inflata* *Polymesoda nicaraguana*	Littorinidae	*Littoraria zebra* *Littoraria varia* *Littoraria fasciata*
Teredinidae	*Bankia gouldi*	Melampidae	*Melampus carolianus* *Ellobium stagnalis*
Veneridae	*Protothaca asperrima* *Chione subrugosa*	Cerithidae	*Cerithidium stercusmuscarum*
Solecurtidae	*Tagelus peruvianus*	Potamidae	*Rhynocoryne humbolti* *Cerithidia montagnei* *Cerithidia valida* *Cerithidia mazatlanica*
Mytilidae	*Mytella guyanensis*	Thaididae	*Thais kiosquiformis* *Morula lugubris*
Nassariidae	*Nassarius versicolor* *Nassarius luteostoma****	Neritidae	*Theodoxus luteofasciatus*
Ostreidae	*Crassostrea rhizophorae* *Ostrea palmuta* *Ostrea columbiensis*		
Donacidae	*Iphigenia altior*		

* originaria del Atlántico, recientemente introducida al Pacífico

Los moluscos (Tabla 2) representan uno de los componentes más importantes en estos bosques. La distribución dentro del manglar muestra patrones espaciales claramente diferenciables. Elementos de familias típicamente filtradoras (e.g. *Veneridae, Donacidae* o *Arcidae*) son más abundantes en la parte externa del manglar en bancos de lodo desprovistos de vegetación o entre las raíces de *Rhizophora* sp. Las poblaciones de *Anadara* sp, de gran importancia comercial, son encontradas en estos sitios.

Sobre estas raíces, poblaciones de *Thais kiosquiformis* y *Morula lugubris* se encuentran en densidades de 10 individuos/0.25 m^2, alimentándose de cirripedios que crecen sobre las raíces de *Rhizophora* sp (Perry, 1988). Debido a que la zona externa del manglar está constantemente expuesta a la inundación mareal, las poblaciones de moluscos en esta zona son muy estables.

En la parte interna del bosque el panorama es diferente. Especies de gastrópodos detritívoros como *Theodoxus luteofasciatus* y *Melampus carolianus*, dominantes en la parte interna del bosque donde la acumulación de material vegetal es mayor, sufren mortalidades masivas al inicio de la estación seca, desapareciendo de la mayor parte de las áreas internas del manglar. Con el inicio de la estación lluviosa estas zonas vuelven a repoblarse alcanzando, en el caso de *T. luteofasciatus* densidades de hasta 100 individuos/m^2.

La abundancia de moluscos que se alimentan de troncos en descomposición (e.g. *Ellobium stagnalis*) es mayor en manglares de climas húmedos y lluviosos donde se favorece la descomposición de los troncos.

En troncos y suelos del manglar se encuentra una gran cantidad de crustáceos (Tabla 3) que también muestran diferencias de distribución entre la parte interna y externa del bosque (Crane, 1941; 1947). Crustáceos filtradores como los cirripedios (*Chtmalus panamensis, Balanus* sp) son encontrados sobre raíces de árboles en las zonas diariamente inundadas por mareas. En el suelo de estas zonas *Squilla* sp cava madrigueras de gran profundidad. En la zona de canales, *Callinectes arcuatus* y *C. toxotes* se desplazan continuamente entre los canales y los cuerpos de agua principal, alimentándose de poliquetos, peces, cangrejos y residuos vegetales (Aquino, 1982). Se observan además en esta zona, especies arborícolas que se alimentan del follaje (e.g. *Aratus pisonii*) y especies de cangrejos como *Pachygrapsus transversus* que requieren de hábitats constantemente inundados.

En esta zona el material vegetal proveniente de las plantas de *Rhizophora*, así como de algas y diatomeas bénticas es importante para los cangrejos (Aquino, 1982). En las raíces de *Rhizophora* cercanas al canal, la presencia del isópodo perforador *Sphaeroma peruvianum* reduce en un 50% el crecimiento de las raíces (Perry, 1988).

En las partes internas del bosque los cangrejos terrestres (*Ucides occidentalis, Cardisoma crasum,* y *Sesarma occidentalis*, Aquino, 1982; Bright, 1977) son los elementos más comunes. Estas dos últimas especies dominan en el borde interno del bosque (área supralitoral) alimentándose de restos de mangle, gramíneas y otros residuos vegetales.

Los manglares del Pacífico centroamericano proveen un importante hábitat para un gran número de especies de peces (Tabla 4), especialmente en las fases juveniles. Szelistowski (1990) reportó que el 71.9% de las especies encontradas en un área de manglar en Costa Rica se encontraban en fases larvales o juveniles.

Las variaciones en salinidad y turbidez, entre la época seca y lluviosa son importantes en los estuarios del pacífico centroamericano. La fauna íctica muestra por lo tanto, importantes patrones temporales y espaciales en su composición y abundancia, de acuerdo a esas variaciones. Peces como *Lutjanus colorado* y *L. novenfasciatus* están restringidos a ambientes meso y polihalinos por lo que durante la época lluviosa las poblaciones se desplazan hacia el área de las bocas estuarinas alejándose del influjo de agua dulce proveniente de los ríos. Durante la época seca al disminuir el caudal de los ríos las poblacioes se desplazan hacia las partes internas del estuario. Otros grupos como los sciánidos *Bairdiella armata, B. ensifera* toleran condiciones meso, oligo y polihalinas por lo que su distribución temporal en los manglares y estuarios asociados es más estable.

El papel de los manglares como criaderos para crustáceos y peces ha sido abundantemente tratado en la literatura (Szelistowski, 1990). Sin embargo, su importancia para otros grupos faunísticos no ha sido adecuadamente enfatizada. Los manglares vienen jugando en los últimos años el papel de refugios ecológicos para muchas especies de las planicies costeras, especialmente mamíferos y aves. En el pacífico centroamericano, la deforestación acelerada que han sufrido las planicies costeras de la costa Pacífica de Centro América, ha motivado la migración de elementos faunísticos hacia los manglares.

Tabla 3. Principales especies de crustáceos encontrados en los manglares de la costa pacífica de Centro América

FAMILIA	ESPECIES	FAMILIA	ESPECIES
Penaeidae	*Penaeus stylirostris* *Penaeus vannamei* *Penaeus occidentalis* *Penaeus californiensis* *Penaeus brevirostris* *Trachypenaeus byrdi* *Trachypenaeus similis* *Trachypenaeus pacificus* *Trachypenaeus foa* *Xiphopenaeus riveti* *Xiphopenaeus kroyeri* *Protorachypene precipra*	Gecarcinidae	*Cardisoma crassum* *Gecarcinus quadratus* *Ucides occidentalis* *Uca princeps* *Uca zacae* *Uca umbratila* *Uca deichmanni* *Uca batuenta* *Uca insignis* *Uca mordax* *Uca inaequalis* *Uca tenuipedis* *Uca saltitanta* *Uca beebei*
Caridae	*Macrobrachium tenellum*	Portunidae	*Callinectes toxotes* *Callinectes arcuatus*
Artemiidae	*Artemia franciscana*	Leucosidae	*Leucosilia jurinei*
Paguridae	*Clybanarius albidigitus* *Clybanarius panamensis* *Clybanarius vittatus* *Calcinus obscurus*	Xanthidae	*Panopeus purpureus* *Eurypanopeus transversus* *Eriphia squamata* *Eurythium tristani* *Micropanope xantusii*
Grapsidae	*Aratus pisonii* *Goniopsis pulchra* *Sesarma sulcatum* *Sesarma occidentalis* *Sesarma rhizophorae* *Pachygrapsus transversus* *Geograpsus lividus*	Coenobitidae	*Coenobita compressus* *Sphaeroma terebrans*
Squillidae	*Squilla aculeata* *Squilla panamensis*		
Cirripedia	*Balanus* spp *Chtamalus panamensis*	Isopoda	*Sphaeroma peruvianum*
Anomura	*Petrochirus californiensis* *Emerita rathbunae*		

Cambios Estructurales y Funcionales

Los manglares de la costa Pacífica de Centro América cubren un área aproximada de 320,000 has. La mayor concentración de área es encontrada en el litoral Pacífico de Panamá (aprox. 165,000 ha) y la menor en Guatemala (aprox.16,000 ha; Tabla 5).

Estas comunidades muestran diferencias sustanciales en su estructura y funcionamiento de acuerdo al sitio, obedeciendo a un gran número de factores y procesos ambientales. Sin embargo es posible generalizar algunos patrones evidentes en estos bosques. El clima, que tanto influye la composición florística y faunística de estos bosques, también afecta considerablemente la estructura y función de los manglares. En áreas con abruptos cambios climáticos, como en el Golfo de Nicoya, Costa Rica, los contrastes estructurales son evidentes. Los manglares de la sección externa del Golfo de Nicoya, reciben precipitaciones entre los 2000-3400 mm/año. Estos bosques muestran áreas basales superiores a los 30 m^2/ha y volúmenes comerciables superiores a los 200 m^3/ha. A escasos 40 km de distancia, en la parte interna del Golfo, la precipitación alcanza valores inferiores a los 1600 mm/año. Aquí los bosques muestran áreas basales y volúmenes comerciales inferiores a los 20 m^2/ha y los 80 m^3/ha, respectivamente (Tabla 6).

Para analizar el efecto del clima sobre la estructura y función de estos bosques, se deben distinguir dos zonas diferentes en un área de manglar:

a) una zona externa, dominada por procesos estuarinos en el frente del manglar. En esta zona, el elemento principal en el balance hídrico del sitio es el agua generada por un proceso de mezcla entre las mareas semidiurnas y el caudal de los ríos asociados al estuario.

Tabla 4. Lista de peces de manglar de la costa pacífica de Centroamérica

FAMILIA	ESPECIE	NOMBRE COMÚN
Lutjanidae	*Lutjanus colorado* *Lutjanus novenfasciatus* *Lutjanus argentiventris* *Lutjanus guttatus* *Lutjanus aratus*	Pargo colorado Pargo negro, dentón Pargo amarillo, pargueta Manchado, pargo lunar Pargo blanco
Centropomidae	*Centropomus pectinatus* *Centropomus robalito* *Centropomus unionensis* *Centropomus nigrescens*	Robalo, chiquigüite Robalo, aleta Robalo Robalo
Pomadasydae	*Pomadasys macracanthus* *Pomadasys leuciscus* *Pomadasys bayanus* *Anisotremus dowi*	Vieja, ruco Roncador, roche Roncador Viejo
Scianidae	*Bairdiella armata* *Bairdiela ensifera* *Menticirrhus panamensis* *Ophioscion typicus* *Cynoscion stolzmani* *Cynoscion squamipinnis* *Cynoscion albus*	Corvina Corvina, panchana Corvina Zorra Chinas corvina corvina aguada corvina reina
Tetraodontidae	*Sphoeroides rosemblatii* (no descrito) *Sphoeroides annulatus* *Arothon hisppidus*	Cucho, timburil Cucho, sapo Cucho
Gramnistidae	*Rypticus nigripinnis*	Pez jabón
Cyprinodontidae	*Oxyzygonectes dovii*	Ojos blancos
Engraulidae	*Anchoa panamensis* *Anchoa starksi* *Anchovia macrolepidota* *Anchovia rastralis* *Lycengraulis poeyi*	Anchoa, bocona Anchoa Anchoa, sardina bocona Menjuda Anchoa, bocona
Bothidae	*Citharichthys gilberti*	Pez hoja, caite
Soleidae	*Trinectes fonsecensis*	Pez hoja
Cynoglossidae	*Symphurus elongatus* *Symphurus* sp *Symphurus williansi* (no descrito)	Lenguado
Mugilidae	*Mugil curema* *Agonostomus monticola* *Mugil cephalus* *Chanos chanos*	Lisa, chimbera Machín, tepemachín Liebrancha tusa
Atherinidae	*Melaniris guatemalensis*	
Polynemidae	*Polydactylus approximans*	Venado, Bobo
Gerreidae	*Diapterus peruvianus* *Eucinostomus currani* *Eucinostomus argenteus* *Eucinostomus gracilis* *Diapterus aureolus*	Palmita Choveco Pichincha Mojarra Iscanala
Carangidae	*Caranx caninus* *Oligoplites saurus* *Oligoplites altus* *Oligoplites mundus* *Selene brevoortii*	Jurel Sierrilla Sierrilla Cucha, sierrita Palometa, caballa
Clupeidae	*Lile stolifera* *Opistonema libertate* *Ilisha furthi*	Sardina, sardina boquita Sardina Arenque rollizo
Poecilidae	*Poeciliopsis turrubarensis*	Olomina

Tabla 4 (Continuaciión)

FAMILIA	ESPECIE	NOMBRE COMÚN
Belonidae	*Strongylura scapularis* *Tylosurus acus*	Pez aguja Pez aguja
Hemiramphidae	*Hemirhamphus unifasciatus* *Hemirhamphus gilli*	Medio pico Medio pico
Labridae	*Halichoeres chierchiae*	
Scombridae	*Scomberomorus sierra*	Macarela
Dasyatidae	*Dasyatis longus*	Raya de estilete
Sphyraenidae	*Sphyraena* sp	Barracudas
Ariidae	*Ariopsis seemani* *Arius dowi* *Galeichtys jordani* *Bagre panamensis*	Chimbilaco, cuminate Cuminate, bagre Guicho Bagre negro
Synodontidae	*Synodus scituliceps*	Pez lagartija
Gobiidae	*Gobionellus sagittula* *Evorthodus minutus* *Erotelis armiger* *Microgobius crocatus* *Hyporhamphus snyderi*	Chupapiedra Pipones culebrilla Chupapiedra Chupapiedra
Gobiesocidae	*Tomicodon abuelorum*	Chupapiedra
Eleotridae	*Dormitator latifrons*	Vieja
Albulidae	*Albula vulpes*	Pez Zorro
Cichlidae	*Cichlasoma macracanthus*	Mojarra negra
Elopidae	*Elops saurus*	Macabillo, platano
Pomacentridae	*Abudefduf troschelli*	Burrito
Diodontidae	*Diodon holocanthus*	Zorroespin
Kifosidae	No identificado	Chopa
Uranoscopidae	*Astroscopus zephyreus*	Astrólogo
Chaetodontidae	*Chaetodon humeralis*	Señorita
Serranidae	*Ephinephelus analogus* *Ephinephelus itajara*	Tigre Mero
Balistidae	*Suflamen veerres*	Tunco
Lepisosteidae	*Lepisosteus tropicus*	Machorra
Syngnathidae	*Hipocampus ingens*	Caballito de mar

Tabla 5. Estimaciones de la cobertura de manglares (ha) para la costa pacífica de Centro América. El área total es 343,760

COSTA RICA	NICARAGUA	PANAMA
Puerto Soley 200 Tamarindo 400 Golfo de Nicoya 15,176 Damas/Palo Seco 2,312 Sierpe/Terraba 717,37 Coto Colorado 875 Otras Areas 4,592	Estero Real 19,410 Padre Ramos 4,590 Corinto/Poneloya 10,700 Peñitas/Juan Venado 2,420 Puerto Sandino 1,990 Otras Areas 200	Golfo de Chiriqui 44,688 Golfo de Montijo 23,439 Península Azuero 6,213 Bahía de Parita 11,553 Bahía de Chame 5,044 Bahía de Panamá 26,192 Golfo San Miguel 46,489 Otras Areas 1,350
Total 41,292	**Total 39,310**	**Total 164,968**
GUATEMALA	**EL SALVADOR**	**HONDURAS**
Manchón 10,850 Monterrico 4,325 Otras Areas 911	Golfo de Fonseca 4,657 Jiquilisco 19,847 Jaltepeque 5,385 Otras Areas 5,346	Golfo de Fonseca 46,869
Total 16,086	**Total 35,235**	**Total 46,869**

Tabla 6. Estimaciones de áreas basales y volúmenes de madera para diferentes rodales de manglar de la costa Pacífica de Centro América bajo condiciones secas estacionales (S) o condiciones más húmedas (H)

Géneros	Volumen m^3/ha	Area Basal m^2/ha	Localidad	Ref.
Rhizophora sp	21-77	-	Estero Real, Nicaragua (S)	1
" "	163	-	Playa Garza, Costa Rica (H)	2
" "	116	-	El Encanto, Costa Rica (H)	3
" "	129	-	Tripa Pollo, Costa Rica (H)	3
" "	107	-	Bahia Chismuyo, Honduras (S)	4
" "	80	-	San Lorenzo, Honduras (S)	4
" "	109	-	San Bernardo, Honduras (S)	4
" "	-	12.5	Osa, Costa Rica (H)	5
" "	-	25.1	Darien, Panama (H)	6
" "	-	17.4	Tivives, Costa Rica (S)	7
" "	-	14.9	Barranca, Costa Rica (S)	8
" "	-	19.0	Santa Rosa, Costa Rica (S)	8
" "	-	16.8	Chiquimulilla, Guatemala (S)	11
Pelliciera sp	117	-	Playa Garza, Costa Rica (H)	2
" "	306	-	El Encanto, Costa Rica (H)	3
" "	71	-	Tripa Pollo, Costa Rica (H)	3
" "	-	10.6	Damas, Costa Rica (H)	9
" "	-	7.2	Tivives, Costa Rica (S)	9
Avicennia sp	7-23	-	Estero Real, Nicaragua (S)	1
" "	165	-	Bahia Chismuyo, Honduras (S)	4
" "	121	-	San Lorenzo, Honduras (S)	4
" "	206	-	San Bernardo, Honduras (S)	4
" "	-	41	Tivives, Costa Rica (S)	10
" "	-	15	Barranca, Costa Rica (S)	8
Laguncularia sp	1-2	-	Estero Real, Nicaragua (S)	1
" "	8.1	-	Bahia Chismuyo, Honduras (S)	4
" "	7.2	-	San Lorenzo, Honduras (S)	4
" "	7.6	-	San Bernardo, Honduras (S)	4

1/IRENA, 1986; 2/ Chong, 1988; 3/Sanchez, 1986; 4/COHDEFOR, 1987; 5/ Holdridge *et al*., 1971; 6/Golley *et al*., 1969; 7/Jiménez, 1988b; 8/Pool *et al*., 1977; 9/Jiménez, datos no publ.; 10/Jiménez, 1990. 11/López, 1990

b) una zona interna, dominada por procesos terrígenos en la que las mareas inundan estacionalmente la zona, dependiendo de las variaciones estacionales en el rango de marea o en el caudal de los ríos asociados. En esta zona los procesos de escorrentía superficial, infiltración de aguas, lluvia y evapotranspiración son los elementos reguladores del balance hídrico de la zona (Fig. 5).

En climas secos estacionales, los bosques de Rhizophora ubicados en la parte externa del bosque muestran incrementos en área basal relativamente altos (0.22 m^2/ ha año, Jiménez, 1988b) si se les compara con crecimientos en la zona interna dominada por *Avicennia*. La mortalidad difiere también entre la zona interna y externa del bosque. La disponibilidad de agua mareal en la parte externa del bosque hace que éste muestre una menor mortalidad en todas las clases de tamaño, al comparársele con las altas tasas de mortalidad encontradas en la parte interna del bosque (Jiménez, 1990).

El desarrollo estructural en manglares bajo climas secos estacionales, es escaso en la zona interna del bosque. Aquí dominan extensos rodales de *A. germinans*. Las áreas basales en estos rodales varían de 15 a 7 m^2/ha y las alturas raramente sobrepasan los 15 m. Los procesos de evaporación en estas zonas acumulan las sales traídas por las mareas, aumentando la concentración desde valores cercanos a los del agua de mar (35 ppm) en las áreas adyacentes a los canales hasta valores superiores a las 170 ppm. en el borde de las albinas. En estas zonas, la vegetación muestra un patrón decreciente en su altura, a lo largo del gradiente de salinidad en el suelo, alcanzando alturas inferiores a los 0.5 m en las partes más internas del bosque en donde la salinidad intersticial puede superar 90 ‰. La vegetación (arbustos de *A. germinans*) desaparece completamente cuando las salinidades del suelo superan las 100 ‰ (Soto y Jiménez, 1982).

Debido a este fenómeno las áreas de manglar del Golfo de Fonseca están rodeadas por más de 14,000 ha de albinas. La extensión de estas albinas varía de un sitio a otro dependiendo de la geomorfología de la zona y la amplitud de las mareas. El aporte sedimentario de ríos como el Choluteca y el Nacaome favoreció la formación de extensos

Figura 5. Zonación de un manglar de acuerdo a los regimenes hídricos a los que está expuesto. La zona externa está expuesta a la inundación diaria de marea y agua estuarina. En la zona interna la escorrentía terrígena y la evapotranspiración son los elementos mas importantes en el balance hídrico del sitio

bancos en donde se forman albinas. Las albinas presentan dos formas distintas: planas y onduladas. Las onduladas presentan depresiones donde se acumula agua de lluvia y de marea. Estas depresiones son frecuentemente colonizadas por vegetación y ampliamente usadas por grandes poblaciones de aves que aprovechan la ocurrencia de poblaciones de algas, moluscos y crustáceos asociadas a estas depresiones. El segundo tipo de albinas es más regular en su topografía y al estar desprovistas de fauna y vegetación tienen un

menor valor ecológico. En este tipo de albina, el afloramiento de aguas infiltradas provenientes del continente, permite la aparición de una banda de vegetación de manglar contigua al bosque tropical seco, *Laguncularia racemosa, Conocarpus erecta* y *Avicennia germinans* son los componentes principales de esta banda.

En aquellas áreas de alta precipitación, no existen albinas. Sin embargo, la división del manglar en dos grandes áreas: un frente afectado por procesos marinos y una parte interna influenciada por procesos terrígenos, se mantiene. El desarrollo estructural de la masa boscosa externa, en climas lluviosos, es mayor que en climas secos estacionales. Las salinidades de la masa de agua irrigando está zona son, en promedio, menores (15-25 ‰) que en climas secos estacionales (20-35 ‰).

La parte interna de estos bosques está influenciada por el gran aporte de agua dulce. Los gradientes de salinidad encontrados en estos bosques presentan un patrón inverso a los encontrados bajo climas secos. Las salinidades del suelo disminuyen hacia tierra adentro alcanzando durante algunas épocas del a o las 0 ‰. en la sección interna. El desarrollo estructural bajo estas condiciones es el máximo encontrado en bosques de manglar de Centro América, alcanzando en muchas áreas entre 30-45 m^2/ha. El borde interno del manglar está dominado por una banda de vegetación típica de pantanos de agua dulce y es corriente encontrar un traslape importante entre estas zonas pantanosas y la vegetación de manglar. Los elementos arbóreos más comunes en esta banda de traslape son *Avicennia germinans, Mora oleifera, Pterocarpus officinalis, Symphonia globulifera, Anona glabra* y *Muellera frutescens*. Debido a la abundancia de agua dulce el sotobosque es también más abundante dominando componentes como *Hymennocalys littoralis, Rhabdadenia biflora, Crinum erubescens* y *Pavonia spicata*. Es notorio como en este tipo de bosques las poblaciones de *Avicennia* se ven notablemente reducidas en extensión. Mientras en sitios secos estacionales *Avicennia* presenta ex- tensos rodales, en la parte interna del bosque, en sitios lluviosos *Avicennia* está representada por una angosta zona entre las poblaciones de *Rhizophora* y el pantano. Las causas de la zonación en estas áreas parece estar estrechamente ligada a procesos de competencia interespecífica donde *Avicennia* es excluida de la mayor parte de su rango potencial (Jiménez y Sauter, 1991).

Sin embargo, la ocurrencia de escorrentía dentro de un sitio puede modificar sustancialmente estos patrones estructurales. Areas de manglar, bajo clima seco estacional, pueden recibir abundante escorrentía gracias al aporte de ríos que drenan áreas montañosas con alta precipitación. La influencia de la escorrentía terrestre permite un mayor desarrollo estructural, especialmente en las áreas internas del bosque irrigadas por ríos, quebradas o escorrentía superficial. Estas zonas son ocupadas generalmente por extensos rodales de *A. bicolor* que alcanzan muy altos desarrollos estructurales (Jiménez, 1990). Estos bosques poseen altas densidades (más de 4,000 plantas mayores de 50 cm en altura en una hectárea) y una gran área basal (más de 40 m^2/ha). Debido al amplio suministro de agua dulce las salinidades del suelo son, en cualquier época del año, inferiores a las 50 ppm y el crecimiento en estos bosques es relativamente alto (incrementos en diámetro a la altura del pecho, DAP, de hasta 0.35 cm/año, incrementos en área basal cercanos a 0.4 $m^2.ha^{-1}.año^{-1}$). La dinámica de estos bosques es en general más compleja que en otro tipo de manglares (Jiménez, 1990) y el mantenimiento de la escorrentía terrestre es de vital importancia. En algunas de estas áreas (*e.g*. Barra de Santiago, El Salvador) se encuentran en el margen interno del manglar zonas pantanosas de agua dulce, dominadas por *Thalia geniculata* y *Typha dominguensis.* Estas áreas pantanosas, mantenidas por escorrentía o infiltración, funcionan como reservorios, que durante las época seca se convierten en la principal fuente de agua dulce para los manglares adyacentes.

Los patrones climáticos e hidrológicos también afectan los procesos fenológicos. En climas secos estacionales, se observa una fuerte dependencia de la fenología reproductiva de estos bosques con el balance hídrico de lo sitios (Jiménez, 1988a). La floración en la mayoría de las especies ocurre a inicios de la estación seca cuando todavía existen reservas considerables de agua en el suelo. Durante la estación seca el desarrollo del fruto se reduce notablemente, reiniciando su crecimiento durante los meses de junio y julio cuando las lluvias han recargado el suelo de agua (Jiménez, 1990). La caída de frutos se da a mediados o finales de la estación lluviosa (agosto-noviembre), cuando las salinidades del suelo son mínimas y el nivel freático alcanza los mayores niveles. El tiempo de maduración del propágulo varía entre 7-8 meses para *A. bicolor* y *R. racemosa. A. germinans* presenta flores y frutos 2-3 meses más tarde que *A. bicolor* (Jiménez, 1988a). Este desplazamiento temporal en la fenología reproductiva de *A. germinans* parece estar asociado a procesos de competencia interespecífica con *A. bicolor* (Jiménez, 1990). La asincronía reproductiva, especialmente en la zona interna del bosque es muy baja. En los márgenes de los canales, la asincronía aumenta al aumentar la frecuencia e

intensidad de las inundaciones mareales y por ende la disponibilidad de agua en el sustrato.

En climas lluviosos, con menos estacionalidad, los patrones fenológicos son muy similares. Sin embargo, la asincronía reproductiva es mayor en las partes internas del bosque. La mayor disponibilidad de agua en el sustrato permite la ocurrencia de desviaciones importantes en el patrón fenológico del bosque. *Pelliciera rhizophorae*, por ejemplo, cuando se encuentra en su límite norte de distribución (*v.g.* Península de Nicoya) muestra patrones fenológicos muy claros (flores de diciembre a marzo y frutos de junio a agosto). Bajo climas más lluviosos se observa una mayor asincronía en las poblaciones, e importantes sectores de la población muestran importantes desviaciones del patrón fenológico de climas secos.

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Hydrological and Hydrogeochemical Variations in Mangrove Ecosystems

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Abstract

Mangrove systems differ greatly with respect to hydrological and hydrogeochemical parameters which principally vary because of tidal processes, rainfall events, evapotranspiration, and differences in microtopography. Hydrological conditions in mangrove systems control structure and production and regularly cause changes in the hydrogeochemical signatures of waters and suspended matter in mangrove wetlands. Outwelling of organic carbon and other materials from mangrove systems is probably not the rule, but rate, direction, and quality of material transport vary greatly in response to tidal flooding and rainfall events, sometimes causing ebb-directed or seaward transport of mangrove and terrestrial materials and sometimes landward transport of ocean-derived materials. We conclude that results from transport and material balance studies in mangrove systems should be looked at with suspicion and only accepted after hydrological and hydrogeochemical variability have been properly accounted for.

Resumen

Los sistemas de manglar son muy diferentes respecto a los parámetros hidrológicos e hidroquímicos que los describen, los cuales varían principalmente debido a los procesos de marea, eventos de precipitación, evapotranspiración y diferencias en la microtopografía. Las condiciones hidrológicas en los sistemas de manglar controlan la estructura y producción y regularmente causan cambios en las *huellas* geoquímicas del agua y materia en suspensión de los pantanos de manglar. El drenado de carbón orgánico y otros materiales de los sistemas de manglar no es probablemente la regla, pero la tasa, dirección y calidad del material transportado varía considerablemente en respuesta a eventos de inundación por la marea y precipitación, a veces causando reflujo o transporte hacia el mar de materiales del manglar y terrestres y a veces hacia el continente transportando materiales provenientes del océano. Se concluye, que los resultados del transporte y estudio del balance de materiales en los sistemas de manglar serían vistos con desconfianza y únicamente aceptados después de que ha sido considerada la variabilidad hidrológica e hidrogeoquímica.

Introduction

Mangrove vegetation comprises a dominant coastal habitat in tropical areas and is one of the most productive ecosystems on earth. In the Americas, mangroves consist of only six species from four genera, as compared to 45 genera and more than 70 species in the Indo-Pacific (UNESCO, 1987).

Mangroves constitute a valuable renewable resource, which is rapidly being destroyed by population expansion and development. Mangrove trees are harvested for lumber and charcoal, and marginal mangrove areas are drained for urban and industrial development, agriculture, and aquaculture. The most devastating impact may be due to excavation of aquaculture ponds in mangrove wetlands. Still, mangroves support higher sustainable productivity than does pond aquaculture activities and other uses of mangrove wetlands (Turner, 1985; UNESCO, 1985; UNESCO 1986a).

Mangrove wetlands occur along both marine and brackish coastal margins and are typically inundated by tides and freshwater flooding at least intermittently. Lugo and Snedekar (1974) distinguished between five types of mangrove forests based on physionomy in marginal mangrove systems in Florida. Although a milestone publication, their classification has often been applied uncritically to mangrove ecosystems elsewhere. More significant than the classification scheme, Lugo and Snedekar (1974) stressed that both physiognomy and formation of mangrove forests are largely controlled by tidal and terrestrial drainage within mangrove wetlands. They suggested that hydrological difference from site to site is the dominant factor in controlling mangrove structure and productivity.

The influence of hydrological processes on mangrove systems, e.g. flooding, sea level rise, and rainfall, has usually been lumped with geomorphic processes and not received adequate attention. It is our contention that hydrological and geochemical processes jointly exert significant control in mangrove systems. In many cases, hydrogeochemical processes may explain the majority of the variability in structure and productivity in mangrove units.

Hydrological processes together with micro-variations in topography clearly play a central role in dynamic processes in mangrove ecosystems (Wolanski *et al*., 1980; Wolanski and Ridd, 1986; Kjerfve, 1986; Boto and Wellington, 1988; Kjerfve, 1990; Ovalle *et al*., 1990; Wattayakorn *et al*., 1990; Ong *et al*., 1991; Itthipatachai *et al*., 1991). Hydrological processes include weather impacts, climate variability, rainfall and runoff characteristics, groundwater flow and storage, frequency and extent of tidal inundation, water and soil salinity, wave exposure, and inundation due to river flooding are clearly of fundamental importance to how mangrove systems function (Thom, 1967; Coleman *et al*., 1970; Blasco, 1984; Twilley, 1985; Woodroffe, 1985a,b,c; Kjerfve, 1986; and UNESCO, 1986b; Ovalle *et al*., 1990; Ong *et al*., 1991).

Hydrological Variability in Mangroves

Mangroves are salt-tolerant trees and grow most prolifically along low-lying depositional coast and deltas, where the substrate is predominantly made up of clay and silt rather than sand. Rains and subsequent river floods carry alluvial muds and sands to tidal flats, forming a substrate for mangrove colonization. Although some mangrove species grow on sand, gravel, or rock shores, these substrates are abrasive and cause considerable damage to mangrove seedlings (Bird and Rosengren, 1986). Thus, mangroves ideally colonize fine-grained alluvial mud and flats deposited by river runoff particular in deltas, and along protected shorelines of bays, estuaries, and lagoons (Thom, 1984). During flash floods, extreme quantities of alluvium can be deposited rapidly and may cause initial destruction to mangroves before rebuilding commences.

Mangroves are subject to either regular or occasional inundation by water of riverine, estuarine, or oceanic origin. Waters inundating mangroves regularly can have salinities up to 37 ppt without adversely impacting the function of mangroves, as long as the trees are protected from wave action and substantial currents. The area flooded during each tidal cycle increases with increasing tidal range along depositional, low-lying tropical coasts. This is where the most extensive mangrove wetlands exist. A good example is the Amapa coast in northern Brazil, where the tidal range reaches 6 m and Amazon-derived sediment deposits form an enormous expanse of mangrove habitats. Where the tidal range is large, however, the extreme high and low tide margins cannot easily be colonized by mangroves because the alternating periods of

exposure and submersion are too long. Along the seaward margin of mangrove systems, strong tidal currents can also inhibit mangroves from settling and serve to export seedlings to other areas. Along the landward margin, stunted and dying mangrove trees are often occurring adjacent to an extensive zone of non-vegetated bare sand, where high evaporation rates and a pan-shaped micro-topography have lead to hypersaline interstitial conditions which do not even support mangrove trees (Macnae, 1966; Spenceley, 1976; Galloway, 1982; Blasco, 1984).

Mangroves grow in both humid and arid climates, but production and species diversity are greatest in humid equatorial areas, where rainfall is plentiful and evenly distributed throughout the year. The ratio of rainfall to evapotranspiration exerts a critical control on mangrove production.

Differences in rainfall lead to leaching, which can cause substantial nutrient export from mangroves, in particular nitrate (Ovalle *et al*., 1990), as a function of plant type, season, and rainfall periodicity (Boto, 1982). In climates that remain humid throughout the year, soils are continuously leached of salts by heavy but evenly distributed rainfall, which yields constantly low and stable salinity levels. In arid climates with marked seasonal rainfall distribution, in contrast, the drought periods lead to high evapotrans-piration rates, and consequently high soil salinities. During the rainy season, this situation reverses, and the soil salinity drops. As a consequence, mangrove species biomass and other growth variables are substantially lower in arid regions than in humid regions.

A useful method for expressing aridity is to compute the ratio of annual precipitation, P, and annual potential evapotranspiration PET. When PET is greater than P, i.e. when the water loss from a saturated surface is greater than the addition by rainfall, a local water deficit results. UNESCO (1979) listed four degrees of aridity based on **1)** the ratio P/PET; **2)** temperature regimes; **3)** drought periods; and **4)** temperature of the coldest month. Blasco (1984) found that 90% of the world's mangroves grow in humid regions where P/PET > 0.75, e.g. Amapa, Brazil, and the Pacific coast of Colombia; some mangroves grow in sub-humid climates where 0.50 <P/PET > 0.75, e.g. Yucatan, Mexico; very few mangroves grow in semi-arid conditions where 0.20<P/PET <0.50, but the coast of Ecuador is an example; and mangroves are almost non-existent in arid climates where P/PET <0.20. Mangroves are subject to destruction by tropical storms. Stoddart (1962) studied the effects of Hurricane *Hattie* in October 1961, on mangrove stands in Belize. He reported that defoliation of *Rhizophora*, *Avicennia*, *Laguncularia*, and *Conocarpus* occurred over a 30-40 km wide zone north and south of the storm track. Mangroves exposed to flooding, high wave action, and hurricane winds suffered far more defoliation than those exposed to high winds alone (Stoddart, 1971). A survey four years after the hurricane Hattie showed that most of the defoliation resulted in mangrove death, with no evidence of subsequent recolonization (Stoddart, 1965, 1971).

Hydrogeochemical Variability in Mangroves

Variations in rainfall and differences between dry and wet climates, result in hydrogeochemical variations in mangrove pore waters and creek waters, especially with respect to alkalinity and concentrations of nutrients, such as phosphate, silicate, ammonia, and nitrate. The importance of rainfall and the effects of rainfall on variations in hydro-geochemistry in a Brazilian mangrove system is shown in Figure 1. During the initial sampling phase in the Itacuruça

Experimental Forest, a cold front accompanied by heavy precipitation impacted the study area, causing marked fluctuations in creek hydrology and hydrogeochemistry. Salinity and total alkalinity normally displays characteristic tidal variations, but the tidal fluctuations diminished during the rain event as the concentrations were strongly reduced. Rains are significant in that they wash salts from mangrove soils and pore waters, which is of utmost importance in maintaining soil salinity at levels favorable for sustaining mangrove trees. Rains are also important in that they bring vital nutrients to mangrove systems. For example, nitrate and silica exhibited concentration peaks early during sampling in response to tidal water level rise (Fig. 1). This increased groundwater input to the mangrove creek, resulting in a type of piston effect pushing ground waters into the creek, and giving the creek waters the observed hydro-geochemical groundwater signature, i.e. low ionic content and low total alkalinity with high nitrate and silica concentrations (Ovalle *et al*., 1990).

Any hydrogeochemical model of mangrove ecosystems should consider not only tidal effects but also the impact of rain. At low tide, creek waters are often dominated by inflow of mangrove pore waters, which usually are enriched in ammonium, carbonates, silica, and phosphate, and is recognized by a strong negative redox potential (Blackburn, 1986; Agosta, 1985). Nitrification of pore water derived

Figure 1. Hydrological and hydrogeochemical variations in a tidal mangrove creek in the Itacurusa Experimental Forest, Baía de Sepetiba, Brazil, in March 1987, exemplified by time series of silicate, nitrate, alkalinity, salinity, and tidal variation. The importance of intense rainfall 1000-1500 hours can be seen in the subsequent variations in the other parameters

ammonium readily occurs under high temperature and low dissolved oxygen, typical of mangrove waters (Nedwell, 1975). At the start of flood tides, sea water enriched in dissolved oxygen, salinity, and chlorides usually interact with mudflat pore waters before entering tidal creeks, resulting in high ammonium, nitrate, and silicate concentrations in creek waters (Agosta, 1985). As the water level rises, mangrove pore water migration into tidal creeks decreases as mangrove sediments become inundated.

Salinity, chloride, and dissolved oxygen concentrations together with pH increase in tidal mangrove creeks. Recharge of mangrove pore waters may then occur, in particular where active heavy crab burrowing enhances the hydraulic conductivity of sediments (Warren and Underwood, 1986). At low tide, pore waters again migrate into tidal mangrove creeks, and pH, dissolved oxygen, and chloride decreases, whereas ammonia, silicate, phosphate, and nitrate increase (Ovalle *et al*., 1990).

This pattern, however, can be highly affected by rainfall. First, nutrient-poor rain water dilutes creek and mangrove waters and filters out tidal variability. Second, there is an increase in pore water transport to tidal creek waters, which become enriched in silicate and phosphate. When rain falls during low tide, the pore water outflow to tidal creeks is usually greatly enhanced (Ovalle *et al*., 1990). Therefore, the resultant model of hydrogeochemistry of mangroves is complex and highly time and site specific

Material Transport in Mangrove Systems

E Transport of materials, in particular carbon, through and from mangrove wetlands has received a lot of attention (Wolanski and Bunt, 1980; Twilley, 1985; Woodroffe 1985a,b,c; Wattayakorn *et al.*, 1990). Outwelling of detritus from mangrove wetlands possibly represents the major source of carbon for coastal food chains in tropical coastal waters. Various studies (Macnae, 1974; Martusubroto and Naamin, 1977; Turner, 1985) have related shrimp production to the size of mangrove areas in different parts of the world, although a cause-effect relation has not been successfully demonstrated. Also, mangrove transport studies have often been based on sampling for short durations and sometimes employed questionable methodology.

Recent studies have yielded new insights to the transport of materials through mangrove wetlands (Table 1). It appears that outwelling is not the rule. In fact, most studies concluded that more carbon is either metabolized in situ or buried in sediments, than is exported to adjacent coastal systems. This raises the question of the validity of the outwelling paradigms in mangrove ecosystems (Lacerda and Rezende, 1990). The export of materials varies by two orders of magnitude as a function of mangrove forest type and location (Table 1). Further, the variation of tidal export or import of constituents during a tidal cycle is generally larger than the net values by several orders of magnitude, raising the question of the significance of the measured or calculated net transport. Thus, tidal asymmetries, pulses of constituent transports, and coarse sampling or errors in measurements can all results in net values on the same order of magnitude. As a consequence, the net export/import usually varies greatly from one tidal cycle to the next (Woodroffe 1985a,b,c).

As an example, consider the total suspended solid (TSS) transport through a mangrove tidal creek in a 6.2-hectare Brazilian mangrove system (Fig. 2). The area is characterized by 1.4 m semidiurnal spring tides and 0.4 m quarter-diurnal neap tides. The data (Table 2) were collected during four quarter-diurnal and one semi-diurnal tidal cycle during the passage of a front. The four quarter-diurnal cycles resulted in an import of 218 kg, an export of 122 kg, and a net import of 96 kg of TSS or a net import rate of -1.1 g s^{-1}. The spring tide resulted in an import of 165 kg, an export of 240 kg, and a net export of 75 kg of TSS or a net export rate of 3.6 g s^{-1}. Not only was the rate of transport different between spring and neap tides, but the direction of transport was opposite as well. Outwelling occurred during the spring tide with the frontal passage, whereas TSS import was the rule during the neap tide cycles. The particulate carbon transport (POC) in the creek showed similar behavior (Fig. 3; Table 2). Outwelling of POC occurred during the spring tide, whereas POC import took place during the neap tides. It is evident that variations in tidal processes, weather events, and conditions existing prior to sampling all enter in controlling to what extent a mangrove system either will export or import materials during a particular sampling interval.

Table 1. Estimates of carbon export from various mangrove systems

Reference	Production (ton/ha/y)	Export (ton/ha/y)	Export (%)
Lugo and Snedaker (1975)	3.1 (POC)	1.8	58.1
Heald (1969)	4.9 (POC)	2.1	42.9
Lugo *et al*. (1980)	2.7 (POC+DOC)	0.7	25.9
Boto and Bunt (1981)	4.5 (POC)	4.2	94.0
Rezende (1988)	5.1 (POC)	0.9	17.6
Flores-Verdugo *et al*. (1987)	6.1 (POC)	5.4	88.5
Woodroffe (1985c)	4.2 (POC)	1.1	26.2
Twilley (1985)	2.9 (POC+DOC)	0.6	22.0
Lee (1989)	6.2 (POC)	0.0	0.3
Itthipatachai *et al*. (1991)	0.73 (leaves)	0.0-0.09	0.3-12.5

Figure 2. Total suspended solids (mg/l) flux in a tidal mangrove creek in the Itacurusa Experimental Forest, Baía de Sepetiba, Brazil, during (a) four quarter-diurnal neap tidal cycles (16-17 June 1987); and (b) a single spring tide cycle (17 March 1987)

Table 2. Net material fluxes (Rezende, 1988) in the Itacuruça Experimental Mangrove Forest, Baía de Sepetiba, Brazil, expressed as net flux in mass per tidal cycle and hectare. Positive sign indicates export and negative sign import

Date 1987	Water Balance ($m^{3)}$	Zn (g)	Cd (mg)	POC (kg)	TSS (kg)
Spring Tide					
17 March	>0	+ 21	+ 471	+ 1.2	+ 12
Neap Tide					
16 June	+ 135	- 8	- 52	- 0.6	- 14
16 June	+ 150	+ 3	+ 36	+ 0.4	+ 7
17 June	- 62	- 6	- 45	- 0.6	- 16
17 June	+ 10	+ 5	+ 21	+ 0.5	+ 7

The magnitude and direction of the net carbon flux is one relevant quantity, but the mass balance approach is neither well suited to express the quality nor the origin of carbon cycling through mangrove systems. Using stable carbon isotopes, Rezende *et al*. (1990) showed that a sizable fraction of carbon transported through mangrove systems is of marine phytoplankton origin ($^{13}C/^{12}C$ = -20.5 ‰) rather than originating within the mangrove system ($^{13}C/^{12}C$ = -26.5 ‰) (Rondelli *et al*., 1984). The fraction of POC of marine varied from 2% to 30% with sometimes 84%. It seems that carbon balance studies which do not take into consideration the import of POC from adjacent marine systems may overestimate carbon production in mangroves. The transport of POC in the Brazilian creek (Fig. 4) is illustrative. During the spring tide, flood currents brought organic carbon, almost totally of marine origin, as indicated by $^{13}C/^{12}C$ = -21.8 ‰, into the mangrove system. In contrast, ebb currents carried organic carbon, 80% of which originated in the mangrove system, as indicated by $^{13}C/^{12}C$ = -24.6 ‰. During the neap tides, the difference in the source of organic carbon is poorly defined with both ebb and flood currents transporting a

Figure 3. Organic carbon (mg/g of TSS) flux in a tidal mangrove creek in the Itacurusa Experimental Forest, Baía de Sepetiba, Brazil, during (a) four quarter-diurnal neap tidal cycles (16-17 June 1987); and (b) a single spring tide cycle (17 March 1987)

Figure 4. Organic carbon in a tidal mangrove creek in the Itacurusa Experimental Forest, Baía de Sepetiba, Brazil, during (a) four quarter-diurnal neap tidal cycles (16-17 June 1987); and (b) a single spring tide cycle (17 March 1987). The $^{13}C/^{12}C$ ratios are close to the mangrove end member (-26.5) at low tide and close to the marine end member (-20.5) at high tide

Figure 5. Cadmium (g g^{-1} of TSS) flux in a tidal mangrove creek in the Itacurusa Experimental Forest, Baía de Sepetiba, Brazil, during (a) four quarter-diurnal neap tidal cycles; and (b) a single spring tide cycle.

Figure 6. Zinc (g g^{-1} of TSS) flux in a tidal mangrove creek in the Itacurusa Experimental Forest, Baía de Sepetiba, Brazil, during (a) four quarter-diurnal neap tidal cycles; and (b) a single spring tide cycle.803-777-2572/4529

mixture of carbon from the two main sources. Independent of tidal phase, there is usually a significant contribution of marine POC flowing through a mangrove system. This suggests that mangrove carbon balances, which do not account for a marine carbon source, probably overestimate the outwelling of organic carbon and the rate of mangrove production.

Trace metals can provide useful information on the factors controlling the transport of constituents through mangrove ecosystems. For example, the behavior of particulate zinc (Zn) and cadmium (Cd) in the tidal mangrove creek in Brazil was also measured during the sampling of organic carbon (Figs. 5, 6). The transport of the two metals is consistent with the transport of

TSS and POC. The spring tide resulted in a significant export of each trace metal, while the neap tide yielded a small net import of trace metals (Table 2).

The determination of net constituent fluxes is by no means an easy or trivial task. Direct measurements of transport require repeated measurements of constituent concentration and horizontal flow systematically during one or more tidal cycles (e.g. Kjerfve, 1990). Just because the average flood concentration might be significantly greater than the average ebb tide concentration or vice versa, even when the net water balance is zero, does not guarantee that a constituent is being either exported or imported. For example, consider regular time series concentration and discharge measurements every 1.5 lunar hours for one tidal cycle (Table 3). The net water balance is zero, the flood tide concentration is on the average substantially greater than the average ebb tide concentration, and, still, the measured constituent is exported from the system. In this case, it would have been easy to make the opposite, and erroneous, conclusion based on intuition rather than appropriate calculations.

Table 3. An example data set demonstrating net export from a system although the net water balance is zero and the average flood tide concentration is greater than the average ebb tide concentration. A positive flux/discharge denotes ebb transport and a negative sign flood transport

	Concentration	Discharge	Flux
ebb tide	2.0	+ 3,000	+ 6,000
	2.0	+ 3,000	+ 6,000
	1.0	+ 1,000	+ 1,000
	1.0	+ 1,000	+ 1,000
	1.5	+ 8,000	+ 14,000
flood tide	3.0	- 1,000	- 3,000
	3.0	- 1,000	- 3,000
	1.0	- 3,000	- 3,000
	1.0	- 3,000	- 3,000
	2.0	- 8,000	- 12,000
Net flux		0	+ 2,000

Conclusions

Hydrological and hydrogeochemical variations in mangrove wetlands are often substantial, and, at least in part, control the kind of mangrove systems that results. These variations include salinity, rainfall intensity, variation in rainfall, and the local type of hydroclimate as defined by the ratio of precipitation to evapotranspiration.

Early studies of material transport in mangrove ecosystems did not include consideration of meteorological and runoff events, which cannot be predicted with confidence. Thus, generalization of the behavior of mangrove systems as exporters or importers of material is often rendered impossible, as one single event can contribute to a significant fraction of total material transport in mangrove wetlands and alter a system from importer to exporter.

The composition and quality of materials moving in and out of mangroves is affected by tidal phase, in particular organic carbon and trace metals. Oceanographic conditions seem to be the major transport process in calculating material balance in a mangrove system.

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8

Procesamiento Digital de Imágenes de Satélite para el Reconocimiento de Patrones en los Manglares

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Resumen

El enfoque principal de este capítulo es describir los estudios de fotointepretación y sensoreamiento remoto con base a las respuestas espectrales de teleobjetivos relativamente homogéneos que caracterizan la estructura física del ambiente costero en particular el del ecosistema de manglar, donde los parámetros físicos condicionan la distribución de las especies vegetales. El método de la fotointerpretación ofrece a las investigaciones en la zona costera componentes indispensables para la evaluación, manejo y usos de sus recursos. Este análisis se basa tanto por la tonalidad como por la textura que caracteriza cada una de las asociaciones vegetales presentes. La interpretación esta referida a la distribución de la densidad de los árboles, al tipo suelo que se observa entre las copas, a las ramas y hojas de una especie. Una vez realizadas las correcciones de algunos atributos sobre las fotografías aéreas, prácticamente todo se puede cuantificar del análisis efectuado, como son distancias, áreas, alturas y más particularmente diámetro de las copas, densidad y porte del árbol, substrato y humedad. Adicionalmente, con los resultados del análisis del sensoreamiento remoto se puede determinar la deficiencia de nutrientes en la comunidad por el uso de diferentes bandas de absorción y reflexión. Con esta metodología se han determinado diez clases de manglares subtropicales considerando sus características de tonalidad, textura y altimetría. Asimismo, es necesario una validación de campo la cual va contribuir con la definición de los patrones de distribución definiendo la clase de foto-interpretación. Además esta técnica ofrece la oportunidad de realizar observaciones sistemáticas en la zona costera para el control del manejo, alteración y degradación de los ecosistemas de manglar.

Abstract

The main focuses of this chapter is describe the studies of photointepretation and remote sensing with fundament to the spectral features of one objective with relatively homogeneous which they characterize the physical structure from the coastal environment in particular of the ecosystem of mangroves, where the physical parameters condition the distribution of the vegetables species. The method of the photo-interpretation offers to the coastal research an indispensable component in order to the evaluation, management and uses of its resources. This analysis is based point of the tonality like as the texture which characterizes each one of the vegetables present associations. The interpretation this referred to the distribution of the density from the trees, to the class soil which is observed among the canopy, the branches and leaves of a species. Once carried out the corrections of some attributes

over the aerial photography, practically all one could quantify from the performed analysis, as they are distances, areas, heights and more particularly diameter from the canopy, density and structure from the tree, substratum and humidity. Furthermore, the findings from the analysis of the remote sensing one could determine the deficiency of nutrients of the community for the use of several bands of absorption and reflection. With this methodology ten classes of subtropical mangroves have been determined considering their attributes of tonality, texture and "height of the trees". Likewise, it is necessary a validation from field which contributes with the definition of the patterns of distribution defining the class of photointerpretation. In addition, this technique offers the opportunity to carry out systematic observations in the coastal zone for the control of the management, alteration and degradation of the ecosystems of mangroves.

Introducción

Las regiones costeras localizadas en los litorales de la zona intertropical del planeta, se destacan por sus características hidro-meteorológicas determinantes en la estructura apropiada del desarrollo de los manglares. Estos sistemas presentan un balance térmico que permite el desarrollo de asociaciones botánicas especializadas al régimen halofito resultante del avance y regreso intermitente de las mareas sobre formaciones sedimentarias de suave gradiente de declive (Herz, 1988).

Los procesos costeros que actuaron desde el periodo terciario durante los cambios climáticos globales, introdujeron en el paisaje costero alteraciones sistemáticas por las fluctuaciones glacio-eustáticas que resultaron en la variación del nivel medio del mar. La dinámica de las aguas en los periodos interglaciares condujo a la sedimentación del ambiente costero en la construcción de la paleografía de las planicies arenosas; el resultado acumulativo de estos procesos naturales promovió la formación de niveles de terrazas marinas originarias de condiciones morfo-genéticas del avance y regreso del mar sobre el litoral.

El nivel medio del mar en el tiempo geológico siempre se mantuvo inestable y actualmente en su estabilidad relativa, se encuentra sujeto a la elevación gradual por el efecto de invernadero, cuya tendencia lineal es de un aumento anual de hasta 1.5 cm (IPCC, 1990).

Estos factores comprueban que las actuales formaciones de los manglares se establecen sobre sedimentos recientes, depositados desde el último evento de transgresión que se remonta entre 3,500 y 5,000 años antes del presente. Son por lo tanto ecosistemas sujetos a la reacomodación constante debido a la adaptación de las especies a la progresión del nivel de las aguas sobre la deposición sedimentaria distribuida en formaciones de terrazas. La geomorfología generada por los procesos marinos, lagunares, fluviomarinos y eólicos induce a una dinámica sedimentaria de gran actividad que organiza el espacio interno de los ecosistemas por una micro-topografía diseñada a partir de la inundación y escurrimiento de las aguas movidas por corrientes de marea (Thom, 1982). Pequeñas elevaciones y depresiones componen las unidades espaciales que comunican los complejos canales de escurrimiento en forma interconectada hasta que se forma un meandro como canal de recepción de las aguas del estuario. De la fijación de cada individuo clasificado en las asociaciones que habitan los bosques de manglar la morfología de la superficie influye en la selección y distribución de los patrones vegetales. En substratos areno-lodoso las semillas y propágulos encuentran condiciones multivariadas en relación a la frecuencia de exposición de las inundaciones por la marea, volumen de agua y mezcla de aguas continentales y marinas, además de sus efectos en los componentes de las aguas intersticiales introducidas en el sustrato según la composición física del sedimento en función de su permeabilidad.

La estabilidad del sustrato y la regularidad de los efectos hidrometeorológicos contribuyen a la estabilidad y conservación de los ecosistemas de manglar. Las condiciones esenciales para el desarrollo de la naturaleza funcional de este tipo de ecosistemas se agregan al aporte de energía electromagnética, manteniendo el microclima y el régimen de asimilación fisiológica de cada especie, de acuerdo con su morfología y estructura interna. La distribución de las especies y su identidad morfométrica da al espacio ocupado por el manglar un contenido estructural que caracteriza la productividad orgánica tan importante en el mantenimiento del ciclo alimentario de la zona costera en que se encuentra instalado. Esta función hace que el sustrato se diferencie en sus propios componentes orgánicos y minerales, que influyen también en la propia geografía de una microzonación interna para la definición de patrones relativos a la productividad de follaje y su área correspondiente. El conocimiento de las micro-unidades caracterizadas por factores de relativa homogeneidad es básica para el cálculo del material fragmentado originario de la liberación de las hojas completándose el ciclo fenológico de cada especie de manglar.

Las especies que componen los manglares llegan a 60 diferentes tipos de árboles y otras 20 a ellas asociadas (Hamilton y Snedaker, 1984), ofreciendo soporte a más de 2,000 especies de animales.

El ambiente resultante de la mezcla de aguas continentales y marinas por la acción de las corrientes, generadas por propagación de las mareas es esencial en la composición de las unidades de manglares. Los movimientos hidráulicos y la propagación de las corrientes, atenuadas por las raíces y troncos, forman un ambiente apropiado para la precipitación del material en suspensión transportado por las aguas estuarinas.

La estructura física de los manglares se mantiene por una diversidad de factores internos que caracterizan gradientes botánicos. Según Wittaker (1953), cada localidad representa las propias condiciones de su clímax, no habiendo razón de discutir esta evidencia, por el sentido de su composición y de la posición relativa en que se encuentra en el ambiente costero.

En general, las hipótesis de gradiente o zonación en el interior de los manglares esta relacionada a los diferentes grados de inundación que influyen en la fisiología de las plantas, en la intención de buscar limites entre distintas asociaciones, cuya fitosociología depende de factores de orden físico, químico o geológico, imprimiéndole una visión geográfica.

Snedaker (1982) acepta como elemento clave, para la identificación de estos patrones, la salinidad que representa un mayor grado de importancia en la organización espacial del ecosistema.

Los gradientes son, sin duda, fundamentales en el estudio de la ecofisiología de las especies, por la dependencia de las variables físicas que condicionan cada subunidad integrada al geosistema.

A pesar de las controversias en relación a los gradientes de algunas sucesiones botánicas en el interior de los manglares, existe una tendencia general de la concentración de *Rhizophora* en su parte exterior, que gradualmente aumenta su porte en el sentido de su Mesozona (Tomlinson, 1957), asumiendo después una faja relativamente estrecha, alturas decrecientes hasta que inicicia la distribución de *Laguncularia y Avicennia*, tornándose menos densa e irregular, hasta su completa dispersión en el borde interno. Este aspecto no es regular, en la mayoría de los casos, dependiendo de la micro-topografía, de los componentes del substrato, de la salinidad intersticial y de la morfología del escurrimiento de las aguas en el ecosistema.

Para que los patrones de zonificación sean homogéneos en relación con la distribución ecológica de los grupos y queden nítidamente definidos, es necesario que la topografía se vuelva regular desde el canal de mareas, con amplio espacio para el desarrollo de los gradientes. No obstante, en la realidad sucede lo contrario, dada la complejidad de los atributos físicos que alteran las estructuras lógicas.

Algunas descripciones de la estructura botánica de los manglares indican que las especies mas comunes alcanzan concentraciones importantes para formar patrones homogéneos (Van Steenis, 1928; Savory, 1953), citado por Tomlinson (1957).

La gran dinámica de regeneración y reciclaje en los bosques, así estructurados, puede alterar las agrupaciones puras, creándose clases transicionales y la reducción o aumento de las demás debido a la alteración de la micro-topografía, por la concentración del substrato orgánico mezclado con partículas arenosas y arcillosas, retenidas durante el flujo de los periodos de inundación. De este escurrimiento superficial resulta la articulación de microdrenajes hasta el canal principal, redistribuyéndose las partículas acumuladas por la propia vegetación, permitiendo el desarrollo de plantas, en una demostración de gran inestabilidad interna del ecosistema. Chapman (1976) incluyó numerosas indicaciones de interferencias, causantes de la pérdida de patrones estructurales en la zonificación en el periodo de sucesión.

La complejidad del ambiente, favorable a la ocupación por especies halofitas, predominantemente, de mangles, fue resumida por Lugo *et al*. (1980) desde diagramas de intercruzamiento de dependencia entre los factores que condicionan el ambiente terrestre y marino. Se puede deducir que el mapeo de la distribución de los patrones clave considera la multiplicidad de factores, conforme el grado de participación de cada uno, al menos se han determinado treinta y cinco componentes esenciales.

Factores Condicionantes de la Estructura Física

No obstante la amplia variedad de distribución de árboles de manglar, derivada de las múltiples combinaciones de los factores que definen la dinámica de cada ambiente, los ecosistemas de manglar presentan, al menos dos franjas distintas: la externa de mayor proximidad al canal y sujeta a intercambio mas frecuente de las aguas de inundación por efecto de la marea,

y otra más interna en el sentido de la zona transicional terrestre, menos sujeta a inundaciones y mas expuesta a la radiación solar, por la dispersión de los árboles de baja estatura sobre sedimentos con concentraciones ligeramente salinas, resultantes de la alta evaporación en esa superficie.

Un factor también selectivo, se fundamenta en la ausencia de mayor proporción de renovación de agua intersticial del manto freático, más activo en los bordes de la superficie sedimentaria, donde la marea actúa hidráulicamente, conforme su ciclo de variación diurna. De distinta permeabilidad, en función de la red hidrográfica, el banco de sedimentos mezclado con materia orgánica, da soporte a las plantas proporcionando sobre la franja externa, una coyuntura mas apropiada de elementos que garantizan su desarrollo diferencial. La permeabilidad, presión hidráulica y evaporación contribuyen decisivamente en esta primera percepción de compartimiento interno del ecosistema.

Por influencia del escurrimiento superficial, los depósitos que quedan fuera de la faja del manglar más concentrada, son desalinizados frecuentemente por la acción de la precipitación de las lluvias, llevando la sal existente en la superficie, por percolación al manto freático de reducida renovación.

Watson (1928), estableció un criterio de zonificación por el análisis de la frecuencia de inundación de las planicies con la variación de la marea, constituyendo cinco clases para un gradiente de 0 a 4.5 m, siendo que las tres primeras se caracterizan por la frecuencia media de 40 a 60 % de mareas de rango alto.

No se debe restringir el tema a un único factor ambiental, a pesar de que en la mayor parte de los casos existe una predominancia, pero siempre esta relacionado a otros de menor interferencia, que cuando sumados ocasionan una variación apreciable sobre la primera.

Las propias circunstancias en que se fija la planta en un cuadro fisiológico, contribuyen para la generación de los gradientes botánicos, restringidas a un intervalo de variación de condicionales físicas en que la especie pueda adaptarse.

Algunos factores bióticos contribuyen en la búsqueda del esclarecimiento y justificación sobre la zonificación en el ambiente ocupado por los manglares. Bajo este criterio, se admite que la propia forma de liberación de los propágulos es responsable del establecimiento selectivo de gradientes, como es observado por Rabinowitz (1978). El peso y la morfología de las semillas en relación a la consistencia del substrato, evidentemente más blando, en la periferia de los bancos junto a los meandros, se fijan fácilmente los más pesados y más largos. En este sentido, algunas experiencias utilizando semillas de diferentes especies, comprueban que la siembra, cuando se hace en la zona inadecuada, tienen poca posibilidad de sobrevivencia en función de la propia selección natural o competencia dictada por los aspectos bióticos.

La longevidad de las hojas definidas en su comportamiento fenológico fue estudiada por Gill y Tomlinson (1971), tomando algunas observaciones en plantas de *Rhizophora mangle*, llegando a una duración de 17 meses máximo con una variación media de 6 a 12 meses. Una serie de factores pueden explicar esa diferencia de edad para una misma especie en una misma localidad, principalmente tomando en cuenta el mes en que la misma hoja es expuesta, se trata pues de árboles siempre verdes. Las hojas de primavera, en general, alcanzan un periodo de vida mas largo del que aquellas formadas en el invierno, entretanto su caída es observada mas frecuentemente en el verano.

El régimen del mantenimiento de las hojas como parte de la biomasa de los manglares y su caída puede representar un proceso biológico regulador o eliminador de sal en las plantas.

Adaime (1985), en estudios recientes sobre la producción y descomposición de las hojas de mangle, en la región lagunar de Cananéia, presenta elementos de importancia básica para entender la dinámica de las copas de los árboles situadas principalmente en la franja exterior (Fig. 1). Ahí la producción foliar aumenta en la estación lluviosa, coincidiendo con los meses del verano, alcanzando los menores valores de julio a septiembre y como citan Pool *et al*. (1977), se expone a la caída de las hojas maduras con la reducción de la salinidad intersticial y en consecuencia de la formación de las hojas nuevas, siendo que esto último puede coincidir con los meses de diciembre, enero y febrero en la estación con índices pluviométricos de gran amplitud. Para el área de estudio (Río Nóbrega), mostrado en la figura 2 y vecino a la unidad considerada para el procesamiento digital; los resultados muestran una producción media anual de 2.216 kg/ha de hojarasca del mangle blanco y 1.540 kg/ha para mangle rojo (Fig.3).

Todo el material liberado por los árboles esta sujeto a transporte por largas distancias, siendo que las hojas recién caídas pueden derivar hasta seis días, para después hundirse y ser transportada con mayor dificultad por las corrientes sub-superficiales.

Figura 1. Aspecto panorámico del sistema estuarino Cananeía-Iguapé (São Paulo-Brasil) a partir de un sector de imagen LANDSAT/TM donde es posible distinguir en composición falso color los ecosistemas de manglares muestreados por Herz (1988)

Teixeira *et al*. (1965), presentan resultados en que se percibe la influencia de la respiración de la comunidad fitoplanctónica, en el sistema lagunar, con valores de tasas de consumo de oxígeno relativamente elevados, siendo que Mesquita (1987) atribuye también altas tasas de consumo por la presencia de bacterias asociadas al material fragmentado de detritos exportados por los esteros en los ecosistemas de los manglares, que sirven de alimento a las otras comunidades biológicas que componen la cadena alimenticia, lo que se ha comprobado en estudios hidroquímicos realizados por Gianesella- Galvâo *et al*. (1986) y Navarra (1986).

La descomposición del material precipitado sobre el substrato se hace inicialmente por la liberación de los elementos solubles de las hojas por lixiviación (Heald, 1969), iniciándose después la degradación de tejidos vegetales mas resistentes, y mas acentuadamente, durante el verano cuando la temperatura del aire y del agua suben a niveles propicios al desarrollo del cambio químico y ataque bioquímico de la materia orgánica, por actividad enzimática y del metabolismo de los microorganismos (Adaime, 1985). Es cierto que en este proceso la presencia de oxígeno es fundamental en la aceleración de las reacciones

Figura 2. Información analógica en par estereoscopio para interpretación visual sobre emulsión pancromática y respectivo resultado de la Fotointerpretación, buscando identificar los patrones de mangle denso alto (azul), mangle denso bajo (rojo), mangle disperso bajo (verde) y *Apicum*/arena (amarillo)

Figura 3. Resultados del levantamiento de campo por radiómetro portátil sobre las tres especies de mangle y respectivas curvas de radiancia obtenidas sobre las imágenes LANDSAT/TM en perfil aproximado a la dirección norte sur

químicas, y con tasas de humedad más reducidas. Los tejidos del mangle negro son mas frágiles a la descomposición que los del mangle rojo, liberando este último mayor cantidad de productos disueltos. Todo lleva a creer que hay una mayor disponibilidad de oxigeno por la renovación de las aguas en las desembocaduras de los canales de la marea.

Heald (1969), verifico también que las hojas de *Rhizophora* alcanzan tasas de descomposición mas elevadas cuando son sometidas a salinidades altas. Por otro lado, Adaime (1987), después de un periodo de cuatro meses de muestreo en Cananéia, notó que las hojas caídas pasan 39% del tiempo en agua salobre con salinidades máximas de 22.9 ‰ y 54 % sumergidas en agua de baja salinidad con un máximo de 12,9 ‰ concluyendo que en treinta días de invierno la contribución de la pérdida del follaje sobre el substrato fue de 18% pasando a 68% en el verano. También en el verano, las hojas alcanzan después de mes y medio a dos meses su duración de vida media, comprobando que *Rhizophora* perdura 58 días, *Laguncularia* 48 días y *Avicennia* 45 días, como característica de ese ambiente subtropical.

Prácticamente la mayoría de las publicaciones dedicadas a estudios fenológicos establecen que la primavera es para los manglares el periodo estacional de la aparición con el mayor número de yemas foliares, modificándose de sobremanera la apariencia de los bosques. En el ciclo de surgimiento, maduración y caída del follaje existen variaciones de copa, con una mayor densidad al inicio del verano y una reducción del área del follaje en el otoño e invierno.

Otro comportamiento fisiológico importante en términos estructurales, es la floración de las tres especies mencionadas, siendo *Avicennia shaueriana* la que presenta yemas florales de primavera, especialmente, entre los meses de agosto a diciembre; *Laguncularia racemosa*

entre febrero y marzo y algunas veces enero y abril, mientras que *Rhizophora mangle* en marzo, abril y mayo en época de otoño en el hemisferio sur y mas precisamente en latitud subtropical (Adaime, 1985).

El ambiente esencial para el desarrollo de los manglares exige condiciones especiales, encontradas en el espacio de transición de las zonas costeras, dotadas de un régimen estuarino o lagunar.

En el océano la salinidad varía entre 33 y 38‰, pero en aguas costeras existe un amplio gradiente de dilución de sal debido a los procesos estuarinos y lagunares cuya mezcla ocasiona salinidades entre 25 y 12‰ llegando a 4‰ junto a la desembocadura de algunos ríos.

No obstante esta reducción de salinidad en determinados ambientes de la zona costera, como aquellos que interactúan con las cuencas hidrográficas continentales, Cintrón *et al*. (1978) señalan que las especies de *Avicennia* son las de mayor tolerancia a la salinidad, ya que resisten valores 2.5 veces mayor que el máximo encontrado en los océanos. En este caso, esta alta concentración se encontraría en áreas de arenas expuestas, sujetas a insolación constante y alta evaporación ocasionando altas concentraciones salinas en el sedimento.

La circulación de las aguas, en el interior de los ambientes costeros, es básica en la dilución de concentraciones salinas del substrato, como también en la regeneración del contenido líquido introducido al manto freático durante los ciclos de la marea.

Esto crea un ambiente de alto potencial de oxi-reducción en una larga franja que cubre niveles aeróbicos (+700 mV) y anaeróbicos (-300 mV). La influencia del ciclo químico en el substrato se observa por la liberación de gases, desde niveles inferiores, debido a la transformación del dióxido de carbono y metano. Otros componentes derivados determinan una progresión de nitrato, nitrógeno, magnesio, manganeso ferroso, férrico, sulfato y sulfhídrico.

Thom (1982), refiriéndose a los patrones de la comunidad definió tres componentes fundamentales de asentamiento ambiental de manglares: geofísico, geomorfológico y biológico.

La variación del nivel del mar por fluctuaciones glacio-eustáticas, por la mecánica de las mareas actuales y por condiciones climáticas propias de la región son factores de orden geofísico, dando a los geomorfológicos tres niveles espaciales de tratamiento: **a)** la sedimentación; **b)** procesos particulares de reflexión del oleaje, aporte fluvial y efectos secundarios de la marea, y finalmente **c)** la micro-topografía de las formas específicas que condicionan las distintas etapas de crecimiento de esta vegetación.

El componente biológico esta íntimamente relacionado a las especies animales y vegetales permitidas por los factores ecológicos de cada región.

De los componentes mencionados, la combinación de los procesos geofísico y geomorfológico (Thom, 1984), producen la coyuntura de elementos físicos necesarios para el soporte de los componentes biológicos. Los cambios geomorfológicos, en tales ambientes, por procesos de erosión y deposición debidos a una gran movilidad temporal, determinan el avance o destrucción de superficies cubiertas por ese tipo de vegetación, creándose diferentes repuestas fisiológicas a los procesos geomorfológicos y conduciendo la adaptación de comunidades ajustadas a la disponibilidad de los factores del componente físico.

Las zonas costeras situadas en regiones tropicales y subtropicales, que están sujetas a los procesos de erosión y acumulación, con alta producción de partículas arenosas, limos, y arcillosas, poseen una dinámica bastante acelerada en la alteración de los contornos litorales.

Numerosas observaciones al respecto se encuentran publicadas, demostrando crecimiento de terrenos y en otros de remoción sedimentaria con apenas la duración de algunos años. La fotointerpretación de levantamientos aéreos desfasados, en Cananéia en un imtervalo de entre diez y treinta años, comprueban alteración de millares de hectáreas que no están registradas en las cartas topográficas y de navegación, debido a la dificultad que existe en la actualización de la información.

Principalmente para la costa brasileña este aspecto es relevante en el estudio de las progresiones de los ambientes de manglar, destacando el aporte multidimensional de los factores ambientales que influyen, directa o indirectamente, en el establecimiento de estos ecosistemas de manglar. Este acondicionamiento geomorfológico, supone la preexistencia de un gradiente climático estacional no limitante.

Chapman (1987) destaca, en una serie de artículos, la importancia de la temperatura y de la precipitación en la biogeografía de los manglares, discutiéndose la relación entre tales variables para la organización de su distribución. Bagnouls y Gaussen (1953) y Walter y Leith (1987), combinaron dos variables para organizar un diagrama, en que la calificación de los tipos de ambiente seco y húmedo esta definida de manera arbitraria, para que el factor limitante del biotipo sea conocido.

Blasco (1984) en sus consideraciones sobre la biogeografía de los manglares, para una cartografía a nivel mundial, concuerda con Saenger *et al*. (1977) sobre la desaparición de esas especies en litorales que presentan 16 ^{o}C de temperatura media, en los meses de enero o julio. Algunas de esas especies en la costa brasileña (*Avicennia shaueriana)* limitadas a la latitud de 29° sur, se encuadran en esta clasificación, debiendo entre tanto recordar que en inviernos ocasionales toleran periodos cortos de 2 ^{o}C a temperatura ambiente.

Las áreas de bajo gradiente térmico son menos selectivas a las especies, que aquellas que varían especialmente sobre intervalos en que los mínimos alcanzan, temperaturas medias menores de 20 ^{o}C. La estabilidad térmica promueve el desarrollo de asociaciones más numerosas en la variedad de especies.

La frecuencia de la temperatura mínima absoluta, la amplitud diurna, la amplitud anual media y la media del mes más frío, al alcanzar valores extremos, inhiben la floración y la producción de semillas.

Las lluvias tienen repercusión en la fisiología de las plantas halófitas y en las propiedades físicas de los suelos, expuestos a las precipitaciones o a las descargas fluviales extremas que reducen la salinidad de las aguas en el interior de los canales de drenaje, de las planicies costeras; Blasco (1984) destaca que tales inestabilidades pluviométricas ocurren en litorales sub-tropicales, marcando su presencia en el mangle ya que reducen las tallas a menos exuberantes.

En efecto en las zonas ecuatoriales se presentan las mayores alturas de los árboles (30-40 m), lo cual se justifica por la distribución regular de las precipitaciones y altas temperaturas durante todo el año. Con estas características el ecosistema dispone de gran diversidad de especies, mayor densidad y mayor altura máxima.

Los periodos de seca pronunciada, pueden llevar a la extinción de muchas especies de mangle. Esto es a partir de las alteraciones que implican en la estabilidad de las soluciones en el manto freático, lo que puede ser comparado al da o causado por prolongados periodos de descarga fluvial, con gran volumen de agua dulce, durante la estación de lluvias. Todas estas inestabilidades de origen climático interfieren directamente en el comportamiento fisiológico de las plantas, por exceso o reducción del potencial salino.

Recientes estudios efectuados por Silva y Herz (1987), comprobaron la importancia de las investigaciones microclimatológicas para los ecosistemas de manglares, al relacionar la temperatura simultánea, registrada en el interior de la planicie de marea y la terraza adyacente, donde se encuentra la vegetación costera. Fueron identificadas tendencias de balance térmico, bastante diferentes, por la característica de regulador térmico del manglar, acumulando radiación solar en el substrato de color negro y también por el alto contenido de agua constantemente renovado. Todo metabolismo de las especies de manglar es dependiente de un balance térmico, extremadamente diverso, de aquel encontrado para la vegetación costera o floresta Atlántica. El hecho de la adaptación térmica de las plantas representativas de este ambiente salino, puede ser verificado en trabajos geológicos y geomorfológicos o edáficos.

Muller (1981) menciona que los manglares modernos podrían estar relacionados a una edad geológica cercana al final del Cretácico (69 $\times$ 10^{6} años), siendo que algunas *Rhizophoras* registran su presencia en el Eoceno (30 $\times$ 10^{6}). Edades que pueden reforzar estos datos podrían estar relacionadas a fases geológicas determinadas por la tectónica de placas, variación en la radiación solar y diferentes concentraciones de dióxido de carbono en la atmósfera, cuando eventos climáticos determinaron la reducción o expansión, de las actuales fronteras zonales. En el Cretácico, la tendencia del conocimiento indica que habría un extenso océano tropical, induciendo la expansión de los mismos por el transporte de propágulos por las corrientes marinas existentes entre los bloques continentales de Tethys y Gondwana.

En los periodos glaciares e interglaciares ocurridos desde el Terciario, la disminución de la extensa distribución de los climas calidos y húmedos, provocó el exterminio de la biota en grandes áreas costeras, no sólo por el frío y reducción de la humedad del aire, sino también por la variación del nivel marino, en relación al nivel medio actual. El sistema hidrográfico, en estas variaciones, se modificó radicalmente por la inmersión y emersión de las plataformas sedimentarias durante el retiro y regreso del mar.

Estudios sobre la variabilidad del nivel del mar, en la costa sudeste del Brasil, realizados por Mesquita y Leite (1986), establecen la tendencia de la elevación del nivel medio del mar por series de análisis de largo plazo con un gradiente que puede llegar a 1.0 cm por año. Esta evidencia coloca en términos actuales la posibilidad de la variación del nivel del mar, por fenómenos Glacio-eustáticos registrados en la escala geológica por Fairbridge (1966).

En el océano Atlántico se encuentra el límite en la costa este a 12° sur, por la influencia de la masa fría de Bengala que avanza hacia latitudes menores en la costa africana, límite que se sitúa

a 29° sur en América del Sur, en la costa oeste, límite de frecuencia de avance de la corriente de las Malvinas. Este escenario seguramente fue diferenciado durante las oscilaciones paleoclimáticas relacionadas a la glacio-eustasia de los últimos 400,000 años (Fairbridge, 1966).

Villwock (1987) sugiere la posibilidad de ocurrencias paleográficas de antiguos manglares, cuyas evidencias se encuentran dentro de turbas plásticas, en depósitos sedimentarios correspondientes a niveles marinos superiores a los actuales, retratando su contenido polínico relativo a fluctuaciones climáticas de periodos largos. En el mismo trabajo hay evidencias de un gran contenido polínico en el cono del Río Grande a 33° 33' Sur, con polen de de bosques de manglares existentes alrededor de 5,100 años A.P. (Lorscheiter, 1975).

La humedad constante del substrato en el interior de los manglares, así como su salinización, está garantizada por la elevación de las aguas por efecto de la marea, a niveles de hasta 307 cm, y hasta 16 cm en marea baja (Mesquita y Harari, 1983), considerando una corrección de 50 cm sobre el nivel cero, reconocido por Miniussi (1958) estando el nivel de calibración o ajuste a 414.3 cm en vez de 364.3 cm.

Las medidas observadas por estos dos autores son distintas para el periodo de 1969 a 1974 con 161.73 cm y 1954 a 1958 corregido a 159 cm. Entre tanto es necesario considerar que los niveles del mar en la región lagunar de Cananéia sufren alteraciones de gran amplitud, según el comportamiento de los vientos regionales y de la presión atmosférica, principalmente por la presencia de los centros de alta presión o "frentes fríos", que elevan las aguas a valores superiores a 300 cm (Mesquita y Leite, 1986). Además de eso, la acumulación de agua por acción eólica, puede variar también en función combinada o aislada de descargas excepcionales en los meses de mayor lluvia.

Una curva de frecuencia para la evaluación de niveles de variación, durante el ciclo anual, puede ser de gran ayuda en el análisis de la progresión de la marea sobre la planicie de inundación donde se desarrollan los manglares, considerando la microtopografía en cada caso. En el patrón general, la marea en Cananéia (Miyao *et al*., 1986) es del tipo mixta predominantemente semi-diurna, la altura media de la marea local es de 81 cm, con medias en sicígia de 120 cm y cuadratura de 26 cm (Mesquita y Harari, 1983).

Miyao *et al*. (1986) observaron la variación de la salinidad durante el invierno y el verano, en series de muestreo periódico para registrar los efectos de las inundaciones y flujos de la marea local; constataron que la salinidad próxima a la barra de Cananéia, entre el Pontal y la isla do Cardoso, fue de 30.5 ‰ en la vertical y en el interior de la laguna en el mar de Cananéia, frente a la Punta del Fraile, los valores se redujeron a 23 ‰. Para el verano el contenido salino fue de 26.3 y 18.6 ‰ demostrando la dilución causada por aguas fluviales que entran en el sistema en periodos pluviales intensos, especialmente en enero.

Las corrientes máximas ocurren, según estos autores, durante la inundación (flujo) con salinidad creciente, ligera estratificación en el periodo de estoa (marea muerta) y salinidad decreciente en vaciante (reflujo), marcando velocidades de entre 8 m/s en superficie hasta 0.6 m/s en el fondo. Una turbulencia consecuente del flujo causa la mezcla entre las aguas, no permitiendo cualquier estratificación que se da solamente en los periodos de estoa.

La presencia de nutrientes como fósforo, nitratos y nitritos sugiere que tales concentraciones están relacionadas a la presencia de ríos y esteros, en el interior del sistema lagunar.

La penetración de las mareas, entre las islas Comprida y de Cananéia, provocan el encuentro de las aguas marcando dos puntos de encuentro, uno en el mar pequeño arriba del Río Cordeiro y Sabaúma y otro en el mar de Cubato junto del Río Guapará (Miniussi, 1959). Los atrasos de pleamar y bajamar son extremadamente importantes para la generación de las corrientes por efecto de gravedad, siendo también responsables por algunos detalles geomorfológicos en los canales principales.

Mesquita y Franca (1987) diferenciaron clases de distribución de los niveles de marea para un periodo de un año, con 429 ocurrencias para 8,784 observaciones horarias (1984), con la cota de 0.882 m, siendo la mayor frecuencia de 18. Este análisis contribuye a la evaluación de la frecuencia de inundación, en diferentes planos sobre la zona entre mares, caracterizada por la micro-topografía del substrato en que el manglar se encuentra instalado. Con el análisis originado por ese grupo de datos, algunas conclusiones sobre la zonificación y gradientes de distribución del manglar, son explicadas por una correlación de la frecuencia de inundación del substrato.

Interpretación Analógica de Imágenes

Sin duda alguna las unidades homogéneas de patrones de tonalidad identificadas pueden ser confundidas, a pesar de ser bastante distintas entre si por su estructura y constitución.

Como segundo parámetro adicional del fotoanálisis se debe considerar los elementos de textura de la distribución de tonalidad, lo que implica en la búsqueda de los efectos estructurales de las superficies relativamente homogéneas reconocidas sobre la imagen por su patrón tonal/textura, capaz de provocar alguna confusión que pueda surgir entre tonalidades semejantes pero de textura diversa.

Para explorar plenamente los elementos de la textura de la fotografía a interpretar, esta debe de cumplir requisitos de la combinación de película y filtro para que las tonalidades resultantes evidencien abruptamente peque as variaciones en contraste resultando en el efecto de corte de la imagen (Colwell, 1960).

Se distingue la textura y la tonalidad por estereoscopía por la percepción de la rugosidad aparente con referencia al punto de observación y a la posición del objeto, resultando en el paralelismo deseado.

Evidentemente, en la evaluación de los diferentes pares estereoscópicos la pregunta de la estructura geométrica, por principio, se condiciona al sistema óptico intermediario entre el sensor y el objeto, ya que se debe considerar que el movimiento de la plataforma provoca distorsiones irregulares en el curso de una línea de vuelo.

Además de los factores considerados es necesario que la altura de vuelo, la resolución de la película, la dimensión de la película, el tipo de cámara fotográfica y el procesamiento en laboratorio alcancen la calidad exigida en la expectativa del fotointerprete. Todas las circunstancias inherentes al sensor fotográfico, directa o indirectamente influyen en los resultados de identificación y clasificación (Rivereau, 1972) por su esencia y compatibilidad con la escala de las fotografías.

Consciente del conjunto de factores que interfieren, el fotointerprete realiza la Fotointerpretación, que se compone de distintas fases de calificación y cuantificación desarrolladas principalmente por la clasificación e identificación de las unidades homogéneas en textura y tonalidad (Wilson, 1960).

El control del trabajo es referido a patrones de gris universales y condiciones de iluminación estable similar a la luz solar (5,600 K), eliminándose los eventuales desvíos provocados al nivel del sujeto por la adopción de dieciséis rangos de variación entre el blanco y el negro, como capacidad media de discriminación por la visión humana.

En el caso de un ambiente costero dominado por manglares pueden ser identificados muchos patrones de conjuntos debido a variaciones de textura y tonalidad, referidas a la densidad de la distribución de los árboles y al suelo aparente entre las copas, ramas y hojas.

La curvatura superior de las copas es responsable de la microtextura que seguramente no es la misma en los cuatro periodos estacionales, especialmente durante la caída y el rebrote de las hojas, cuando la tonalidad en la imagen también se altera. No obstante, la variación temporal, esta vegetación mantiene su característica perenne de siempre verde que marca los gradientes de modo muy claro en todas las estaciones del año.

En fotografías a pequeña escala, la tonalidad indica, sobre todo, trazos de la composición entre las especies, a pesar de su alteración en función de la fecha y hora de la toma de la escena y algunos atributos de la composición de la atmósfera en razón de la altura de vuelo.

Cuando se realizan las correcciones necesarias sobre las fotografías analizadas, prácticamente todo puede ser cuantificado: distancias, áreas, alturas y más particularmente diámetro de las copas, densidad y porte, substrato y humedad. Asociando los criterios a la inspección en superficie para dimensionar el intervalo de variación de los factores determinantes de la clasificación.

En la tarea de la identificación de algunas formas cuya variación diversificada es comprobada repetidamente en la actividad de Fotointerpretación, pueden prepararse transparencias con escalas especiales que facilitan el trabajo de cuantificación. Escalas patrón de tonalidad y textura adoptadas para la clasificación de los patrones seleccionados por la leyenda son ideales para fijar las categorías geocodificadas.

Las clases mas apropiadas a la Fotointerpretación de los manglares sub-tropicales están representadas en diez categorías distintas por sus características de tono, textura y altimetría:

1. **Mangle Denso Alto** - Se constituye especialmente de una asociación de *Rhizophora* y *Laguncularia* distribuidas junto a los esteros o canales estuarinos donde alcanzan su altura máxima con densidades

altamente concentradas entre los troncos que sustentan la gran masa del follaje. El substrato orgánico acumulado en la base de los árboles es mas espeso de que en otras categorías, a pesar de ser casi imperceptible entre las copas en que la especie *Rhizophora* predomina, resultando en tonalidad gris medio y textura granular.

2. Mangle Denso Bajo - Presenta la predominancia de *Laguncularia* sobre las *Rhizophora*, que disminuyendo de altura, estabilizan una superficie que se diferencia de la primera por las copas de menor diámetro. Modifican así su tonalidad a gris más oscuro debido a la apariencia relativa del substrato de menor exhuberancia, por su contenido orgánico, en función de la propia naturaleza de la productividad de esas especies. Su textura es suave (felpudo)

3. Mangle Disperso Alto - Consta de especies distribuidas en porciones aisladas con *Laguncularia* o *Avicennia*, imprimiendo textura mosqueada y tonalidad mixta entre oscuro y gris medio por la alternancia de substrato y arena abajo de las copas separadas.

4. Mangle Disperso Bajo - Contiene extensas áreas con árboles de pequeña altura, abajo de la cota que marca el nivel inferior (3 m) trazada por estereoscopía, presenta tonalidad de gris medio y textura mosqueada derivadas del pequeño diámetro de las copas, de ramas y densidad del follaje menos concentrada.

5. *Apicum* - Compuesto de especies variadas principalmente de *Acrosticum*, *Hibiscus* y *Crinum* que se desarrollan en superficies más elevadas de una microtopográfia de niveles arenosos aislados, o vecinos a las terrazas adyacentes de la zona de contacto. Textura fina sin embargo irregular, de tonalidad variable en que predominan el gris claro o blanco.

6. *Spartina* - Especie que ocupa áreas expuestas especialmente sobre los bancos de arena y lodo periféricos a las formaciones de manglares mas densos. Presenta textura homogénea en tonalidades continuas variando de gris medio a oscuro, sin la interferencia del substrato por la concentración de las plantas.

7. Mangle Degradado - Áreas de corte parcial o total exponiendo el substrato oscuro con troncos cortados o peque os arbustos de regeneración, de textura heterogénea variando de aspecto conforme el estado de degradación ocasionada al ecosistema; define tonalidades más oscuras por la dominancia de la exposición de la materia orgánica descompuesta.

8. Mangle Alterado - Presentando modificaciones estructurales de carácter total o parcial por la instalación de caminos o carreteras, construcciones o rellenos o hasta actividad agrícola o de acuacultura. La textura y tonalidad se hacen dependientes de la diversidad del efecto de alteración sobre las condiciones naturales.

9. Vegetación costera - Uniformemente estructurada, destaca textura gruesa de tonalidad más oscura que de aquella presentada por el manglar denso bajo, sin gradientes altimétricos representativos.

10. Banco de lodo - Periférico a los bancos de *Spartina* o franja externa presentando morfología compatible al escurrimiento de las aguas por los procesos de corrientes de las mareas, dispone de textura extremamente homogénea, variando su tonalidad en función de la concentración de materia orgánica lixiviada en las proximidades de los canales y por la inmersión gradual de los sedimentos con el hundimiento de los bancos.

Es necesario recordar que los patrones de tonalidad y textura de las fotografías permite su acompañamiento por densiometría de reflexión en la eventual necesidad de calibración de las referencias de las escalas de gris, siendo que las trasparencias ofrecen de un modo general gradientes de variación tonal más uniformes y más detallados discriminando más del 30% de la capacidad de los materiales opacos, como las copias en papel.

La búsqueda de datos estructurales en ambientes costeros se remonta a la historia de la fotografía aérea y del desarrollo de la Fotointerpretación, siendo la metodología de interpretación visual aplicada al estudio detallado de los manglares creada en bases mas recientes (Hamilton y Snedaker, 1984). En este punto, el especialista puede distinguir en promedio 16 tonalidades sobre emulsiones monocromáticas, reuniendo desde la posibilidad de la estereoscopía factores de textura combinados en la distinción de altura relativa entre las diferentes unidades estructurales del ecosistema. Los objetivos de un trabajo como este pueden variar según el tipo de levantamiento. Por ejemplo, el mapeo de clases de inundación, altura de las copas de los individuos, de la amplitud y densidad y dominancia de las especies relacionados al desarrollo temporal y, cuyo producto de interpretación esta reducido a fotografías aéreas en escala 1:25,000. Según diversos autores clásicos dedicados a la Fotointerpretación, se reconoce que la cobertura vegetal de bosques homogéneos ofrece cierta dificultad de identificación de especies en escalas mayores de 1:50,000. Para los bosques de manglar esta observación es válida de manera general para el análisis de los individuos que habitan en tales

ecosistemas principalmente para la identificación entre las tres especies más frecuentes *Laguncularia*, *Rhizophora* y *Avicennia*. A partir de muestreos de campo de baja intensidad en las áreas de levantamiento los datos fitosociologicos, fenológicos y morfométricos contribuyen a la definición de clases distribuidas según patrones geométricos en franjas, cuenca, corona, meandro o bajo. Transectos y cuadrantes son excelentes auxiliares en la organización de la visita de campo necesaria para la comprobación de los parámetros considerados en la Fotointerpretación de acuerdo con observaciones efectuadas en Herz (1988) y conclusiones referidas en Chapman (1984) y Hamilton y Snedaker (1984).

No obstante el análisis de tonalidad y textura que diferencía las sub-unidades, la Fotointerpretación implica referenciales que confunden distintos patrones en tonalidad de gris similar. De igual manera con la utilización de equipos de visión estereoscópica, estas superficies de textura uniforme e igual tonalidad representan diferente composición botánica. A pesar de algunas limitaciones como la mencionada, la fotografía aérea convencional ofrece un gran avance en la evaluación de los ecosistemas de manglar y da la oportunidad para la observación sistemática de la zona costera para el control del manejo, alteración y degradación del dominio vegetal de los manglares.

Los resultados de interpretación de fotografías aéreas con recubrimiento lateral (Fig. 2) permiten evaluar la distribución de patrones referidos a una relación de altura de la vegetación con la textura y tonalidad para la selección de sub-unidades de asociaciones de manglar adaptadas a diferentes substratos. En ese aspecto es esencial realizar el trabajo a partir del conocimiento del estado fenológico de las plantas en su comportamiento estacional que puede influir diferencialmente en la exposición del suelo conforme la frecuencia de las hojas en las copas y de su liberación con la consecuente cobertura del substrato húmedo. A través de los principios visuales de la Fotointerpretación el ecosistema representado en la figura 1 puede ser mapeado conforme las unidades relativamente homogéneas, clasificadas en cuatro patrones distintos de manglar conforme la leyenda: manglar denso alto, manglar denso bajo, manglar disperso bajo, superficies arenosas o *Apicum*. El uso de estas categorías expresa elementos cualitativos de utilidad en la evaluación de la biomasa de esa unidad espacial costera situada en la zona sudeste del litoral brasileño como parte del sistema estuario lagunar Cananéia-Iguape (Fig. 1). Herz (1988) estable parámetros cuantitativos sobre el mismo ecosistema, comprobando los límites demarcados en la Fotointerpretación y correspondiente composición botánica (Fig. 2). Conjuntamente a éste parámetro la planimetría efectuada sobre el croquis distingue los valores espaciales de cada categoría identificada de informaciones del sobrevuelo efectuado en 1973 en escala aproximada de 1:35,000.

De estos resultados el patrón de la categoría indicada en azul corresponde a la formación botánica con predominancia de *Rhizophora* en general situada en las proximidades de los meandros y del canal estuarino donde hay mayor posibilidad de inmersión del substrato por la variación de las mareas. Son áreas en que la densidad de individuos es generalmente concentrada y la altura de los árboles más desarrollados es de hasta 15 m sobre la franja, sufriendo reducción de las mismas en sentido opuesto al escurrimiento de las aguas. Normalmente ese patrón sufre transición gradual para la categoría de manglar bajo relativamente concentrado donde hay poca dominancia y mas mezcla entre las dos especies principales. En la figura 2 se indican en rojo las áreas que se encuentran sujetas a menos inundación como consecuencia de la propia micro-topografía del sedimento y substrato. Estas dos categorías ocupan la mayor parte de los ecosistemas de manglar, pues el patrón registrado en verde presenta individuos más aislados y dispersos sobre una superficie menos orgánica y menos húmeda hasta encontrarse en las proximidades de las terrazas marinas mas antiguas con arenas no consolidadas sujetas a la acción eólica incorporando arbustos de algunas Avicenias y especies del *Apicum*. En amarillo se marcan áreas de contacto con la vegetación costera, como una formación transicional a la floresta Atlántica, impuesta a las formaciones sedimentarias construidas durante la transgresión marina ocurrida hace más de 5,000 años.

Quedan así definidos que en el ecosistema mapeado la predominancia de la categoría del manglar denso alto (azul) es del orden de 64.1% de cobertura en los bordes, el manglar denso bajo con 24.8 % y el manglar disperso bajo con 10.2 %. Siendo un indicio de que se trata de un bosque ribere o donde las condiciones del substrato son muy favorables a los manglares especialmente a *Rhizophora* (Fig. 2).

Factores Ambientales que Rigen el Mecanismo de la Interacción de las Radiaciones Electromagnéticas con la Vegetación

El método clásico de mapeo derivado del análisis de fotografías convencionales y no convencionales utilizadas por el levantamiento aéreo, ha contribuido para el conocimiento de la distribución de los manglares, por su capacidad de diferenciar en contrastes sobre emulsiones monocromáticas y policromáticas los efectos de la radiación incidente modificada por la estructura física de tales ecosistemas.

Con el surgimiento de los sensores óptico-electrónicos, de alta resolución espacial y espectral, aumentó la capacidad de producción de la información necesaria para el mejor entendimiento del ambiente intermareal apropiado para el desarrollo de las especies halófitas que habitan en los manglares. Por su capacidad operacional esos instrumentos ofrecen grandes ventajas sobre los sensores fotográficos en razón de la reducción de etapas de procesamiento e interpretación de los datos convencionales de la fotogrametría. Los sensores registran la energía electromagnética reflejada de una superficie en forma analógica que puede ser decodificada según el formato digital en que la imagen es construida por líneas y puntos compatibles a la resolución geométrica o espacial. En el proceso, la imagen así compuesta puede incorporar la selección de diferentes intervalos de radiaciones, operando con resolución espectral variada según el avance tecnológico que caracteriza al sensor.

Las propiedades intrínsecas de los sistemas de detección de información por sensoriamiento remoto, dirigen las investigaciones a metodologías automatizadas donde es posible obtener mayor rendimiento de los resultados registrados sobre el ambiente costero. Hay en el procedimiento científico la preocupación de la integración de diferentes enfoques disciplinarios, en que el conocimiento de la dinámica ambiental, incluye el conocimiento de las propiedades físicas que rigen la energía electromagnética entre sus componentes.

Tratándose las características espectrales de los manglares como objeto de levantamiento, es necesario considerar básicamente las propiedades biológicas en el acondicionamiento de la radiación incidente que será absorbida, transmitida o reflejada por las plantas, y los demás componentes ambientales que introducen variaciones periódicas en el balance energético.

Desde el punto de vista de la naturaleza teórica tales procesos pueden definir las propiedades multiespectrales que rigen la captación y manipulación de datos de sensoriamiento remoto, obtenidos por los más diversos sistemas de sensores orbitales y hasta portátiles.

Como enfoque principal, el tema propuesto en esta investigación, se proyecta en los estudios de las respuestas espectrales de los teleobjetivos relativamente homogéneos que caracterizan la estructura física del ambiente costero, especialmente del ecosistema de manglar, donde los parámetros físicos condicionan la distribución de las especies vegetales que participan en aquella comunidad especializada.

Muchos factores interactúan en las propiedades físicas del ambiente halófito de la zona intermareal, reflejándose en la estructura y morfología botánica, responsables por semblanzas geomorfológicas de superficies derivadas de la acción de componentes hidrometeorológicos en su ritmo estacional acumulativo.

Es prácticamente imposible crear un modelo teórico, que represente la compleja organización de los mecanismos de interacción de la energía a partir de la radiación incidente, entre tanto, para efecto práctico, hay simulaciones que consideran la estructura básica y la fisiología de los elementos principales para calcular el balance de las interacciones.

En la evaluación del ambiente costero el procedimiento de control del flujo de las radiaciones, para la comprobación de las propiedades que rigen el sensoriamiento remoto, debe ser dirigido sectorialmente para que los diferentes procesos físicos lo constituyan. Los manglares, a pesar de restringir grandemente los múltiples efectos encontrados en el ambiente transicional costero, también destacan tres elementos bastante diferenciados en su comportamiento espectral: el substrato, las aguas y la vegetación.

En cualquier esfuerzo realizado en el intento de clasificar patrones relativamente homogéneos por un comportamiento espectral característico de ese ambiente, deben ser consideradas las condicionantes mencionadas en su justa proporción, por el aspecto de distribución de la vegetación tanto en su densidad como en su textura. También se debe tomar en cuenta la exposición del substrato y/o de las aguas o humedad como circunstancia variable, en relación con los ciclos de precipitación, mareas y vientos locales.

Las regiones subtropicales, involucran una dinámica atmosférica de choque entre masas de alta y baja presión, originando regímenes pluviométricos intensos principalmente en el

verano, con buena distribución mensual y en el invierno con episodios concentrados de corta duración. En general con alto contenido de humedad atmosférica, la masa de aire costero induce serias anomalías que perturban la propagación de las radiaciones incidentes, ofreciendo una reducción de la eficiencia de los sensores por el efecto atmosférico.

Hay periodos en que los datos tomados por los sensores orbitales y aerotransportados son menos vulnerables a las alteraciones del efecto atmosférico, siendo tales imágenes apropiadas para un trabajo más eficiente de reconocimiento de patrones espectrales de los blancos costeros. Esa preocupación contribuye expresivamente en la correlación con los datos de apoyo en superficie, obteniéndose mayor ajuste entre lo previsto en los datos multiespectrales de la escena procesada automáticamente y los valores medidos en el campo.

Los periodos de abril/mayo y agosto/septiembre han sido registrados por imágenes MSS y TM o HRV como los de mejor calidad, cuando son examinados los canales de bajo visible, correspondiendo las bandas del azul y del verde en el espectro, en que la turbulencia atmosférica debería ser calificada como un constituyente de ruido indeseable.

La estructura de las plantas, del suelo y de los factores ambientales asociados, están directamente relacionados con los procesos fisiológicos que condicionan la morfología de la copa de los árboles, como superficie reflectora de flujo de radiación solar. Willstatter y Stoll (1916) explican la reflectancia y transmitancia de las radiaciones electromagnéticas por las hojas de los vegetales, principalmente de la porción del espectro visible, como una función de la estructura interna de las interfaces de las bolsas de aire y del tejido esponjoso intermedio entre las dos epidermis. Sinclair (1968), estudiando las mismas características, plantea la hipótesis de la influencia de las paredes intercelulares en el proceso de difusión.

Uno de los aspectos inherentes al comportamiento radiométrico debe ser relacionado a las variables ambientales. La fotosíntesis tiende a desarrollarse inversamente al aumento de la temperatura ambiente, siendo mas intensa en los días fríos que en los días calientes. Como esa tasa esta estrechamente relacionada con la absorción de las radiaciones de onda corta, la actividad de la fotosíntesis se reduce en los días más calientes aumentando la reflectancia de la vegetación principalmente de ondas de la banda del azul y del verde.

Gausman *et al*. (1970) relacionan la reflectancia de las radiaciones de infrarrojo próximo a la mayor presencia de espacios intracelulares ocupados por el aire. De ese modo la reflectancia aumentaría con el aumento de los bolsones de aire en las hojas por el hecho de que la radiación difusa se propaga más de un índice de refracción alto a uno bajo.

La presencia del volumen de agua y aire en las hojas de las especies vegetales es comprobadamente la causa del balance entre la absorción y la reflexión de las radiaciones entre 380 y 1100 nm, pudiendo, en una generalización, ser definido en la dependencia del cálculo del índice de follaje.

En general, los espacios de aire intercelulares de las hojas son notables a partir de un tercio del desarrollo de su tamaño final de maduración siendo su volumen variable en función de las especies vegetales, alcanzando según Sifton (1945) relaciones de 77/1,000 y 713/1,000.

La reflexión de las hojas es predominante en el infrarrojo próximo, destacando al *Citrus* (Myers, 1983), en que 55% de la radiación que penetra hasta el interior de las mismas, es 40 % transmitido y 5 % absorbido, sin embargo, Sinclair (1968) comenta que estos valores varían bastante en relación a la estructura de otras especies.

Pearman (1966) citado por Myers (1983) relata que las plantas que alcanzan la madurez con menores contenidos de clorofila, poseen un mayor nivel de se al reflectora de radiaciones del visible que aquellas más jóvenes con más clorofila. Knipling (1970) estableció que los factores fisiológicos que alcanzan las hojas afectan directamente la reflectancia de la vegetación, que es más pronunciada en la banda del espectro visible que en el infrarrojo próximo. Este cambio reside en la sensitividad de la clorofila, entre tanto en muchos casos ocurre por el cambio de volumen de los componentes de la hoja reduciendo su área externa.

La absorción de la luz entre 500 y 700 nm en las plantas es orientada en presencia de los pigmentos de clorofila *a* y *b*, siendo el intervalo de 750 a 1,350 nm del infrarrojo la banda de alta reflectancia y baja absorción es afectada considerablemente por la estructura interna de las hojas; en un rango entre 1,350 y 2,500 nm la absorción mayor se da entre 1,450 y 1,195 nm por el contendido de agua entre las estructuras y en su propio tejido.

Las hojas jóvenes por su naturaleza contienen menos agua de que las adultas porque cuando son inmaduras están formadas por pequeñas vacuolas llenos de agua (Lundgardh, 1966). Los pigmentos son parte integrante del elemento fluido y no pueden ser separados para efecto de diagnóstico de la influencia del agua en el

régimen de interacciones con la energía electromagnética. Rabinowitch (1951) demostró que la introducción de agua pura en los espacios intercelulares de las hojas aumenta la reflectancia en relación al contenido túrgido de las hojas, habiendo una disminución en la absorción como lo reportan Moss y Loomis (1952) en la mayor parte de la región del visible especialmente en 680 nm. De esta forma las investigaciones de Pearman (1966) confirman esa tendencia pues afirma que la deshidratación natural de las hojas aumenta la reflexión de las radiaciones del visible, debiendo tomar en cuenta esa perdida de agua en cualquier muestreo sobre la vegetación, especialmente en el periodo diurno regulado por la evapotranspiración de las plantas.

En su ciclo funcional la vegetación ocasiona en las hojas una serie de mutaciones impuestas por la variación de los factores ambientales y las fases estacionales del desarrollo floral. Esto debe ser considerado en los estudios sistematizados de monitoreo en relación con las condiciones especificas de huellas espectrales que serán intercomparadas.

Durante su crecimiento, maduración y deterioro, las hojas de los vegetales tienen su contenido de clorofila, proteínas y ácidos nucleicos degradados, siendo sus productos catabólicos dislocados hacia áreas anabólicas activas. En el mismo periodo que caen las mismas con el consecuente cambio de color (amarillo, anaranjado y rojo). Myers (1983) indica que, parcialmente, esto puede ser explicado por la invasión de pigmentos de antociamina cuando la clorofila se pierde o descarga. Esto también puede ocurrir por el cambio del ciclo de los nutrientes, choques térmicos y periodos cortos de exposición a la luz.

La reflectancia en el visible para la hoja madura en presencia del inicio del periodo de degradación de la clorofila, se hace a 550 nm (Knipling, 1970), y a partir de ese estado el aumento de antociamina y pigmentos carotenos causan desvío de la respuesta espectral para la banda del rojo y del azul en la región espectral del visible. El infrarrojo próximo decrece principalmente en su respuesta de reflectancia entre 750 y 1,350 nm, cabe mecionar que este efecto puede ser ocasionado por otros procesos que introducen da os a las células de las hojas.

La madurez de la hoja de una planta viene a representar un factor de importancia en la evaluación de la influencia de la salinidad en las propiedades espectrales de la vegetación. Muestras colectadas en el tercer o cuarto nudo de plantas saturadas, presentan alta reflectancia y baja transmitancia debido al aumento del índice de refracción cuando son comparadas con las hojas mas jóvenes y menos alcanzadas por el escurrimiento.

Muchos estudios documentan a la salinidad como un factor responsable de la alteración de estructuras internas de la hoja. Las adaptaciones morfológicas de vegetación desarrolladas en ambientes de naturaleza salina, repercuten en hojas gruesas de parénquima más desarrollado, menor contenido de clorofila, espacios intercelulares menores, menos estomas, y menos cloroplastos (Myers, 1983). En general las hojas verdes absorben 75% a 90% de las radiaciones de longitud de onda característico del azul (459 nm) y del rojo (680 nm) utilizando esta energía radiante en el proceso de fotosíntesis en este intervalo exactamente a 550 nm donde ocurren el máximo de reflectancias en torno de 20% de la energía incidente.

Estos resultados de las investigaciones condujeron a Thomas (1970) a la identificación de las propiedades de los nutrientes en el interior de la hoja conforme a su relación directa con los pigmentos disponibles, pues la reducción del primero actúa directamente en la caída del segundo. Consecuentemente, los resultados del sensoriamiento remoto pueden influir en la estimación de la deficiencia de nutrientes en las plantas utilizando múltiples canales de información sensibles a las bandas de absorción y de reflexión de las plantas.

Las hojas constituyen el elemento mas importante de la planta desde el punto de vista de conservación de energía. A través de las radiaciones solares acumulan energía de tal modo que su balance térmico no permite los excesos que representan índices peligrosos para la sobrevivencia, entre el frío y el calor, excluyendo cortos periodos transitorios de su estado de adaptación.

El régimen funcional de la planta está condicionado por los factores externos del medio ambiente (destacando la temperatura, la humedad y la luz), es extremamente importante en el desarrollo biológico de la hoja, siendo detectados en la fotosíntesis y demás actividades internas. La radiación aumenta la temperatura de la hoja por la absorción y la evapotranspiración reduce la misma por la liberación del calor latente, siendo que el ambiente puede actuar por convección calentando o enfriando la planta en su contacto con el aire en la zona periférica envolvente.

Además de las consideraciones intrínsecas a la estructura de los vegetales, especialmente de sus hojas, es necesario considerar la forma de obtención de las informaciones espectrales por los instrumentos sensores y radiométricos, tomando en cuenta las circunstancias espacio-temporales durante los levantamientos.

El visor del instrumento sensor sobre las copas de los árboles, define aspectos espaciales cuya geometría califica una coyuntura que, efectivamente, dirigirá la eficiencia de la medida a un grado deseable de precisión. La propia cobertura vegetal atribuye al espacio ciertas características que establecen una textura propia a cada ambiente; cuando se considera el arreglo de un espécimen y de su copa o una asociación de muchos de ellos, las propiedades físicas de la interacción de las radiaciones electromagnéticas son influenciadas por su geometría, incluyéndose la interferencia de la superficie aparente del suelo a través de las aberturas derivadas del patrón de densidad de las copas y/o distribución de los árboles por su dispersión o concentración.

Por principio, la radiometría de la cobertura vegetal debe ser llevada a una geometría de observación que altere los pre-requisitos de una observación directa, bastante próxima del nadir local que deberá corresponder al eje del péndulo en reposo posicionado en el centro del campo de lectura y siempre que se realice, igualándose el área cubierta al elemento de área observado por el satélite utilizado.

Bariou *et al*. (1985) reúnen argumentos bibliográficos sobre esta pregunta, alertando al usuario, a través de una rese a, de los principales procesos de adquisición de los datos espectrales. Las citas referidas integran factores de interferencia de diferentes orígenes. Por ejemplo, la reflectancia bi-direccional para el infrarrojo próximo y medio del visible por ensayos efectuados por Vanderbilt *et al*. (1980) entre ángulos Cenit que varían entre 10 y 60°. Las curvas registradas en ese ensayo muestran la variación de la energía reflejada, manteniéndose la tendencia de proporcionalidad en el infrarrojo, y en el visible, un entre-cruzamiento de las curvas documenta el comportamiento irregular. Otros resultados que demuestran de la variabilidad de la orientación del instrumento en relación a la fuente de luz (iluminante) y al blanco son presentados por Belov (1961) en que el porcentaje de reflectancia se altera en aproximadamente 4% entre las condiciones extremas de medidas.

Para una elevación solar entre once y quince horas y un ángulo de difusión entre 3° y 56°, Rao *et al*. (1979) revelaron que la reflectancia porcentual alcanza variaciones de hasta 40% en la tendencia de la curva de firma espectral para un mismo punto o teleobjetivo.

El posicionamiento de los teleobjetivos en relación al relevo representa un grado de inclinación que influye en la respuesta espectral de la vegetación, siendo este efecto bastante considerado en la clasificación de patrones sobre los datos de imágenes. En el caso de manglares esto no es relevante por ser un ecosistema instalado en la planicie o zona intermareal, donde las variaciones son de pequeño orden en el dominio de la microtopográfia.

Con un aspecto casi plano, la superficie equivalente a los manglares son revestidas por altas concentraciones de materia orgánica fragmentada y descompuesta, mezclada con partículas sedimentarias de origen mineral. Su disposición no es uniforme estando asociada a las microformas, a veces de contenido arenoso predominante. En los sectores en que las hojas son liberadas por los árboles, revisten las formaciones superficiales de espesas camadas de apariencia oscura y húmeda, asociadas a los componentes disueltos del tejido de hojas descompuestas, ocurre gran absorción de energía como un cuerpo negro natural. Como ya se mencionó, esta interferencia es muy importante en la identificación de las clases de distribución de especies y densidad vegetal relativamente a su exposición a la mirada vertical de los instrumentos sensores de las plataformas aéreas y orbitales. La humedad permanente y la alta absorción de energía, principalmente de radiaciones del infrarrojo, garantizan la saturación del aire afectando la evapotranspiración. En estas condiciones la energía recibida por los sensores depende de las propiedades de los constituyentes del teleobjetivo y de la variación de las propiedades dieléctricas o de la temperatura.

Las temperaturas tomadas sobre superficies con vegetación inducen al estudio del balance térmico donde el agua disponible en el suelo es parte esencial del proceso. El substrato de los manglares en que el agua es fácilmente disponible para las plantas y también activamente evaporada, probablemente es una de las causas principales del mantenimiento de temperaturas a veces superiores a las del aire.

Lecturas Radiométricas y Distribución Espacial de los Elementos de Imagen

Cuando se seleccionan los teleobjetivos dominantes por su representatividad en el ambiente costero, la interacción de las radiaciones electromagnéticas en sus propiedades físicas, obedece a un régimen que puede ser modelado teóricamente con algunas restricciones de orden práctico.

Mediciones espectrales pueden ser simuladas

en laboratorio u obtenidas en el ambiente natural, en reconocimientos de superficie o aéreos; los instrumentos de laboratorio miden usualmente la reflectancia hemisférica (o emitancia) y en casos específicos, la transmitancia. Realizadas en peque as muestras sobre las copas, una hoja y su tallo, substrato o suelo en áreas reducidas, los datos resultantes de esa actividad son indispensables para entender el mecanismo de la interacción de la radiación-materia que, sirve de instrumento identificador de los teleobjetivos por su se al espectral, siendo importante tener en cuenta para el laboratorio lo siguiente: **a**) Los instrumentos poseen fuentes de iluminación controlada, **b**) El ambiente donde se procesan las medidas es estable, **c**) El instrumental puede ser complejo sin restricción de volumen, peso y consumo, **d**) La velocidad de observación no es importante, **e**) Soporte logístico existente.

Si por un lado se considera las ventajas de las mediciones condicionadas, hay que precisar que el ambiente de observación no es normal, no reproduciendo las características naturales. La remoción de la muestra para el laboratorio puede perturbar sus propiedades espectrales; la geometría de iluminación y observación no reproduce la reflectancia hemisférica. Para fines de sensoriamiento remoto el elemento de resolución espacial contiene un conglomerado de componentes que solamente los ecosistemas en su estructura natural disponen.

Como conclusión de las apreciaciones de los dos métodos de medición es necesario considerar: que la información radiométrica deben, en la medida de lo posible, realizarse *in situ* donde se observan las propiedades de autoemisión o reflexión de la luz solar. Sin embargo es posible aplicar otras fuentes de iluminación.

En la superficie, las medidas a nivel del suelo no reproducen la generalización espacial de los elementos de imagen de una plataforma orbital, necesarios a la correlación en el procesamiento digital. Por esto, es recomendable utilizar aeronaves como soporte de los radiómetros, que a partir de alturas programadas simula uno o más elementos de resolución geométrica. En este caso la geometría de mirada es idéntica al sistema operacional incluyendo su movilidad que posibilita la colecta de perfiles o puntos de muestreo en una gran variedad de blancos.

No obstante las ventajas mencionadas algunas dificultades interfieren en la calidad de tales resultados, pues los sistemas radiométricos aerotransportados más complejos, exigen calibración y estabilización produciendo datos menos precisos que aquello simulados en laboratorio. El gran volumen de datos necesita sistematización, requiriendo sofisticados métodos de tratamiento, siendo casi impracticable su reducción a elementos específicos de la superficie observada.

Ningún equipo reúne totalmente estos requisitos, siendo necesarias también soluciones tecnológicas que capaciten las unidades para que una automatización facilite la rutina de operación reduciendo los costos del vuelo, aumentando la eficiencia de las mediciones.

La medidas radiométricas en superficie por principio son definidas como la radiancia calculada por el producto de la reflectancia con la irradiancia:

$$I = p\ E/\pi$$

donde: I= radiancia; p = reflectancia; E= irradiancia.

El equipo de lectura óptica, del tipo utilizado en la investigación, no ofrece en su medición la distribución energética del espectro y si su logaritmo. Por lo tanto, se hace necesaria una simples rutina de conversión de datos medidos en su valor energético. Por consiguiente, las lecturas sobre el objeto son consideradas relativas a una referencia que, teóricamente, presenta altísima reflectancia en torno de 98% a partir de una superficie de $BaSO_4$ depositada sobre una placa rígida en solución de alcohol.

Los modelos de estudio de la distribución espacial de los elementos de imagen implican en las definiciones y conceptos que involucran, la idea reduccionista en que el resultado lleva a diferentes niveles de abstracción. En el estudio de la distribución espacial de los elementos de imagen por el reconocimiento de patrones, esa percepción reside en la observación de la escala de trabajo de procesamiento digital y su compatibilidad con la resolución geométrica del sistema sensor.

El elemento de imagen, por si mismo, encierra una señal de abstracción, por su capacidad de cobertura en área de superficie ilustrada como unidad menor de la escena, representa la medida de la radiancia de un espacio compuesto por blanco homogéneo, o relativo cuando la estructura del mismo contenga superficies de diferente propiedad física con relación a su interacción con la energía electromagnética.

Hay por lo tanto un factor limitante sobre la discriminación de los detalles por una imagen, cuya dimensión de sus elementos geométricos sea superior a la de los blancos que constituyen la expectativa de la clasificación. En la mayoría de los casos, cuando son utilizados los datos del mapeador temático (TM) del satélite LANDSAT, el área de un elemento (pixel) de imagen abarca 900 m^2 que son registrados en la imagen por su vector de radiancia en cada uno de los canales,

y de conformidad con la respuesta espectral de aquella área en el suelo por su media de energía reflectora o emitida en dirección al sensor instalado en el satélite.

En razón de ese proceso de transferencia y de codificación de valores en la imagen de los elementos espaciales, estructuran la distribución de patrones por unidad homogénea constituida en clases, existiendo siempre una dificultad de la identificación de sus límites reales. El control del borde de los conjuntos o sub-unidades de una escena tiene su distribución influenciada por el alineamiento de las líneas y columnas de la imagen en relación a la posición de los objetos y sus perímetros de contorno en el suelo.

Las relaciones de vecindad entre los elementos de imagen que marcan el borde de patrones distintos pueden avanzar o retroceder sobre la dirección verdadera, debido a su sobreposición al espacio de acuerdo con la órbita y barrido del sensor, o bien de la proporcionalidad entre las dos categorías vecinas. El porcentaje en área para cada una, en un solo elemento de imagen, resulta en la radiancia media o tendencia del valor espectral predominante, cuando es sobrepuesto al verdadero lugar geométrico del contacto entre las demás interunidades de la escena.

Por principio cuanto mayor sea la resolución espacial del sensor, menor será la perturbación causada por el efecto de borde en relación a la precisión del mapeo de las unidades con su verdadera grandeza en el suelo. El grado de detalle para superficies menores solo es viable a partir de la capacidad de los sistemas en registrar en el área cubiertas por elementos de imagen las variaciones de contorno implícitas a su distribución geográfica.

Saint y Podaire (1982) comparan el sistema HRV del satélite SPOT con resolución de 20m a los resultados producidos en la misma escena por el sistema MSS y TM respectivamente de 80 y 30m de resolución espacial. Una serie de detalles entre los canales que actúan en bandas similares son comparados en reproducciones monocromáticas de la misma área geográfica, permitiendo la visualización del efecto de borde entre los mismos. Concluyen que un blanco discriminado por el sensor HRV con 6,757 elementos pasa a ser representado por 3,095 en el TM y 658 en el MSS; filtrando la escena para determinados elementos de coherencia sobre el blanco establece la relación de 3.676, 1.190 y 55 para cada uno de los detectores, lo que es importante cuando el objetivo es identificar los elementos puros no contaminados por valores de la vecindad. La relación encontrada en aquel experimento depende de la estructura de cada imagen y del direccionamiento de los contornos de los blancos por la alineación de las columnas y líneas, variando evidentemente el efecto del control de borde en la imagen.

Esto influye en la selección de elementos puros caracterizados espectralmente por las propiedades físicas de los materiales, diferenciando mucho la proporción entre los registros de los tres sistemas de sensoreamiento orbitales considerados. Lo cierto es que la probabilidad de menor efecto de borde ocurre en las direcciones próximas a los alineamientos de barrido de los sensores y de la mayor resolución espacial de los mismos, reduciendo la interferencia de elementos de imagen contaminados por áreas vecinas.

Recientemente, Herz *et al*. (1985) abordan la aplicación del índice de vegetación sobre datos TM-LANDSAT, encontrándose en esa resolución la probabilidad de realizar de clasificaciones de los datos para el detalle de clases de manglares que componen la estructura física de tales unidades costeras. Los patrones de detalles fueron comparados con los mapas de interpretación elaborados a escala 1/25,000 y 1/35,000 a partir de interpretación y ajuste de fotos aéreas pancromáticas en estereoscopia.

Para el estudio de los ecosistemas de manglares algunas experiencias anteriores demostraron las ventajas entre resolución espacial de los sensores MSS y TM. Para Herz *et al*. (1985) algunos ensayos efectuados en la zona costera subtropical brasileña llevaron a conclusiones muy claras sobre la utilización de las informaciones del sistema MSS de los satélites LANDSAT. Sobre estos datos tentativas de identificación interna de los patrones sobre algunos ecosistemas de manglares no condujeron a ningún producto que pudiera ser comparado al conocimiento de campo e interpretación de fotografías aéreas, a no ser su área total, considerando los errores generados por el efecto de borde de una estructura de imagen relativamente gruesa considerando el blanco en referencia.

Queda comprobado que el mapeador temático (TM) como sensor orbital tiene una eficiencia mayor en relación al MSS, sobre todo en escalas mayores a 1/100,000 formas particulares de patrones relacionados a gradientes de distribución de la vegetación de los manglares. Si el error de cálculo de área se reduce en relación al cómputo total por unidad, en razón del aumento de resolución geométrica por la reducción del efecto de borde, en las subunidades de los patrones suman mayor error por la complejidad de las formas que acumulan diferencias representativas entre los límites reales. En ese caso el desvío puede variar hasta en 30m sobre la línea límite entre los dos patrones dependiendo de la orientación de las líneas y columnas de la imagen sobre la alineación de los contornos que definen la forma verdadera del espacio identificado espectralmente.

Con la intención de evaluar la radiancia provocada por la reflexión media de áreas de 30 x 30 m en el suelo, equivalentes a un pixel de la imagen, algunas parcelas definirán la forma de distribución de especies y morfología en algunas posiciones representativas de cada perfil morfométrico. En un interés más profundo algunas lecturas radiométrícas entre 400 y 1,050 nm fueron efectuadas con instrumento portátil directamente sobre los blancos principales representados por especies dominantes y diferenciación del substrato.

Durante el verano los experimentos de campo efectuados tanto para pequeñas, como para grandes longitudes de onda en el intervalo mencionado, los patrones identificados en las imágenes principalmente para los dos canales del infrarrojo próximo (TM-4, y TM-5), por su reflectancia muy alta en cobertura vegetal densa, confirman los datos representados en las curvas radiométricas establecidas por radiómetro portátil.

En el comportamiento general queda demostrado la alta absorción del azul, con una reducción sensible a 550 nm para elevarse en el anaranjado / rojo (600-675 nm) para reducirse substancialmente en el infrarrojo próximo. Esto se mantiene para la curva de radiancia apenas en magnitud aunque las lecturas sean hechas sobre substrato variado de lodo o arena predominantes o mixtos.

La baja reflectancia del lodo de contenido predominantemente orgánico hace que la vegetación se caracterice de modo nítido principalmente en la longitud de onda más larga del infrarrojo próximo, siendo la contribución del substrato en términos aditivos muy baja. La mencionada diferenciación de la radiancia por especie pues *Avicennia schaueriana* posee reflectancia más intensa en su potencial relativo que *Rhizophora mangle* y *Laguncularia racemosa*. Esta última no depende del substrato, sin embargo valores mayores se han verificado sobre el substrato de arena conforme a las curvas.

Las diversidades encontradas en los niveles de reflectancia entre las especies instaladas sobre el lodo, llegan a 20 % entre *Rhizophora mangle* y *Laguncularia racemosa*, mostrándose mayor discriminación (al rededor de 30 %) entre *Laguncularia racemosa* y *Avicennia schaueriana*; análisis similar entre las radiancias relativas de *Rhizophora mangle* con *Avicennia schaueriana* destacan solamente 10% de abertura entre las curvas intercomparadas.

De lo anterior se deduce que en las áreas en que los manglares se desarrollan sobre substratos curvos predominantemente orgánicos, registrados por sensores, la tonalidad del gris característica de cada elemento de imagen corresponde a una respuesta relativamente proporcional a la secuencia revelada por los datos radiométricos de apoyo en superficie. En este caso, un brillo (radiancia) más intenso para las tres especies mencionadas sería el comprobante registrado en los canales TM 4 y TM 5. Este mismo efecto sobre substrato más arenoso queda menos evidente observándose en algunos puntos la sobreposición, al igual que en el infrarrojo próximo, pues *Avicennia schaueriana* que presenta alguna elevación de la curva junto al límite superior del espectro experimental, presenta una inversión con *Rhizophora mangle* incluyendo a *Laguncularia racemosa*. Sobre la arena o substrato predominante, los niveles porcentuales son más elevados en el distanciamiento entre las curvas, alcanzando valores de 60% destacándose la reflectancia de *Rhizophora mangle* y mucho más todavía de *Laguncularia racemosa* en casi 100 % sobre la anterior. Por lo tanto, la separación entre la arena, es en parte discutible para la identificación segura entre las especies de manglar en las imágenes orbitales, debiendo aplicarse en esta situación otros recursos en el acceso al reconocimiento de las clases establecidas de los patrones producidos por el sistema computacional.

A partir de las curvas del patrón radiométrico se verifican separadamente las cuatro condiciones en que las tres especies registrarán a la radiometría, estando ellas sobre el lodo, arena, manto de hojas y hojas individualizadas, han demostrando el mismo comportamiento en cuanto a los niveles porcentuales de sus respuestas. Se puede afirmar que es obvio que la contribución del substrato, por la abertura de las copas o espacios interfoliares deja de existir en el análisis del manto de hojas y de la propia hoja cuando la reflectancia es medida.

Las gráficas de reflectancia de los blancos relacionados, agrupados sobre las cuatro condiciones en que fueron observados (lodo, arena, manto de hojas y hoja individual) exhiben la misma secuencia de valores crecientes y diferenciados entre 400 y 1,050 nm. Este comportamiento es esperado en la medida en que las características radiométricas del vegetal son evidenciadas, por la reducida participación del esparcimiento multidireccional, provocado por el múltiple posicionamiento de las hojas y del propio substrato. De este modo, es perfectamente comprensible que la especie vegetal, sobre un substrato lodoso, presente niveles de radiancia más bajos de que aquellos encontrados sobre la arena, pues la presencia de sílice contribuye en la radiación emergente. El manto de hojas y la hoja individualizada registrada por el radiómetro es una tentativa de eliminar esta influencia, causada por la participación de factores aparentes entre las hojas *in natura*.

Como se puede observar en las gráficas experimentales de las tres especies de manglar, la curva característica sobre el lodo es la más baja, cuando se relaciona con la curva característica de la hoja aislada con reflectancia relativa al rededor del 80%. Otras curvas de radiancia sobre hojas aisladas, presentan algunas discrepancias, por ejemplo en los gráficos compuestos para *Avicennia schaueriana* y *Laguncularia racemosa*, un aumento de la reflectancia de 650 y 550 nm, respectivamente, e igualmente para la *Rhizophora mangle*. El pico de 650 nm es imprevisto y por esto causado seguramente por el posicionamiento irregular de la superficie de hoja en relación a la radiación incidente. Algunas partes de la superficie ondulada de la hoja pueden establecer un ángulo de reflexión especular, provocando en alguna longitud de onda una interferencia aditiva, resultando en los incrementos observados. Asimismo, los picos en 550 nm, considerablemente elevados, acompañan la tendencia del aumento característico de la reflectancia vegetal para pequeñas longitudes de onda.

En las curvas para el manto de hojas se nota la tendencia general de elevación y una inversión a 950 nm, reduciendo cerca de 10% con relación al nivel de reflectancia del intervalo anterior. comparándose esos resultados a la curva patrón, se identifica la misma depresión a 850 nm que se mantiene a 950 nm. El arreglo presenta respuestas más características que de la hoja individualizada eliminándose de cierta forma las contribuciones ilegítimas de las medidas por hoja. De ese modo se reprodujo una buena calidad de resultados de muestras representativas y estudio en el ecosistema.

Es marcado el aumento que ocurre en la reflectancia de las especies sobre la arena, particularmente *Laguncularia racemosa* que aumenta hasta en un 25% el nivel de respuesta reflectora, presentando *Rhizophora mangle* un aumento de 15% y *Avicennia schaueriana* apenas 5%. Esto no se justifica por el substrato, pero si por la propia especie que presenta una distribución diferenciada de área del follaje expuesta a la radiación. También se debe considerar que diferencias morfológicas entre las tres especies son causantes de desvíos relacionados con la apertura entre ramas y hojas, como por ejemplo *Laguncularia racemosa* que tiene sus troncos y ramas más esparcidos, causando mayor apertura para que el substrato interfiera en el resultado de la lectura. Para *Avicennia schaueriana* la verticalización como el entrelazamiento y sobreposición de las ramas y hojas no permite una exposición tan acentuada del substrato, es indiferente el tipo de substrato cuando son registradas, por los sensores multiespectrales.

Procesamiento Digital de Imágenes

La información digital derivada de la transformación de datos aéreos orbitales permite identificar la distribución geográfica de patrones ambientales sobre imágenes multiespectrales, que son procesadas por equipo automático a partir de algoritmos especiales.

La organización sistemática de una imagen se refiere a la ordenación espacial articulada en líneas y puntos de resolución geométrica conocida, en el caso del mapeador temático (TM) del satélite LANDSAT-5, equivalente a 30 m para los intervalos espectrales del visible e infrarrojo próximo. Esa unidad representa áreas de 900 m^2 distinguidas por coordenadas de posición y el valor de radiancia corresponde al intervalo espectral de cada banda del sensor, medido en la escala relativa de 252 niveles digitales.

Por la versatilidad de la intercomparación y combinación de valores espectrales de los diferentes intervalos radiométricos, encontrada en la automatización, las imágenes en formato digital permiten realizar la clasificación temática de patrones referidos al comportamiento de interacción de los materiales con la energía electromagnética. El ajuste de los coeficientes estadísticos atribuidos por los algoritmos de procesamiento automático resulta en el conocimiento de la distribución espacial según la clase del atributo de imagen.

Específicamente para los ecosistemas de manglares las especies vegetales que lo habitan, forman asociaciones cuyo comportamiento espectral se puede determinar por su dominancia y densidad. Entre tanto, la morfología y el ciclo fenológico de los individuos representan factores de variación que inciden también en el aspecto de la cobertura del suelo abajo de las copas, visible en el registro de los sensores. Considerada esa dinámica, el control efectivo del reconocimiento de patrones, viene a ser esencial para el trabajo de procesamiento de la información obtenida por sensores remotos multiespectrales. Cuando se comparan imágenes de diferentes periodos, esos factores quedan bastante evidenciados en la estructura de las imágenes, como puede ser verificado en la figura 4, donde están representadas informaciones obtenidas de un mismo ecosistema en distintos periodos estacionales (Río Baguaçu) como parte del sistema costero Figura 1. A la izquierda de la referida Figura 4 el

Figura 4. Resultado del procesamiento digital de sectores de imagen del satélite LANDSAT-5, sistema mapeador Temático, utilizando los canales TM3, TM4 y TM5 y algoritmos de máxima verosimilitud para la obtención de las clases representativas de patrones espectrales por densidad/substrato en el ecosistema de manglar del Río Baguaçu próximo a Cananéia (25°00' S).

paso orbital del satélite LANDSAT-5 (órbita 220 pt. 77 qd. D) del 22 de mayo de 1985 representa la situación de otoño, y a la derecha la misma área levantada el 14 de septiembre de 1986 en primavera. Para una comparación visual entre los dos periodos, se identifica con cierta facilidad la mayor exhuberancia de las copas para la primavera y la influencia del substrato por la reducción de la masa del follaje en los árboles en pleno otoño.

Basados en el conocimiento previo del comportamiento radiometríco de los manglares (Fig. 3) se eligieron para componer la información multiespectral a ser procesada tres bandas del Mapeador Temático TM3 (0.63-0.69 m), TM4 (0.76-0.90 m) y TM5 (1.55-1.75 m) siendo el primero caracterizado por radiaciones del visible predominantes en el anaranjado/rojo y los dos últimos por radiaciones del infrarrojo próximo donde hay mayor reflectancia de la vegetación.

Debido a la reducida extensión del área ocupada por este manglar, la transferencia de las unidades de resolución de la imagen en proporción 1:1 (pixel x byte) que es la escala original de 1:56,000, fue alterada por interpolación geométrica, reduciéndose el área de cada pixel de 30 m x 30 m a 7.9 m x 7.9 m resultando en nueva escala de 1:15,000. En este procedimiento, la utilización de un interpolador bilínear capaz de alterar la estructura original de la imagen fue aplicado sin degenerar su eficiencia.

La discriminación radiométrica de las unidades espaciales fue aumentada cor la aplicación de filtros del tipo paso alto, en que los detalles son realzados en las zonas de contraste transicional, con una demarcación más nítida entre superficies diferenciadas en relación a la se al registrada. Una de las prácticas de implementación del filtro para el realce de la imagen, consiste en la conversión a partir de una matriz de ventana, que se mueve sobre la misma ocupando siete columnas por siete líneas (matriz 7×7).

Para proceder al procesamiento con mayor grado de eficiencia, la aplicación del artificio, permite separar el área total del manglar de las demás superficies adyacentes, eliminándose de los inconvenientes al producto de análisis, evitándose también desvíos estadísticos que degeneran los parámetros de control en la clasificación de los datos. Preparada de esa forma la imagen recibe después el tratamiento previo, los atributos seleccionados por el procesamiento final aplicándose el método de la máxima probabilidad. Categorías preestablecidas en función de la estructura de la imagen presentada en la figura 1, en que son identificadas las superficies homogéneas para los patrones de manglar denso alto, manglar denso bajo, manglar disperso bajo y *Apicum*, se incluyen al final como leyenda.

Las matrices compuestas para las dos imágenes presentaron, respectivamente para el oto o y primavera un entorno estadístico de alta eficiencia, habiendo para el punto 16.3 una exactitud promedio entre 97.46% y 97.76% con abstención de 0.44% y 0.80%, sobre el universo de datos considerados sectorialmente en la imagen. En cuanto a la capacidad de discriminación del método, para el límite entre las clases consideradas el nivel de confusión medio varió de 2.10% a 1.44%. El resultado final del mapa temático se encuentra detallado en la Figura 4, en que las dos situaciones ambientales demuestran diferencias sensibles en su distribución, según las cuatro clases seleccionadas. Una comparación estadística puede ser encontrada en la Tabla 1, donde la interpretación visual presenta un desvío bastante representativo al compararse con el método digital, confirmándose en parte el alto grado de subjetividad del control de los contornos de las subunidades a pesar de la ventaja de la estereoscopía (Fig. 2).

Es sorprendente la coherencia entre el procesamiento destacando dos episodios temporales, siendo necesario tomar en consideración los datos de la Tabla 1 la variación ambiental entre la imagen de otoño y primavera, principalmente en el que se refiere al cálculo de la cobertura vegetal en función de la fenología de las especies asociadas. El producto observado en la evaluación digital para la imagen de otoño (22 de mayo de 1985) introduce números de área para las clases de manglar denso alto (azul), manglar denso bajo (rojo) y manglar disperso bajo (verde) superiores a los encontrados para la primavera en la Tabla 1. Se justifica el hecho por ser el periodo de otoño el final del ciclo de maduración de las hojas dándose inicio a la liberación de las hojas.

En el inicio de la primavera se expone de modo más directo el substrato por la reducción del área foliar. Son diferencias sensibles que advierten su presencia en las dos clases en que el manglar se encuentra más disperso o en contacto con las arenas y el *Apicum*. Espectralmente, la señal registrada en las bandas TM3, TM4 y TM5, aumenta en el periodo de la primavera para las áreas con vegetación en función del balance del contenido de aire y agua en el interior de las hojas permitiendo radiancias más intensas. Hay que considerar en esta afirmación la declinación solar del ciclo estacional que contribuye también para ese efecto; cabe entre tanto observar que la tendencia general del perfil radiometríco es posible obtener oscilaciones localizadas que pueden caracterizar la respuesta de la predominancia de una de las especies.

Tabla 1. Resumen de los datos de cálculo del área mapeada por los métodos analógico y digital para los diferentes patrones identificados en la variedad de asociaciones por densidad y frecuencia de individuos en Río Baguacú

Clase	Color	Unidad	Interp. visual (Aerofoto)	Digital MAXVER BRUTO-85	Digital MAXVER BRUTO-86	Visual x BRUTO-85	Visual x BRUTO-86	BRUTO-86 x BRUTO-86
Manglar denso alto	Azul	km^2	1.50	0.998	0.974	-0.502	-0.526	-0.024
		%	64.10	39.100	38.200	-50.300	-54.000	-2.500
Manglar denso bajo	Rojo	km^2	0.58	1.073	0.861	+0.493	+0.281	-2.212
		%	24.80	42.000	33.700	+85.000	+48.400	-24.600
Manglar disperso bajo	Verde	km^2	0.24	0.441	0.576	+0.201	+0.327	+0.126
		%	10.20	17.300	22.200	+83.700	+136.200	+28.600
Apicum	Amarillo	km^2	0.02	0.040	0.151	+0.020-	+0.131	+0.111
		%	0.90	1.600	5.900	+100	+655.000	+277.500
TOTAL		km^2	2.34	2.552	2.553	+0.212	+0.213	+0.001
		%	100	100	100	+9.100	+9.100	0.000

En la clase de manglar denso alto la predominancia verificada fue la de *Rhizophora* para más de 90%, habiendo junto al límite interno variaciones que incorporan en algunos casos hasta 70% de *Laguncularia*. Por la posición del perfil y parcelas el hecho se comprueba, que el mismo a veces representa valores de interfaces en la zona transicional. Es innegable, inclusive apoyando las consideraciones por las curvas radiometrícas de la figura 3, que la señal mas intensa es característica de la especie *Rhizophora*, en general predominante en la clase de manglar denso alto representado en azul en la figura 4. Le sigue en secuencia el manglar denso bajo con la predominancia de *Laguncularia*, se destaca espectralmente en la clase siguiente por su discriminación radiometríca principalmente en el intervalo del infrarrojo próximo, donde las curvas radiométricas se alejan del valor de radiancia entre las tres especies consideradas.

En el sector de menor concentración de la biomasa considerada como tercera representación de la leyenda el manglar disperso bajo en verde hay una mezcla de las dos especies principales a veces incluyendo ejemplares aislados de *Avicennia*, lo que corresponde a la disminución de la radiancia en la condición exclusiva de las tres especies, pudiendo existir en diferentes substratos un resultado de interacción múltiple. Las especies instaladas en el substrato arenoso pueden tener la potencialidad de las radiaciones reflejadas acrecentando la radiancia final registrada por el sensor. Conforme el levantamiento local con radiómetro portátil (Fig. 3), lo que puede representar un cierto nivel de confusión.

La precisión alcanzada por el método descrito en Herz (1988) ofrece al investigador componentes indispensables para el planeamiento integrado de los sistemas costeros tropicales indicando la distribución geográfica de diferentes patrones de productividad de material fragmentado introducido por los manglares en los estuarios tropicales. Este levantamiento, utilizando técnicas de sensoriamiento remoto, cuando se complementa con las demás investigaciones de superficie, integrando datos físicos, químicos, geológicos y biológicos permitirá conocer la dinámica de la distribución de las poblaciones de organismos marinos que dependen de las propiedades del ambiente estuarino. La masa de partículas y compuestos orgánicos transportados por las corrientes, monitoreada por las técnicas de la oceanografía, constituirá depósitos diversificados para el desarrollo de la cadena alimenticia apropiada a la sustentación de especies de crustáceos, moluscos y peces de importancia como recursos renovables costeros.

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Mangrove Physiology: the Challenge of Salt, Heat, and Light Stress Under Recurrent Flooding

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Abstract

Mangroves have developed a wide array of morphological and physiological traits that deal successfully with salt stress and oxygen demands for root function. Water uptake from an environment enriched in highly permeable ions, mainly chloride and sodium, require the capability of excluding ions at the root level, get rid of the excess of salts taken up, or develop compartments where large amounts of salt can be accumulated without the risk of damaging the photosynthetic apparatus. These alternatives have significant physiological costs associated. Energy demands are particularly strong for maintaining ion selectivity (high K^+/Na^+ ratios relative to soil water) and membrane stability. These processes depend on the supply of carbohydrates from the leaf canopy as energy source, and the supply of oxygen for the respiratory chain to operate efficiently. Development of aerenchyma-rich roots has been shown to be essential for successful growth of mangroves. Salt excretion is efficient in maintaining a salt balance at the leaf level, but requires large amounts of photosynthetic energy for the excretory tissues to operate continuously. The presence of hypodermises, or water parenchyma usually found in mangrove leaves, has been associated with the differential accumulation of sodium and chloride at the leaf level. The operation of salt accumulating compartments demands photosynthates both for structure development and for pumping ions into the specialized tissues.

Compartmentalization is crucial for separating salt sensitive enzymes in the cytoplasm and cell organelles from the incoming salts in the transpiratory stream. Maintenance of appropriate hydration of the cytoplasm and organelles appears to be related to the accumulation of “compatible solutes”, particularly organic nitrogen compounds and cyclitols.

Restrictions of water uptake of mangrove trees from a highly saline substrate reduce the evaporative cooling of the photosynthetic surfaces. This is potentially harmful in tropical and subtropical, high temperature, high irradiation, environments because it may lead to photoinhibition and heat damage of the photosynthetic machinery. Mechanisms avoiding these damages are mostly related with reduction of incident radiation (leaf inclination and size) and perhaps buffering of thermal changes (leaf succulence). In fact, within the same species leaf size decreases with increasing aridity and/or salinity, but also nutrient availability, of the coastal environment.

Mangal communities generally show a well defined zonation, with particular species substituting one another along gradients of salinity, and duration of tidal flooding. This zonation results from the competitive exclusion of species differing in their tolerance to salinity and/or anoxic soils. Zonation,

therefore, is highly dependent on the general climatic conditions where the mangrove forests are found. In relatively arid coastal environments salinity increases landwards, resulting in the formation of areas where salinity levels change strongly during the rainy and dry seasons, avoiding permanent establishment of higher plants. In humid coastal areas, on the contrary, salinity decreases landwards, therefore mangrove forests change slowly into brackish and swampy communities, where many non-salt tolerant tree species can develop successfully.

Resumen

Los manglares han desarrollado una amplia organización de rasgos morfológicos y fisiológicos que tratan exitosamente con el estrés de sal y las demandas de oxígeno para las funciones de las raíces. La toma de agua desde un ambiente enriquecido en iones altamente permeables, principalmente cloruros y sodio, requieren la capacidad de exclusión a nivel de las raíces, deshacerse del exceso de sales absorbidas, o desarrolla compartimentos donde grandes cantidades de sal pueden ser acumuladas sin el riesgo de dañar el aparato fotosintético. Estas alternativas tienen asociado un significativo costo fisiológico. La demanda de energía son particularmente fuertes para el mantenimiento de la selectividad iónica (alta relación de K^+/Na^+ relativa al agua del suelo) y estabilidad de la membrana. Estos procesos dependen del suministro de carbohidratos desde las hojas del dosel como fuente de energía, y el suministro de oxígeno para la cadena respiratoria operar eficientemente. El desarrollo de raíces ricas en aerénquimas ha demostrado ser esencial para el exitoso crecimiento de los manglares. La excreción de sal es eficiente en el mantenimiento del balance de sal en el nivel de la hoja, pero requiere de grandes cantidades de energía fotosintética para que los tejidos excretores operen continuamente. La presencia de hipodermis o parénquima de agua usualmente encontrado en las hojas del manglar, ha sido asociado con la acumulación diferencial de sodio y cloruros a nivel de la hoja. La operación de acumulando sal, los compartimentos demandan fotosíntesis tanto para las estructuras de desarrollo y para bombeo de iones dentro de los tejidos especializados.

La compartimentalización es crucial para las enzimas sensitivas a la separación de la sal en el citoplasma y los organelos celulares que entran en la corriente respiratoria. El mantenimiento de hidratación apropiada del citoplasma y organelos parece estar relacionada a la acumulación de “solutos compatibles” particularmente compuestos de nitrógeno orgánico y ciclitoles.

Las restricciones en el consumo de agua de los árboles de manglar de un sustrato altamente salino, reduce el enfriamiento evaporítico de las superficies fotosintéticas. Esto es particularmente dañino en ambientes tropicales y subtropicales, de alta temperatura y elevada radiación solar debido a que pueden resultar en fotoinhibición y el calor daña la maquinaria fotosintética. Los mecanismos que evitan estos daños están principalmente relacionados con la reducción de radiación incidental (inclinación y tamaño de la hoja) y quizás el amortiguamiento de los cambios climáticos (hojas suculentas). En efecto, dentro de las mismas especies el tamaño de la hoja decrece con el incremento de la aridez y/o salinidad, pero también la disponibilidad de nutrientes del ambiente costero. Las comunidades de manglar generalmente muestran una zonación bien definida, con especies particulares sustituyendo una a la otra a lo largo de de los gradientes de salinidad y duración de la inundación mareal. Ésta zonación Resulta de la exclusión competitiva de las especies difiriendo en su tolerancia a la salinidad y/o suelos anóxicos. Por lo tanto, la zonación es altamente dependiente de las condiciones climáticas generales donde los bosques de manglar se encuentran. En ambientes costeros relativamente áridos, la salinidad incrementa hacia el continente, resultando en la formación de áreas donde los niveles de salinidad varíian fuertemente entre las estaciones de lluvias y secas, evitando establecimientos permanentes de plantas superiores. En áreas costeras húmedas, por el contrario, la salinidad disminuye hacia el continente, por lo tanto los bosques de manglar cambian lentamente en comunidades salobres a pantanosas, donde muchas especies de árboles no tolerantes a la sal pueden desarrollarse exitosamente..

Introduction

True mangroves are “tropical trees restricted to intertidal and adjacent communities” (Tomlinson, 1986), growing in saline, generally anoxic soils, under climatic conditions characterized by a combination of high temperature and irradiance (Stewart and Popp, 1987). They are typical halophytes developing up to reproductive stage in sea water, accumulating large amounts of sodium chloride in their cell vacuoles (Walter and Steiner, 1936). Salt, water, and energy balances, therefore, constitute simultaneous constraints for mangrove photosynthetic productivity. These constraints acquire particular significance in mangal habitats where supply of fresh water through rainfall or riverine flow is severely restricted during periods of more than a month duration. An additional factor of stress which has received comparatively little attention is the role

of nutrient supply in modulating the responses of mangroves to environmental stresses (Boto, 1983). In a modeling study Lugo *et al*. (1976) concluded that nutrient supply to mangrove ecosystems is predominantly associated with terrestrial drainage, which is nutrient rich compared to sea water. Development of management strategies of natural and man-made mangrove ecosystems has to be based on an integrative approach, considering the multivariate interactions of the above factors.

In this chapter I will focuses on the ecophysiology of photosynthesis and water relations of true mangroves, that is, plants which can complete their life cycle in sea water, and require a certain salinity level for optimum development. The responses of the photosynthetic apparatus to water logging and salinity under natural conditions will be used as a basis for understanding structure and species composition of mangrove communities in arid and humid coastal environments. With this approach I am tacitly assuming that differences in fresh water availability will be closely associated with nutrient inputs from the land. The paper includes most relevant papers on physiology of mangroves; however, it does not provide a full literature list of all recently papers published on the subject. There are a number of recent reviews and books on the ecology and physiology of mangroves which are highly recommendable for the interested readers. Tomlinson (1986) wrote an authoritative account on mangroves which clarifies their botanical status and biogeography. A book covering most relevant aspects of ecology and productivity of mangroves was published by Hutchings and Saenger (1987). It includes a comprehensive literature review and constitute a very good guide for the work carried out in Australian mangroves. Two excellent reviews dealing specifically with ecophysiological aspects are those of Stewart and Popp (1987) and Ball (1988a).

Environmental Constraints and Ecophysiological Adaptations

Understanding of variations in structure, and distribution of species in mangrove communities requires a precise knowledge of the fresh water sources from terrestrial drainage. Walter and Steiner (1936) differentiated among coastal, estuarine, and coral reefs mangrove communities. Lugo and Snedaker (1974) proposed a more detailed classification of mangrove ecosystems including: **a)** riverine mangroves growing on river floodplains where lateral flow of water of low salinity predominates; **b)** basin mangroves growing in depressions where water flows are slow and the seasonal vertical flow predominate over the lateral flow; **c)** fringe mangroves growing at the edge of the sea or other water bodies directly exposed to vertical water fluctuations; and **d)** mangrove “islands” which may occur at the sea as overwash island or inland as mangrove “hammocks”. Basically these types are differentiated according to the level of salinity stress and the availability of nutrients. In this respect, riverine (or estuarine) mangroves are the most complex because of the irregular distribution of saline and fresh water. Mangrove communities growing on coral reefs are always protected against wave impacts. The mangrove trees grow directly on top of the coral rock above the sea water level during low tides. These communities generally do not show a clear structural pattern.

Coastal mangroves (fringe mangroves) may be found growing in arid or wet coast lines, differing in the amount of drainage water available and seasonally of rainfall (Walter 1977). In wet coast lines salinity decreases landwards, so that maximum salinity is found at the fringe itself towards the sea side (36 ‰ salinity, about 1000 mmol/kg osmotic active solutes, or approximately 25 bars of osmotic pressure at 25 ^{o}C). Landwards this level is reduced during the rainy season as a consequence of rainfall *in situ* or freshwater drainage from land. In the back of the mangrove community, salinity can fall to zero, but daily and seasonal oscillations of salinity can be observed according to the tidal regime and the distribution of rainfall. In arid coasts (or with highly seasonal rainfall) on the contrary, salinity increases landwards, because in the coastal areas covered by sea water at high tide the soil solution is concentrated during low tide creating conditions of hypersalinity. Behind the mangrove community areas of extreme salinity oscillations during the year are created, low salinity at the soil surface during the rainy season, and almost salt saturated soil solution during the dry season. These areas are hostile to any kind of vegetation and constitute vegetation-less salt flats in many coastal areas in the tropics (Walter and Steiner, 1936; Walter 1977; Medina *et al*., 1989). These two contrasting hydrological regimes determine community structure according to salinity tolerance in dry coastal areas, and capability of fast resource utilization in wet coasts. In both cases salinity stress and nutrient availability can be detected trough the analysis of osmolality and mineral composition of mangrove tissues.

There are about 38 species considered as true mangroves because of their distribution and apparent salinity requirements. These species are distributed in only 8 families and most of the

species are confined to the Australasian tropics (Tomlinson, 1986) (Table 1). The following genera of mangroves present secretory structures in the leaves that in some cases have been shown to secrete salts, mainly sodium chloride: *Aegialitis*, *Aegiceras, Avicennia, Laguncularia* and *Sonneratia*. From these species most studies have been conducted in species of the genus *Avicennia*.

Flooding and Gaseous Exchange at the Root Level

As plant communities living in the intertidal zone mangroves are frequently flooded. This causes a reduction in the oxygen partial pressure at the root level which might impair the processes of ion uptake due to the disturbance of the respiratory metabolism in root cells. Most mangrove species develop strongly aerenchymatic aerial roots, which play a role in the oxygenation of underground root tissues, and provide ways for expelling gases originated in aerobic or anaerobic respiratory processes (Table 2). Three genera of mangroves, however, do not develop aerial roots, and they are presumably less resistant to flooding as may be inferred from their distribution in mangrove communities (Tomlinson 1986). The anatomical description of the aerial roots of the mangroves is outside of the scope of this chapter, and the reader is referred to the excellent accounts published by Gill and Tomlinson (1971), and Tomlinson (1986).

Diffusion of gases through the lenticels and the highly developed aerenchyma of the underground roots is probably a most important mechanism for supplying growing root tips with oxygen and to get rid of the excess of CO_2 produced by root respiration. In addition, diurnal variations in internal gas pressure in aerial roots have been shown to play a role in gas exchange, particularly in aerial roots under a daily flooding regime (Scholander *et al*., 1955). When pneumatophores of *Avicenia germinans* are completely covered by water during high tide, the internal gas pressure decreases rapidly, as a consequence of the fast consumption of oxygen in the respiration of root cells, and the relatively high solubility in water of the resulting CO_2. The underpressure developed in this process is about 0.5 bars, but the water can not enter the pneumatophores, because the hydrostatic pressure is not enough to overcome the surface tension at this level. At low tide, air penetrates easily through the pores providing oxygen to the respiring cells. This mechanism is not operative, or is not so effective, in aerial roots not submitted to flooding. Mangrove roots in these areas, are always relatively superficial, therefore, aereation is probably guaranteed by diffusion (Scholander *et al*., 1955; Tomlinson 1986).

Table 1. Families and genera of true mangroves based on their distribution and apparent requirements of saline environments (from Tomlinson 1986)

Family and Genera		No. of species	American species
Anniaceae			
	Avicennia	9	*A. germinans* *A. schaueriana*
Combretaceae			
	Laguncularia	1	*L. racemosa*
	Lumnitzera	3	
	Conocarpus	1	*C. erectus*
Meliaceae			
	Xylocarpus	3	
Myrsinaceae			
	Aegiceras	2	
Pellicieraceae			
	Pelliciera	1	*P. rhizophoreae*
Plumbaginaceae			
	Aegialitis	2	
Rhizophoraceae			
	Bruguiera	6	
	Ceriops	2	
	Kandelia	1	
	Rhizophora	3	*R. mangle* *R. racemosa*
Sonneratiaceae			
	Sonneratia	5	
Total: 13 genera		**39 species**	**7 American species**

Table 2. Types of aerial root systems in strict mangroves (Gill and Tomlinson 1971)

Morphological adaptations of the root system to flooding	Genera of mangroves
Stilt roots	*Rhizophora, Bruguiera, Ceriops, Avicennia* (sporadically)
Pneumatophores	*Avicennia, Sonneratia, Laguncularia* (facultative)
Root knees	*Bruguiera* and *Ceriops, Lumnitzera, Xylocarpus*
Plank roots	*Xylocarpus*
Fluted buttresses	*Pelliciera*
Without special aerial roots	*Aegiceras, Aegialitis, Kandelia*

In *Avicenia marina* the pneumatophores present little resistance to oxygen diffusion, the structure of the pneumatophores represent a compromise between the needs for expedite gas exchange and the need to exclude water (Curran, 1985). In the horizontal roots oxygen can diffuse freely and differences in oxygen concentration along these roots are unlikely in healthy roots.

Avicenia germinans can oxidize the substrate surrounding its roots in considerable extension, and when air supply trough the pneumatophores is impeded by flooding the reduction of the rhizosphere is rapid and reach levels similar to unrooted soils (Thibodeau and Nickerson, 1986). Roots of *Rhizophora mangle*, however, although developing a thick aerenchyma when underground (Gill and Tomlinson, 1971) are not able to oxidize their rhizosphere to a similar extent. These differences are probably associated with the distribution of these two species in natural conditions. *Avicennia* spp grow quite actively in heavy soils which may be flooded for prolonged periods, while *Rhizophora* spp occupies generally areas which are flooded periodically, but with continuous movement of water, probably facilitating aeration of the upper soil layers.

In six months old seedlings of *Avicenia germinans* flooding can increase mortality, and induces the activity of alcohol dehydrogenase (Steward and Popp, 1987). This biochemical response is of general occurrence in higher plants submitted to flooding. In adult plants this effect is probably of lesser importance because anaerobiosis is prevented by the development of pneumatophores. This increase in the activity of ADH can be counteracted by the addition of NaCl, but the nature of the effect is not well understood (Steward and Popp, 1987).

Salinity Stress and Osmotic Relationships in Mangroves

Growth of mangrove species under different salinities

Mangroves can be found in nature growing in a large range of salinities. It appears, however, that there exists a differentiation in the salinity tolerance at least of the adult plants. In South America, *Rhizophora mangle* and Laguncularia racemosa are frequently found growing best at salinities near sea water level or below, while *Avicennia germinans* is found growing at salinities near sea water and above (Lugo and Snedaker, 1974; Cintrón *et al*., 1978). Frequently the occurrence of zonation of mangrove species along salinity gradients is obscured by the complexities of the hydrological regime, particularly in estuarine mangroves. The analyses of leaf sap osmolality indicate the long-term salinity conditions of the species occurring in mangrove communities (Walter and Steiner 1936). The general differences in salinity of the preferred sites of occurrence of mangrove and some associated mangal species was shown by Harris (1934) in Florida through the analysis of leaf saps (Fig. 1). *Avicennia germinans* has the highest average value (38.5 bars) and can reach values above 50 bars. *Rhizophora mangle* and *Laguncularia racemosa* are similar in the distribution of their osmotic pressure values. The associate species *Conocarpus erectus* and *Acrostichum aureum* show average values that indicate clearly their occurrence in low salinity sites. These results correspond to the salinity tolerance of adult plants.

On the other hand, growth experiments conducted with seedlings during periods varying from a few weeks to several months indicate that optimum growth of several mangrove species is reached at salinities well below that of sea water. In *Rhizophora mangle* Pannier (1959) measured a maximum production of leaves and roots in 6 months old seedlings at 25% of sea water without added nutrients; similar growth response to salinity, but with added nutrients, was reported for 12 months old seedlings of *R. stylosa* (Clough, 1984). For *Avicennia marina* Downton (1982) recorded maximum growth in 11 months old seedlings growing at salinities equivalent to 25 to 50% sea water, while Burchett et al. (1984) and Clough (1984) for the same species recorded optimal growth at 25% sea water. Lower salinities for optimum growth

Figure 1. Box plots of the osmotic pressures of leaf sap measured in true mangrove and associated species in a range of habitats in Florida (with data from Harris 1934). The osmotic pressures were measured with a crioscopic method.

have been reported in Africa for *Avicennia marina* (Naidoo, 1987) and *Bruguiera gymnorrhyza* (Naidoo, 1990). Increase in growth induced by salinity around 40% of sea water has been recently confirmed for *Rhizophora mangle* (Werner and Stelzer, 1990). The improvement in organic matter production induced by NaCl reflects the halophytic character of true mangroves, and is certainly associated with improved water relations (Werner and Stelzer, 1990).

Ball (1988a) measured maximum growth rates of *Avicennia marina* at 50% sea water, while *Aegiceras corniculatum* reached maximum growth at 10% sea water (Clarke and Hannon, 1970). However, when the seedlings are mature and not dependent on the reserves provided by the mother tree, growth decreases with salinity from 50 to 500 mmol m^{-3}, *A. corniculatum* being more sensitive than *A. marina* (Ball, 1988b).

Salt balance

Roots developing in an aqueous high saline environment absorb salts readily, which are transported to the leaves in the transpiration stream. Ions such as Cl^- and Na^+ are highly permeable in most root cells of higher plants. The concentration of sodium chloride in the xylem sap has been used as an indicator of the degree of exclusion of salts at the root level. Scholander *et al*. (1962) showed that mangrove species with salt-secreting glands in their leaves have usually higher NaCl concentrations in the xylem sap than those without those structures (Table 3).

In all cases NaCl concentration in xylem sap is well below that in sea water (36‰). That means that if all the species are absorbing water from the sea, NaCl is being efficiently rejected at the root level. There is no indication in the original paper of Scholander *et al*. (1962) that the root systems of all the species investigated were absorbing water from sources of similar salinity.

The actual Cl^- concentration in the xylem sap varies with concentration of the bathing solution of the roots. It was proposed that those species with the lowest Cl^- concentrations in the xylem sap were those which act as salt excluders at the root level (Scholander *et al*., 1962), while the species with higher concentration were those which have the capability of secreting salt by special salt glands in the leaves. It is clear, however, that irrespective of the actual Cl^- concentration in the xylem sap, transpiring mangrove leaves do accumulate large amounts of Cl^- and Na^+ in their leaves (Popp, 1984). The degree of salt exclusion may vary from species to species, and also in relation to the actual saline concentration of soil solution in which the roots are growing.

Table 3. Concentration of salt in xylem sap (Scholander *et al*. 1962)

	NaCl [g/l]	Leaves with salt secreting glands
Rhizophora mucronata	0.2-0.4	-
Sonneratia alba	0.2-0.5	-
Bruguiera cf. *exaristata*	0.3-0.5	-
Aegiceras corniculatum	0.8-2.8	+
Avicennia marina	1.2-4.0	+
Aegialitis annulata	3.6-8.0	+

The accumulation of salt in the leaves is also a function of leaf age. Old leaves have always higher salt content in their sap. This accumulation tends to be compensated by an increase in leaf succulence (water content per unit leaf area). The increase in leaf succulence with salinity of the growth medium has been shown under natural conditions in *Laguncularia racemosa* (Biebl and Kinzel 1965), and *Rhizophora mangle* (Camillieri and Ribi 1983), and under cultivated conditions in *Rhizophora mangle* (Werner and Stelzer 1990), *Rhizophora stylosa* and *Avicennia marina* (Clough 1984). The increase in succulence with leaf age has been also shown by Atkinson *et al*., 1967 in *Rhizophora mucronata*, and in this species it correlated with increases in Na^+ and Cl^- contents, both on a whole leaf basis and on a leaf water basis. The studies in *Laguncularia racemosa* leaves of increasing age showed that the pro-gressive increase in Na^+ and Cl^- concentration per unit leaf area was almost quantitatively compensated by a similar increase in the leaf water content. The result is that the concentrations of those ions per unit of leaf water remain almost constant (Fig. 2).

The difference in membrane permeability reflected in the salt concentration of the xylem sap of mangrove species with and without active salt secreting glands is observed when seedlings of those species are cultivated under the same salinity conditions. *Avicennia marina* accumulates more Na^+ and Cl^- ions than *Rhizophora stylosa* growing in nutrient solutions with exactly the same salt composition (Clough, 1984). With higher salt concentrations of the solution the Na^+ content of *Avicennia marina* increased continuously, while the K^+ content either remained constant or increased slightly. In *Rhizophora stylosa* to the contrary, Na^+ content stabilized after 25% of sea water but K^+ concentration decreased steadily. These differences in ion absorption might be associated with the salinity tolerance of these species under natural conditions. The differences in K^+ uptake relative to Na^+ uptake at increasing levels of salinity can be appropriately expressed as selectivity ratios (Pitman, 1965). This ratio is

Figure 2. Variations in the concentration of Cl^- per unit leaf area or per unit leaf water, and the content of cations in leaf sap expressed per unit leaf area. On an area basis the amount of Cl^- and Na^+ is showed to increase with the degree of succulence of the leaves. That is not the case for K^+ and Ca_2^+. Notice that the Cl^- concentration per unit leaf water remains constant indicating that the ion uptake is accompanied by water uptake (data from Biebl and Kinzel, 1965).

calculated from the K^+/Na^+ ratio in the plant tissue divided by the K^+/Na^+ ratio in the nutrient solution (Table 4).

The strong preference for K^+ absorption in the presence of large amounts of Na^+ was demonstrated by Rains and Epstein (1967) in *Avicennia marina*. In this species the operation of two absorption mechanisms with different affinities for K^+ was demonstrated. These two mechanisms are of general occurrence in higher plants. In *Avicennia marina* the Michaelis

constant for the mechanism 1 was 0.2 mM, or about 10 times higher than the values recorded for other species, although it has the same specificity (Rains and Epstein, 1967). At 1 mM K^+ and 0.5 mM Ca^{2+} in the external solution the absorption of K^+ was interfered by the presence of Na^+ only when the Na^+/K^+ ratio was above 100. The mechanism 2 however, operating at K^+ concentrations above 10 mM K^+ and 10 mM Ca^{2+} (at a similar level as in sea water), the K^+ absorption was not interfered by concentrations of Na^+ as high as 500 mM, therefore showing a much higher specificity than that of the mechanism 2 described for non-halophytes. In sea water K^+ concentration is around 12 mM, therefore the insensitivity of mechanism 2 to high Na concentrations is of high ecological significance. The operation of this mechanism 2 with high preference for K^+ does not impede the uptake of Na^+ but raises the K^+/Na^+ ratio from about 1/40 in sea water, to 1/7 in the leaf tissues.

The operation of similar mechanisms at the cellular level in other mangrove species has not been documented yet, although such studies may provide a basic physiological explanation for the zonation of mangroves. Indirect evidences for differential ion permeability in mangroves species with and without salt-excreting glands in their leaves may be implied from studies of the composition of the xylem sap. Atkinson *et al*. (1967) measured the transport of sodium chloride through transpiration in the xylem sap of intact trees of *Rhizophora mucronata* and *Aegialitis annulata* growing under natural conditions in northern Australia. The concentration of Cl^- in the xylem sap was smaller in *Rhizophora mucronata* compared to that of *Aegialitis annulata* (17 vs 85-122 mmol Cl^-/l, res-pectively). In a sequence of leaf pairs of increasing age of *Rhizophora mucronata* the total Na^+ and Cl^- contents per leaf increased markedly with age, as a result of the accumulation of about 17 mol of Cl^- per leaf per day. The K^+ content however, decreased markedly. The concentration of Na^+ and Cl^- on a leaf water basis remained nearly constant (515-522 mmol Cl^-/l leaf sap), indicating that the leaf water content also increased. In *Aegialitis annulata*, on the contrary, both Na^+ and Cl^- content diminished with increasing leaf age, although the daily input of Cl^- to the leaf was about 100 mol per day. This results from the salt secreting activity of glands in the adaxial leaf surface. The secretion was mainly NaCl but it contained also a small fraction of K. In the intact tree the secretion takes place mainly during the day time.

Scholander *et al.* (1962) measured the activity of salt-secreting glands in several mangroves species. They covered mangrove leaves with oil drops to avoid drying of the secreted solution. The solution accumulated under the oil drop and could be collected with microburettes for chemical analyses. It was found that the daily course of salt excretion was very pronounced during the day in *Aegialitis annulata*, less pronounced in *Aegiceras corniculatum* and absent in *Avicennia marina*. For the latter species the same lack of a day-night pattern of secretion was reported by Waisel *et al*. (1986). Nearly 90% of the secreted salts was NaCl, and only 4% of the Cl^- was matched by K^+. The concentration of NaCl in the secretion varied between 1.8 and 4.8% in *Aegialitis annulata* and between 0.9 and 2.9% in *Aegiceras corniculatum*, while in *Avicennia marina* it reached 4.1%. Similar results for secretion composition have been reported by Ball (1988) for *Aegiceras corniculatum* and *Avicennia marina*. In these species the rate of secretion increases with the salinity of the nutrient solution. The highest values of Cl^- secretion were 343 nmol Cl m^{-2} s^{-1} for *Aegiceras corniculatum* (at 500 mol m^{-3} NaCl in the solution and 6 mb leaf-air vapor pressure deficit), and 264 mmol Cl^- m^{-2} s^{-1} for *Avicennia marina* (500 $molm^{-3}$ NaCl and 24 mb vpd). These rates were measured in whole seedlings. The salt balance of these two species shows some interesting patterns (Table 5). In *Aegiceras corniculatum* the species with lower salt tolerance, the net water use efficiency is higher at 50 mol m-3 NaCl (approximately 10% sea water), while in *Avicennia marina* the highest value is reached at 500 mol m^{-3} NaCl. Salt uptake increases with salinity in nutrient solution in both species, but the efficiency of salt secretion, both at the whole plant and at the leaf level, is quite higher in *Aegiceras corniculatum* compared to *Avicennia marina*.

In whole seedlings of *Avicennia marina* the rate of salt excretion is larger during the night and increases with salinity of the root-bathing solution (Drennan and Pammeter, 1982). Concentration of Na+ in xylem sap and roots increased linearly with salinity of the nutrient solution. However, in the leaves the concentration reached a plateau at about 50% of sea water, amounting to 1.5 mmol Na per g dry weight.

Under hypersaline conditions in nature Waisel *et al*. (1986) showed that for the salt balance of the salt-excreting species *Avicennia marina* the most important process is the rejection of salt at the root level (about 80%). The measurements were performed on trees of this species growing under natural conditions in a site at the Red Sea characterized by very high salinities (0.70 M ≈ 41 ‰). It was calculated that 0.77 mmol NaCl per g dry weight per day were being transported to the leaf, instead of the 3.57 that would be expected from the concentration of the Red Sea water and the transpiration rates measured

Table 4. Selectivity ratios ($S_{K.Na}$= (K_t/Na_t)/(K_c/Na_c) in leaf and root tissues of *Avicennia marina* and *Rhizophora stylosa* cultivated under different salinities (from Clough, 1984)

Species and Tissue		$S_{K \cdot Na}$ % sea water				
		0	25	50	65	100
A. marina	leaves	0.1	10.1	12.1	17.0	11.1
	roots	0.2	14.6	16.4	18.7	18.1
R. stylosa	leaves	0.2	11.1	9.4	10.3	7.0
	roots	0.1	2.1	4.2	4.4	3.2

Table 5. Salt balance of seedling of salt excreting species *Aegiceras corniculatum* and *Avicennia marina* (from Ball, 1988)

	A. cornuculatum			*A. marina*		
Growth salinity (mol m^{-3} NaCl)	50	250	500	50	250	500
Net water use efficiency (mg dr.wt. mol^{-3} water)	73.8	45.0	41.4	81.0	79.2	91.8
Net Cl^{-1} uptake (μmol Cl^{-1} mol^{-1} water)						
total uptake	91.2	144.4	195.3	102.1	150.9	283.3
secretion	28.7	85.6	157.0	13.4	64.2	94.8
%	31	59	80	13	43	33
Salt balance at the leaf level						
total Cl^- flow to leaf	54.8	111.6	173.9	47.6	98.8	142.1
%	52	77	90	28	65	67

(a reduction of about 80%). This exclusion may have had taken place through the process of ultrafiltration as proposed by Scholander (1968). The amount of salt excretion reached 0.302 mmol NaCl per g dry weight per 24 hours, corresponding to about 40% of the actual amount transported by the transpiration stream to the leaves. The conclusion is that salt secretion in this species, at the salinities of the waters where it is growing, is not sufficient to account for the relative constancy of the salt content of the leaves. Another important role of secretion discussed by the authors is the selective character of the secretion. Almost all the salts secreted is NaCl, this could contribute to maintain a favorable K^+/Na^+ ratio in the leaf cells. This may allow the cells to metabolize normally in spite of the high total salt content.

With excised leaves of *A. marina* Boon and Allaway (1986) measured rates of excretion of Cl^- of up to 3.5 mol m^{-2} s^{-1} when the petioles of the excised leaves were immersed in concentrated solutions of NaCl. The maximum rates of Cl^- secretion were reached at an external concentration of 1 M NaCl. The rate of secretion was reduced at very high concentrations (>2.0 M). These rates are one order of magnitude higher than those measured in intact plants in the field.

The experiments discussed in this section indicate that the exclusion of salts at the root level is the most important process for reduction of salt uptake for all mangrove species, both with and without salt-secreting glands in the leaves. In all mangrove species studied the salt concentration in the xylem sap increases linearly with the concentration of the solution bathing the roots. The salt-secreting mangroves have always higher salt concentrations in their xylem sap, but the rate of salt accumulation in the leaves is partially reduced by the activity of the salt-secreting glands. Finally, the salt tolerance at high levels of salinity is apparently associated with the capability of maintaining a high K^+/Na^+ ratio in the plant tissues.

Compartmentation of salt

The relative fast rates of salt accumulation due to salt transport in the transpiration stream leads to the accumulation of large amounts of salts in the leaf tissues of mangrove species (Steward and Popp, 1987). However, when transpiration rates are measured and the amount of salt that should be delivered to the leaves is calculated, the actual amount found in the leaves is considerably smaller. The missing salt is

probably removed during transportation through the stem xylem and accumulated in stem parenchyma, or retranslocated from the leaves. Stem tissues can have similar salt concentrations as the leaves, at least in the case of *Avicennia germinans* (Steward and Popp, 1987).

The salt reaching the leaves is incorporated into the vacuoles to a great extent as is usual in halophytes (Harvey *et al*., 1981). The distribution within the leaves, however, can be highly asymmetric. Practically all mangrove species are characterized by the development of a hypodermic in the adaxial side of the leaf (Walter and Steiner, 1936; Tomlinson 1986). This hypodermics is hyaline, and it thickness increases with substrate salinity. Therefore it has been proposed that it may act as a salt accumulating tissue. Walter and Steiner (1936) showed the accumulation of salt in this tissue using histochemical techniques. More recently, Werner and Stelzer (1990) used energy-dispersive X-ray microprobe analysis to measure the distribution of sodium chloride within leaf tissues. It was shown that the concentration of Na^+ was lowest in the mesophyll and epidermises of leaves from seedlings of *Rhizophora mangle* grown in salt solutions containing 200 mol m^{-3} NaCl (Fig. 3). The distribution of K^+ was more homogeneous in the different leaf tissues, but the control had clearly higher K^+ contents than the salt treated plants. How this discrimination takes place is probably explained by the pathways of transpiration water.

Cytoplasm-Vacuole Osmotic Relationships: The Role of Organic Osmolites

The large amounts of salt accumulated mainly in the leaf tissues, but also in stems and roots, create special osmotic conditions at the cellular level. Probably most of these salts are accumulated in the vacuoles, maintaining the salt sensitive enzymes in the cytoplasm separated from high saline concentrations. This leads to a reduction of the water potential of the cytoplasm, either through dehydration (decrease in matrix potential) or by the accumulation of organic osmolites, which do not impair enzymatic functioning even at relatively high concentrations (compatible solutes). A number of these organic osmolites, increasingly synthesized at high salinities, have been described in mangroves (Popp 1984b, Popp *et al*., 1984). Several cyclitols, nitrogen compounds including aminoacids, have been described and occur in a wide range of concentrations (Table 6). The role of these compatible solutes is probably the maintenance of an appropriate degree of cytoplasm hydration for enzyme function.

Figure 3. Differences in K^+ and Na^+ concentration in leaf tissues of *Rhizophora mangle* grown in salt-free nutrient solution and a nutrient solution with 200 mol m^{-3} NaCl. Measurements were conducted in fractured leaves using X-ray microprobe analysis (data from Werner and Stelzer, 1990).

Table 6. Concentration of organic solutes of low molecular weight in mangroves (from Stewart and Popp 1987)

Species	Solute	mol m^{-3} tissue water
Aegialitis annulata	pinitol chiroinositol proline	105 150 28
Aegiceras corniculatum	mannitol	230
Avicennia marina	glicin betaine	61
Bruguiera gymnorrhiza	pinitol	80
Ceriops tagal	pinitol	150
Lumnitzera littorea	mannitol	110
Rhizophora apiculata	pinitol	220
Sonneratia alba	mannitol	200
Xylocarpus mekongensis	proline	57

Photosynthesis and Water Relations of Mangroves

Mangroves grow in environments characterized by high irradiation, and, at least in tropical latitudes, homogeneous and high temperatures throughout the year. Under these conditions the demands for water to cover daily transpirational losses are very high. Water uptake from a saline substrate imposes severe osmotic restrictions, and as discussed before, leads to strong accumulation of salt in the transpiring surfaces. Transpiration rates of mangrove species under natural conditions are relatively low compared to non-halophytic vegetation (Moore *et al*., 1973; Lugo *et al*., 1975; Miller *et al*., 1975), therefore the potential damage by overheating due to insufficient evaporative cooling of the leaf surfaces is a serious ecological constraint for mangroves in nature. Photosynthetic rates are correspondingly low, therefore mangroves are exposed to a large excess of excitation energy leading potentially to problems of photoinhibition of the photosynthetic apparatus (Björkman *et al.*, 1988).

In a large survey of photosynthesis of mangrove species under natural conditions conducted by Clough and Sim (1989), a number of patterns relating photosynthesis and conductance with leaf-air vapor pressure deficits (vpd) and substrate salinity have been established. *Avicennia marina* consistently had the higher photosynthetic rates, and leaf conductances. In a particular locality all species showed the same fractional reduction of assimilation with leaf conductance, therefore they had similar internal CO_2 concentrations at irradiances above 800 μmol m^{-2} s^{-1}, and the same water use efficiency (Fig. 4). Stomatal conductance and assimilation rate decreased with salinity and increased vpds. It is concluded that in mangroves water use efficiency increases with stress (increased salinity and lowered vpds).

Figure 4. Relationship between leaf conductance and photosynthetic rate of mangrove species with (•) and without salt excreting glands (o). Salt excreting species: *Avicennia marina*, *A. officinalis*, *Aegiceras corniculatum*, *Aegialitis annulata*. Non-salt excreting species: *Rhizophora apiculata*, *R. mucronata*, *R. stylosa* (data from Clough and Sim 1989).

The survey of Clough and Sim (1989) confirm previous measurements on *Rhizophora stylosa* (Andrews and Muller, 1985). In this species photosynthesis under natural conditions reach maximum levels of around 10-11 μmol CO_2 m^{-2} s^{-1}, and there was a linear relationship between photosynthesis and leaf conductance, therefore allowing the maintenance of a nearly constant ci under a large range of conditions (ca. 166 μbar). Maximum leaf conductances were always around 100 mmol m^{-2} s^{-1}. The water use efficiency was high under these conditions. (5.3, 3.9, 4.7, 5.1 and 5.0 mmol CO_2/mol H_2O). It was shown that leaf inclination was very important for temperature regulation. In a leaf held

horizontally the leaf-air temperature difference reached 11 ^{o}C in a clear day. Photosynthetic gas exchange was shown to be strongly sensitive to leaf temperature and leaf-air vpd.

The analysis of CO_2 uptake, oxygen photon yields, and fluorescence kinetics in leaves of several mangrove species growing naturally at different degrees of sun exposure showed that leaves under full sun are partially photoinhibited (Björkman *et al*., 1988, see Table 7). It was found that shade leaves have a photon yield of O_2 evolution as high as non-mangrove leaves, their fluorescence characteristics were normal, therefore the energy conversion efficiency was unaffected by the high salinity. Sun leaves had markedly depressed photon yields and fluorescence was severely quenched showing that the efficiency of the photo-chemistry of photosystem II was reduced. No such depression was detected in sun leaves of non-mangrove species growing in adjacent non-saline sites. The reduction in efficiency of energy conversion could be reversed by shading sun leaves, but in general more than a week was required to reach the efficiency of shade leaves. Plants cultivated under full sun but with 10% sea water had conversion efficiencies slightly higher than those of plants grown with full strength sea water, but salinity had little influence on the increase of efficiency upon shading. The measurements indicate that the reduced efficiency is due to a large increase in the rate constant of radiationless energy dissipation in the antenna chlorophyll rather than a damage to photosystem II reaction centers. The apparent quantum yield was reduced in leaves grown under fully exposed conditions, probably with angles smaller than 45°.

Under natural conditions healthy mangrove leaves have usually high degree of leaf inclination, a factor reducing considerably the amount of radiation effectively impinging upon the leaf. Ball *et al*. (1988) showed that degree of leaf inclination is quite significant in mangrove species of northern Australia, accounting for a large reduction of the heat load of the mangrove leaves. Shaded leaves were larger, had a higher projected fraction of leaf area, and were less succulent than leaves growing under full sun (Table 8). These observations are associated with the fact that mangroves are conservative in their water use, but living in an environment of high radiation the most effective way of avoiding overheating without evaporative cooling is reducing the absorbed light energy.

Growing under saline conditions in high radiation environments is certainly a severe stress for mangroves, but true mangrove requires a certain level of NaCl in their substrate for optimal growth. However, the reports indicating that the photochemical activity of photosystem II of isolated chloroplasts and thylacoids of *Avicennia marina* are stimulated in their electron transport and oxygen evolution by concentrations up to 500 mM NaCl (Critchley, 1982) have been shown to be an artifact of the chloroplast isolation procedure (Ball and Anderson, 1986). In halophytes salt concentration in cytoplasmic compartments are usually much smaller than that of the vacuoles (Harvey *et al*., 1981) reflecting the sensitivity of enzymes to high levels of Na^+ and Cl^-.

The photosynthetic rate and leaf conductance of mangroves may be affected both by transient changes in salinity and long term exposure to high saline concentrations. Seedlings of *Avicennia marina* submitted to increasing salinities, showed a decrease in photosynthesis from 14.9 ± 0.7 μmol CO_2 at 50 mM NaCl to 9.1 ±1.0 at 500 mM NaCl (nearly full sea water) (Ball and Farquhar, 1984a). Similarly, conductance was reduced from about 250 to 80-100 mmol m^{-2} s^{-1}. It is shown that the CO_2 dependent part of the curve was not affected by salinity, while CO_2 saturation point remained similar but rates of CO_2 uptake decreased considerably with salinity. These short term changes were substantially reversible. Apparently the salt accumulated during the 8 days periods reduced photosynthetic rates at the end of the experiment only by a small amount.

Table 7. Variations of apparent quantum yield leaves grown under full exposure or partial shade of mangrove species on northern Australia (Björkman *et al*., 1988)

Species	Exposure	ϕO_2 (mol O_2 mol^{-1} photons)
Aegialitis annulata	Partial shade Exposed	0.078 0.054
Aegiceras corniculatum	shade Exposed	0.084 0.044
Avicennia marina	Partial shade Exposed	0.078 0.043
Rhizophora stylosa	Partial shade Exposed	0.075 0.047
Sonneratia alba	80° leaf angle 47°	0.078 0.036

Table 8. Variation in the leaf inclination with the degree of exposure in five mangrove species in Hinchinbrook Island, North Queensland (Ball *et al*., 1988). (The projected fraction of leaf area= cos α, where a is the angle of the leaf respective to the horizontal; exposure is expressed as shade (Sh), medium sun (MS), and full sun (FS)

Species	Exposure	Leaf Area (cm^2)	Projected fraction	Succulence (g/m^2)
B. gymnorrhiza	Sh	67 ± 5	0.83 ± 0.04	236.5 ± 8.0
	MS	70 ± 14	0.79 ± 0.01	332.0 ± 35.4
	FS	58	0.56	262.5
R. apiculata	Sh	78 ± 9	0.94 ± 0.01	262.4 ± 21.9
	MS	75 ± 5	0.60 ± 0.04	285.9 ± 16.8
	FS	69 ± 7	0.37 ± 0.09	384.4 ± 41.1
R. stylosa	Sh	61 ± 7	0.95 ± 0.03	258.5
	MS	60 ± 20	0.57 ± 0.04	321.4 ± 11.2
	FS	44 ± 2	0.30 ± 0.03	387.9 ± 35.5
C. tagal	Sh	49 ± 1	0.93 ± 0.03	310.1 ± 9.2
	MS	20 ±3	0.63 ± 0.05	351.9 ± 33.9
	FS	8 ± 1	0.36 ± 0.08	463.2 ± 55.4

The effects of long term increases in salinities and contrasting leaf-air vapor pressure deficits (vpd) on mangrove species with different salt tolerance indicate that the photosynthetic rate is affected by vpd certainly through a reduction of leaf conductance (Ball and Farquhar, 1984b). *Aegiceras corniculatum* appears to be more sensitive to salinity than Avicennia marina but both species respond quickly to reductions in vpd. Particularly at salt concentrations near 100% sea water photosynthetic rate of *Aegiceras corniculatum* is strongly reduced, even at low vpds, being less than half of that of *A. marina* , while at low salinities (10% sea water) there are no differences in the photosynthetic rates of both species. Part of the lower tolerance of *Aegiceras corniculatum* to high salinity might be explained by the rapid reduction of the K^+/Na^+ ratio with increasing salinity.

The measurement of the natural abundance of carbon 13 in plant tissues has been used effectively to establish the type of photosynthetic pathway operating in higher plants (Farquhar *et al*., 1989). The theory of enzymatic and diffusive fractionation during CO_2 uptake in photosynthesis of C3 plants establishes a linear relationship between the ratio of internal to external CO_2 concentrations in the leaves and their water use efficiency (Farquhar *et al*., 1982). All mangrove species measured have $\delta^{13}C$ values typical of C3 plants, with a range of values extending from -32‰ in *Ceriops tagal* to -26.3 ‰ in *Xylocarpus australasicum* (Andrews *et al*., 1984). Higher $\delta^{13}C$ values are indicative of higher water use efficiency, because photosynthesis is more limited by diffusion (lower stomatal conductance) than by the carboxylation step. Mangrove species have higher water use efficiencies under saline conditions (Clough and Sim, 1989) or drought (Smith *et al*., 1989), it is then expected that mangroves from drier sites (lower fresh water availability) or higher salinities will have higher $\delta^{13}C$ values. Some indications that this is the case have been advanced by Farquhar *et al*., (1982).

Salinity and Seasonal Variations in Performance in True Mangroves and Associates

Throughout this chapter I have dealt with *true mangroves*, those tree species growing in the intertidal zone in tropical shores. The implication is that true mangroves have a comparatively high salinity resistance, and that they require salt for their optimum development. The absence of certain amount of NaCl is not only detrimental to their competitive capacity against non-halophytes, but also increases their mortality. Many of the species labeled as associate mangroves (Tomlinson, 1986) do not require salt for their optimum development but may be quite salt tolerant. Two common associate species of the mangrove communities in the american tropics are *Conocarpus erectus* (Combretaceae) and *Acrostichum aureum*, the mangrove fern.

Conocarpus erectus grows in the back of mangrove communities, frequently outside of the influence of the tides. In many circumstances, however, it grows in coastal areas where the incidence of salt spray or salt water in the

underground can modify strongly their leaf succulence and photosynthetic charac- teristics. Smith *et al*. (1989) studied the occurrence of *Avicennia germinans*, the most salt tolerant mangrove species in the neotropics, and *Conocarpus erectus* in vegetation islands in salt flats of northern Venezuela. It was shown that *Conocarpus erectus* can accumulate quite large amounts of NaCl in their leaves, particularly during the dry season, but the Na^+/K^+ ratios are much higher than those of *Avicennia germinans* (Table 9). The different sources of soil water for the two species in these complex vegetation are revealed by the concentration of ions in the leaf sap. In spite of the higher transpiration rates of *Conocarpus erectus* during the dry season, the concentration of Na^+ and Cl^- were nearly 40% lower, while the K^+ content was 60% lower compa- red to *Avicennia germinans*. The photosynthetic capacity of *C. erectus* appeared to be more sensitive both to the larger vpds and higher soil salinities experienced during the dry season.

The case of the mangrove fern is also indicative of differences in the availability of fresh water, in spite of its co-occurrence with true mangrove species in the same communities. In sites of increasing salinity of interstitial water in the northern coast of Puerto Rico *Acrostichum aureum* had always lower osmolalities than *Laguncularia racemosa* and *Rhizophora mangle* (Medina *et al*., 1990; see Table 10).

Figure 5. Relationship between δD and $\delta^{18}O$ values measured in plant tissues of hardwood hammock species and true mangrove species growing on keys of southern Florida. The squares show the range of expected values for ocean water and freshwater. Ocean water is richer both in oxygen 18 and deuterium than fresh water (redrawn from Sternberg *et al*., 1989)

Table 9. Seasonal variations of gas exchange characteristics, cell sap osmolality and Na^+ and Cl^- content in *Avicennia germinans* and *Conocarpus erectus* growing in salt flats (From Smith *et al*., 1989)

	Avicennia germinans		***Conocarpus erectus***	
	Rainy season	**Dry season**	**Rainy season**	**Dry season**
Osmolality (mmol kg^{-1})	1300	2650	760	1640
Cl^- (mol m^{-3})	744	935	421	600
Na^+	261	891	154	504
K^+	130	107	49	35
Na^+/K^+	2.0	8.3	3.1	14.4
Photosynthetic rate near saturation (µmol m^{-2} s^{-1})	5.61	3.87	4.27	2.07
Total net CO_2 uptake during the light period (mmol m^{-2} 12 h^{-1})	173	105	133	40
Total transpiration per light period (mol H_2O m^{-2} $(12h)^{-1}$)	101	31	154	8
Water use efficiency during the light period (mol CO_2 mol^{-1} H_2O)	1.7×10^{-3}	3.3×10^{-3}	1.3×10^{-3}	4.3×10^{-3}

Table 10. Comparison of osmotic pressure (at 25 °C) and Na^+ and Cl^- contents of leaf sap of the associate species *Acrostichum aureum* growing together with *Laguncularia racemosa* and *Rhizophora mangle* (from Medina *et al*., 1990)

Species	Interstitial water salinity		Leaf sap osmolality		Cl^-	Na^+	Cl^-/Na^+
	mmol/kg	π MPa	mmol/kg	π MPa	mol m^{-3}	mol m^{-3}	
A. aureum	520	1.28	914	2.26	240	89	2.7
L. *racemosa*			1138	2.81	490	269	1.8
R. mangle			1422	2.51	461	434	1.1
A. aureum	565	1.39	989	2.44	279	121	2.3
L. racemosa			1183	2.92	465	428	1.1
R. mangle			1527	3.77	571	427	1.3
A. aureum	839	2.07	1019	2.52	282	119	2.4
L. racemosa			1243	3.07	561	354	1.6

Besides, the Cl^-/Na^+ ratios are always higher in the *Acrostichum aureum*, indicating differences in permeability against these two ions. The occurrence of *Acrostichum aureum* in mangrove communities is restricted to wet coasts or to estuarine environments, with a large supply of fresh water at least during most of the year. The supply of fresh water is necessary for the successful sexual reproduction of the fern, because the gametophytic generation appears to be very salt sensitive, compared to the large salt tolerance of the sporophytic generation (Medina *et al*., 1990).

The proportion of fresh water supply to different species in a mangrove community can be accurately estimated mea-suring the abundance of stable isotopes of hydrogen and oxygen. In mangrove communities found on keys in southern Florida Sternberg *et al.* (1989) measured the relative utilization of freshwater and ocean water using this technique. They concluded that plants occurring towards the center of the key were using mostly fresh water, while those growing near the edge were using ocean water. The distribution of δD and $\delta^{18}O$ values of hardwood hammock species and those of typical mangrove species shows clearly the range of variation in the source of water (Fig. 5). Mangrove species appear to use both fresh-and ocean water, while the hardwood hammock species are practically restricted to freshwater sources. This technique may prove to be valuable in clarifying complex zonations, particularly in estuarine mangroves.

Concluding Remarks and Suggestions for Further Research

From the previous discussion on the physiology of mangrove species several points may be highlighted as orientation for further research:

1. Mangrove species are good indicators of long term salinity in their environment. The level of exposure to salinity can be assessed through the analysis of the ionic composition of the leaves, root, and stem saps. Analysis of xylem sap in particular, may be useful for the assessment of short term pollution and changes in the availability of fresh water. Xylem sap composition reflects the differential permeability of root cells membranes and therefore can be used as a sensitive indicator of metabolic or physical disturbances at the root level. Mangrove ecosystems occur in the land-sea interface, and are geared to produce organic matter under high levels of environmental stresses. Their physiological analysis, therefore, has a large potential as a tool to detect environmental change.

2. The occurrence, concentration, and induction of synthesis of organic osmolites is an important field of research which will shed light on the tolerance mechanisms of the cytoplasm towards high osmotic concentration in the vacuoles.

3. Analyses of cell permeability, as exemplified by the studies on *Avicennia* marina, have to be extended to other species with different tolerance to environmental salinity. These studies could contribute to explain the distribution of mangrove species

in nature, and more important, may provide the basis to understand salinity tolerance in higher plants, particularly the maintenance of high K^+ levels in the presence of large amounts of Na^+. Modern molecular techniques may help to introduce such characteristics into crop plants and contribute to the fulfillment of a very old dream, the irrigation of farm lands with sea water.

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The Productivity and Nutrient Cycling of Mangrove Ecosystems

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Abstract

This chapter will look at two ecological functions of mangroves, productivity and nutrient cycling, from the perspective of the environment setting of tropical coastal environments. The main objective is to demonstrate how the geomorphological type of coastal environments can constrain the function as well as structure, of mangrove ecosystems. Together with an understanding of ecological processes of mangrove, we may be able to develop greater generality of the diverse properties of mangrove ecosystems. The influence of these external energies on the productivity and nutrient cycling will determine the role of mangroves in habitat and water quality in the coastal zone.

There are many intrasystem processes that are linked to hydrology of coastal regions that influence the productivity and nutrient dynamics of mangroves. It is evident that the function of mangroves, as determined by productivity and nutrient cycling, are constrained by the forcing functions in an environmental setting by establishing certain patterns of intrasystem processes. Some quantitative examples of this concept are presented, such as effect of latitude, soil salinity, and phosphorous content in rivers on the biomass and productivity in mangroves. In addition, the outwelling of organic matter will vary according to amplitude and frequency of tides. Other functions such as nitrogen fixation, leading to continued confusion as whether mangroves are nutrient sources or sinks of coastal waters.

This review suggest that the regeneration rates of natural forest will vary with latitude, ranging from 25 years at 20º to 30º compared to 100 years at latitudes less than 10º. This is because the potential biomass that can develop at the lower latitudes requires longer time constants for forest to research maturity.

Resumen

Este capítulo trata de dos funciones ecológicas de los ecosistemas de manglar como son la productividad y el reciclamiento de nutrientes, desde la perspectiva del establecimiento ambiental en el medio tropical costero. El objetivo principal es demostrar como la geomorfología de la zona costera puede restringir las funciones así como la estructura de los ecosistemas de manglar. En el entendimiento conjunto de los procesos ecológicos del manglar, que pueden ser capaces de desarrollar mayores generalidades de las diferentes propiedades de los ecosistemas de manglar. Es determinante la influencia externa de los flujos de energía físico - ambiental sobre la productividad y reciclamiento de los nutrientes que determinara el papel ecológico de los manglares como un hábitat en la zona costera así como un regulador de la calidad del agua.

Existen muchos procesos intrasistemas que están vinculados con las regiones costeras y que influyen en la productividad y dinámica de los nutrientes de los manglares. Es evidente que el manglar es determinante en el funcionamiento de la productividad y reciclamiento de nutrientes los cuales son limitados por los mecanismos de producción en cada localidad establecida ya que interactúan ciertos patrones de procesos intrasistemas. Para ejemplificar este concepto se presentan algunos ejemplos cuantitativos, tales como los efectos de la latitud, la salinidad del suelo, el contenido de fósforo en los ríos, sobre la biomasa y productividad de los manglares. Además, la exportación de materia orgánica variará de acuerdo con la amplitud y frecuencia de las mareas.

Esta revisión sugiere que las tasas de regeneración natural de los bosques variarán con la latitud fluctuando de 25 años en 20 a 30º comparado con 100 años en latitudes menores de 10º. Esto es debido a la biomasa potencial que pueden desarrollar en las latitudes más bajas requiere de un periodo mas largo para que el bosque alcance su madurez.

Introduction

The importance of the physical nature of coastal environments on the development of communities has been well documented for a variety of marine ecosystems (Hedgpeth 1957). However, mangrove ecology has been dominated by autecological investigations of botanical interests, with less understanding of community dynamics. While there are numerous studies on selective aspects of community dynamics such as litter productivity and vegetative zonation, few attempts have been made to synthesize this information in the context of the physical settings of mangroves in the tropical intertidal zone. The function of mangrove ecosystems, such as productivity and nutrient cycling, have particular importance to understanding the ecology of adjacent marine ecosystems. The coupling of mangroves to coastal waters is considered an important link to the support of economically important fisheries. In addition, mangroves provide important timber products for construction and energy in many developing countries. Recently, there has been increased pressure on mangrove resources in the coastal zone from increased populations and economic enterprises such as shrimp farming. This chapter will look at two ecological functions of mangroves, productivity and nutrient cycling, from the perspective of the environmental setting of tropical coastal environments. This approach will be to integrate the findings of numerous studies to apply generality to conceptual models of mangrove ecosystems. This generality of the function of mangrove ecosystems will help in the development of mangrove management plans to address problems of tropical coastal resources.

Thom (1982) proposed that the combination of geophysical energies with the geomorphology of the coastal zone is important to establishing the ecological characteristics of mangroves. According to Thom, the landform characteristics of a coastal region together with environmental processes control the basic patterns in the structure of coastal forests. He identified five basic types or classes of environmental settings where mangroves occur based on the relative influence of river, tide, and wave energies on coastal processes as follows (Fig. 1):

Setting I - allochthonous coasts of low tidal range that tend to form deltas;

Setting II - allochthonous coasts with terrigenous materials that are also influenced by strong tidal currents resulting in shoals and mud flats;

Setting III - coasts with minor river influence and autochthonous materials resulting in the formation of bays and lagoons dominated by higher wave energy;

Setting IV - coasts with combination of settings I and III having high wave energy and river discharge;

Setting V - drowned river valley complex.

The geophysical energies that were used by Thom to determine specific types of environmental settings include rainfall, river discharge, tidal amplitude, turbidity, and wave power. These geophysical energies are the dominant forcing functions of mangroves and collectively represent the energy signature of mangroves (Fig. 2).

Thom (1982) focused on terrigenous physical settings to describe patterns in mangrove structure and paid less attention to reef environmental settings. Reef mangroves exist in unique types of environmental settings dominated by carbonate processes and nutrient poor sediments. The geology and ecology of these types of mangroves have been the focus of several recent research efforts, and will be included in this review as a sixth (VI) type of environmental setting. The structure and function of these reef communities will provide an interesting contrast to those mangroves influence more by terrigenous materials. The combinations of these energies, together with the environmental setting, explain the direction and rate of change in community structure.

Figure 1. The five basic groups of coastal mangrove formations (from Thom, 1982)

On a regional scale, the geomorphology or stability of landform is viewed as one of the important factors that explain the diverse patterns of growth in coastal wetlands. The stability of coastal environments allow for development of a variety of plant communities depending on more local factors associated with hydrology. The microtopographic factors of a region determine many of the soil conditions that control the patterns of forest zonation and growth. These physical and chemical conditions of soil, together with biological factors such as predation and resource utilization, are the ecological factors that determine the diversity in community development.

There is a combination of scales to view the patterns of mangrove development that include both the geomorphological and ecological factors that control the ecology of mangroves. The relative influence of geological and biological factors on the structure of coastal wetlands has been confusing, as has been the importance of these factors on the function of mangrove ecosystems. In areas of high geophysical energies, such as in river and tide dominated estuaries (type I and II, Fig. 1), the influence of biological factors on the structure and function of mangrove communities are usually insignificant. However, patterns of mangrove development in environmental settings dominated by wind energy, such as lagoons (type III and VI, Fig. 1), may be influenced more by ecological factors such as competition and predation. Also, those areas with rapid changes in landform relative to the time constant of community development, caused by biological interactions, will determine what factors influence the ecology of mangroves. Those environmental settings, such as bays and lagoons that are more geologically stable may be sites where ecological factors are commonly observed.

The use of environmental settings by Thom to explain mangrove processes from a geomorphological perspective is similar to the use of forcing functions to describe the ecological function of mangrove ecosystems (Twilley, 1988; Twilley 1995). Coastal geomorphology and hydrology have been used to develop several different schemes to classify the physiognomy and zonation of mangrove forests (Lugo and Snedaker, 1974; Watson, 1928). However, the ecological processes or function of coastal forests may also be related to coastal processes. Environmental processes such as tides, rivers, and waves that influence forest structure also determine the function of wetlands (Gosselink and Turner, 1978; Twilley, 1988). Thus the productivity, nutrient cycling, and coupling of these ecological processes with coastal waters may be specific according to the geomorphology and geophysical characteristics of coastal ecosystems (Twilley, 1988). This review will focus on the functions of mangrove ecosystems as controlled by the physical nature

Figure 2. The forcing functions that constitute the energy signature of mangrove ecosystems. T is turbidity caused by total suspended material, O = organic matter, N = nutrients, S = salt content, and L = larvae (from Twilley,1995)

of coastal environments. The objective of this chapter is to demonstrate how the geomorphological type of coastal environments can constrain the function, as well as structure, of mangrove ecosystems. Together with an understanding of the ecological processes of mangroves, we may be able to develop greater generality of the diverse properties of mangrove ecosystems.

Community Structure and Distribution

Composition and Classification

Mangroves refer to a group of forested wetlands that inhabit tropical and subtropical coast generally between 25° N and 25° S latitude that are inundated and drained by tides (Lugo and Snedaker, 1974, Fig. 3). On the east coast of Africa, in Australia, and in New Zealand they extend 10-15° further south, and in Japan they reach about 7° further north (Kuenzler, 1974). In the United States, mangroves occur along the tropical and subtropical coasts south of Cedar Keys in Florida and generally south of Port Isabel, Texas. With the exception of a few isolated, scrubby stands of black mangrove in the Mississippi deltaic plain, mangroves are absent from the northern Gulf Coast, which is dominated by salt marshes. The global distribution of mangroves was estimated from World Resources 1986, a report by the World Resources Institute, at 24.00 $\times$ 10^6 ha dominating the river-dominated delta, lagoon and estuarine coastal environments (Fig. 3). Other estimates of mangrove area range from 15.47 to 30 x 10^6 ha, with an average of 21.8 $\times$ 10^6 ha (Lugo *et al*., 1990, Table 4.1). The largest area of mangroves occurs in the 0° to 10° zone with 10.07 x 10^6 ha compared to only 0.25 $\times$ 10^6 ha in the 30° to 40° latitudes (Fig. 3). Some of the variation in estimates of mangrove area depends on whether the subtropical regions are included. The region above 20° latitude includes a minor component of mangrove area, but includes the major mangrove research sites, such as south Florida, USA.

Figure 3. The distribution of mangrove area (north and south latitude) in the tropical and subtropical regions of the world

Mangroves are considered a group of halophytic species from 12 genera in 8 different families (Waisel, 1972; Lugo and Snedaker, 1974). Fewer than 10 species are found in the newworld and a total of 36 have been described from the Indo West Pacific area (Macnae, 1968, Fig. 3). The number of species included as mangrove depends on the inland extension of the intertidal zone as they may occur from subtidal to supratidal (Lugo and Snedaker, 1974; Tomlinson, 1986). Schimper (1903) defined mangrove to include the formation of plants below the high tide mark, and "true" mangrove species occur in only part of the intertidal zone. Thus *Nypa* swamps are commonly excluded as mangrove associations. Mangrove usually refers to the specific plant or to whole plant associations which are also called mangrove forests. MacNae (1968) introduced the word mangal to refer to whole swamp associations, which is synonymous with mangrove ecosystems.

Mangroves are usually classified into one of three systems depending on which attributes of this diverse group of wetlands are emphasized (Hutchings and Saenger, 1987). Structural attributes include the physical dimensions of the forest such as tree height, density and canopy formation. The use of a geomorphological approach was described above using the energy spectrum of the coast (Thom, 1982). A combination of the two systems uses both the physiographic and structural attributes of the forests together with local conditions of topography and hydrology into an ecological classification system (Lugo and Snedaker, 1974). This ecological scheme uses the dominant environmental factors to classify mangrove forests in the Caribbean into six types, although recently this scheme has been reduced to riverine, fringe and basin forests (Fig. 4). Four species of mangrove (*Rhizophora mangle*, *Avicennia germinans*, *Laguncularia racemosa*, and *Conocarpus erectus*) occur in varying mixtures of vegetation, as well as monospecific stands. The formation and physiognomy of these forest types appear to be controlled strongly by local patterns of tides and terrestrial surface drainage. Local patterns in tidal inundation have long been related to the structure and distribution of mangrove forest (Watson, 1928; Chapman, 1944; Walsh, 1974; Chapman, 1976).

These two basic types of classification systems, geomorphological and ecological, can be used together to describe the environmental factors that control the attributes of forest structure. The geomorphological scheme is a regional scale description of the coastal environmental setting. Thus the description of the mangrove as either in a river-dominated delta (type I in Fig. 1) or wave-dominated lagoon (type III, Fig. 1) indicates the type of forcing functions that will influence the mangrove forest (Fig. 2). The ecological classification, such as either fringe, basin, or dwarf, describe the microtopographic effects of hydrology on the formation of forest types (Fig. 4). Within the regional boundaries of an environmental setting there may exist all six ecological types of mangrove forest depending on the local effects of tides, waves, and river flow. For example Terminos Lagoon, which has a type III environmental setting, has riverine, fringe, basin, and dwarf forests due to the local interactions of river and tides with the microtopography of the forest (Day *et al*., 1987).

Zonation

Observations of intertidal wetlands in many different areas of the tropics reveal similar spatial patterns of distribution of mangroves (Chapman, 1976). Often the distribution takes the form of bands or zones of different associations of plants that are similar from one location to another. Zonation occurs at several different spatial scales (Day *et al*., 1989). At the broadest level there is latitudinal scale zonation, where climate plays the major role in affecting distributional patterns. At an intermediate scale, there is coastal drainage basin zonation, where mean water salinity and coastal morphology are important in determining zonation patterns. Finally, local zonation occurs along tidal creeks as a result of elevation changes and variation in tidal exchanges as one move inland from a tidal creek. This local "patchiness" is caused by adjustment of plants to various factors that are influenced by the microtopography of intertidal areas. Such zonation provides insight into how different plants are adapted to and otherwise alter environmental gradients of the intertidal zone.

On a broad latitudinal scale, zonation of coastal wetlands is affected primarily by climate, particularly temperature. As indicated earlier, mangroves grow in the tropical and sub-tropical regions to about 30°N. Where freezes occur more than once or twice a year, salt marshes replace mangroves. Mangroves generally extend to subtropical zones where the temperature in the coldest month does not fall below 20°C. The genus *Avicennia*, which has broadest distribution in subtropical environment, can tolerate a minimum temperature from 10° in Brazil, 12.7 ^{o}C in Florida and 15.5 ^{o}C in northern Red Sea (Chapman, 1977). The global influence of temperature is evident in comparing the restricted distribution of mangroves along Pacific coast of South America associated with cold Humboldt current. In comparison, one of the largest areas of mangroves in the new world is located along the Atlantic coast of South America due to southerly flowing warm water (Fig. 3).

Figure 4. The six mangrove community types (from Odum *et al*., 1982 as modified from Lugo and Snedaker, 1974)

The regional zonation of mangroves depends on moisture content of intertidal soils which is controlled by the balance of rainfall (P), river, tides, and evapotranspiration (ET) (Fig. 5). The latter is linked to seasonal patterns of temperature. Pool *et al*. (1977) showed that the structure of mangrove forests in the Caribbean was limited in dry life zones based on relative amounts of precipitation and evapotranspiration (Holdridge, 1967). In coastal tropical regions where ET/R is greater than 1, freshwater input to the coast is an important factor to patterns of mangrove zonation since rivers may subsidize the availability of water loss to ET. Along the Guayas River estuary, Ecuador, ET/R ratios are high, and mangroves are restricted to a narrow

Figure 5. Energy flow model of the ecological processes of mangroves as influenced by the forcing functions of coastal environments (from Cintrón *et al*.,1978; symbols from Odum 1971)

band of the intertidal zone due to the influence of the Guayas River (Schaeffer-Novelli, 1983). The ratio of freshwater input to evapotranspiration controls moisture content of sediments and can be a strong influence on the zonation of vegetation.

Local zonation is the result in differential response of mangroves to environmental gradients caused by the microtopographic effects of frequency and duration of tides in intertidal zone. Some of the most important factors are elevation, drainage, and associated soil characteristics. Tidal exchange and soil type are important in determining the oxidation reduction state of the soil and the level of hypersaline conditions in the higher elevations of intertidal zone. In mangrove swamps there is often a distinct elevation gradient from the water's edge to the upland boundary, and often a streamside levee or berm borders coastal waters. The physiognomy of mangroves is more robust in this zone along the waters edge. This is where fringe mangroves occur, identified by their taller forms compared to more inland vegetation. The characteristics of fringing forested wetlands have been described by Lugo (1990).

In higher elevations of the intertidal zone, more inland salt pannes often form, where seasonal moisture deficits exist in tidally flooded land causing areas of hypersalinity (Fig. 6). In mangrove areas, these areas void of vegetation are often called salinas These salt pannes or salinas are zones of higher salinity that prevent colonization by all but the most salt adapted plants. Under conditions of extreme or prolonged dryness, there may be little or no vegetation in the tidal zone. Halophytes such as *Salicornia* often grow in a narrow zone between the salinas and mangroves growing in the lower tidal plain. The areal distribution of salinas may shift in response to climatic changes. Cintrón *et al*. (1978) found that mortality rates of mangroves in the upper regions of intertidal zone in Puerto Rico changed depending on annual cycles of precipitation. In Senegal, the area of wetland vegetation in coastal lagoons declined in 1975 due to southern movement of Sahel drought (Twilley, 1985b). Macnae (1968) has shown similar patterns for the Queensland coast mangrove communities, where the changes in rainfall regions are rapid over short distances along the coast. These areas may recolonize and fluctuate as response to shifts in climate that determine the availability of water.

Succession

Succession in mangroves has often been equated with zonation (Davis, 1940), wherein "pioneer species" would be found in the fringe

Figure 6. Response of structural indices of mangroves to increase in soil water salinity for several sites in Puerto Rico (from Cintrón *et al*. 1978)

Figure 7. Changes in the structure of a basin mangrove forest in Rookery Bay, Florida, from 1971 to 1987 based on tree density (>0.25 diameter at breast height), basal area, and biomass (based on allometric relationships by Cintrón and Schaeffer-Novelli 1984). The forest was damaged by a hurricane in 1967. Mean and standard deviation based on four 10 m x 10 m plots. Summarized from data in Warner (1990)

zones, and vegetational changes more landward would "recapitulate" the successional sequence in terrestrial communities. Zonation in mangrove communities has variously been accounted for by a number of biological factors including salinity tolerance of individual species (e.g. Snedaker, 1982), seedling dispersal patterns resulting from different sizes of mangrove propagules (Rabinowitz, 1978), differential predation by grapsid crabs (Smith, 1987), and interspecific competition (Ball, 1980). Snedaker (1982) proposed the establishment of stable monospecific zones wherein each species is best adapted to flourish due to the interaction of physiological tolerances of species with environmental conditions. The consideration of changes in mangrove communities in a strictly spatial rather than temporal pattern has contributed to the lack of understanding of succession in these forested wetlands.

Zones of mixed species composition have been thought of primarily as transition zones or ecotones between monospecific zones and as such have been interpreted as being temporary responses to disturbance (Lugo and Snedaker, 1974; Lugo, 1980). However, recent analyses of vegetation transects by Warner (1990) have shown that mixed associations of mangroves may be stable communities of the coastal landscape (Fig. 7). This 10 m wide transect in Rookery Bay mangroves extends 50 m inland from shore and is divided into 5-10 m long plots.

The first plot is in a fringe mangrove, and the other four plots in a mixed basin mangrove forest. The forests was damaged by a hurricane in 1965, and the regeneration is demonstrated by high density and low biomass in 1971 compared to 1987. A decline in density and increase in basal area is typical of a developing forest. Biomass was stable by 1987 indicating a mature forest within 20 years following disturbance. The interesting pattern in the basin forest surveyed is the stability of the mixed vegetation during the 17 year period. Patterson (1986) showed that mixed species zones occupied similar percentage of the landscape in southwestern Florida from 1952 to 1984. Both Lugo (1980) and Snedaker (1982) concluded that zonation patterns in mangroves represent steady state adjustments rather than successional stages.

This concept of a steady state landscape as it applies to mangroves is supported by the work of Thom (1967). Thom (1967) demonstrated that the zonation and structure of mangrove forests in Tabasco, Mexico are responsive to eustatic changes in sea level, and that mangrove zones can be viewed as steady state zones migrating toward or away from the sea, depending on its level. He postulated that mangrove zones were responsive to geomorphological changes in the regions where they grow. He considered substratum and water regime to be the important factors controlling zonation, and that each species, within its tolerance range to salinity, finds its place in the environmental gradient created by the regimes of substratum and water flow. According to Thom, biological factors are only secondary in the elimination of species that are first selected according to geophysical processes in the region. However, in those coastal areas with lower geophysical energies, the influence from biological factors in establishing zonation and change in time will be significant. In those areas the zonation of mangroves may more likely represent a successional sequence, yet mangrove zones may not invariably recapitulate successional seres. Instead, the “zonation” of mangroves may be a result of all the external sources acting on a locality.

The structure of mangrove forests is influenced by a combination of geomorphological, climatic, and ecological factors that determine the patterns of zonation along shoreline (Fig. 5). The trajectory of vegetation dynamics are constrained by the geomorphological and climatic characteristics of coastal environment, and modified by the ecological interactions within a mangrove forest. Thus general patterns may be observed within geographic regions, but there are diverse patterns globally based on different land forms that occur in tropical coastlines. In addition, changes in environmental settings caused by drought, subsidence, or tropical cyclones can interrupt patterns in vegetation development. Since seldom do we have sufficient long term records to distinguish these patterns in mangroves, there are no models of mangrove succession that can be applied outside specific geographical boundaries. However, development of models of mangrove succession should include the fundamental geologic, climatic, and ecological functions such as in figure 5 to account for the diverse coastal conditions.

Biomass and Productivity

Biomass

Estimates of mangrove biomass are usually restricted to aboveground structures and in many cases, only include the timber that can be harvested from the forest. The distribution of biomass in sixteen sites throughout the tropics indicates that higher values occur at lower latitudes (Fig. 8). Cintrón and Schaeffer-Novelli (1984) found that mangrove tree height, which is a good indicator of forest biomass, increased at lower latitudes in the neotropics according to the model: $Y = 45.8 - 1.28(X)$ ($r^2 = 0.75$); where Y is tree height (m) and X is latitude north or south. The sensitive response of mangrove biomass and tree height to relatively small changes in latitude is related to the influence of temperature and occurrence of frost on the structure of these ecosystems (Lugo and Patterson-Zucca, 1977). Thus, solar energy represents a major constraint on the distribution and maximum biomass in mangrove ecosystems (Fig. 2). Figure 8a indicates the upper limit of mangrove biomass that may occur in any tropical region depending on latitude.

Mangrove biomass varies dramatically for any given latitude, for example values less than 50 mg/ha occur at 10 and 35°, while maximum biomass is about 400 and 100 mg/ha, respectively (Fig. 8). Thus while the upper limits of mangrove biomass may occur at lower latitudes, there are local effects that may limit the potential for forest development at all latitudes. These local effects include topography and hydrology, including the effects of river and tides on soil characteristics (Fig. 5). Cintrón *et al*. (1978) found that with increasing salinity the values of a number of structural and functional parameters decreased (Fig. 6). These included litterfall, tree density, basal area (total cross-sectional area of trunks), and tree height. For example, tree height (Y, m) of mangroves in Puerto Rico is inversely related to soil salinity by the equation:

Figure 8. Biomass and litter productivity for mangrove forests throughout the world (from Twilley *et al*., 1992)

$$Y= -0.20(X) + 16.58 \ (r^2 = 0.72)$$

where X is soil salinity in ‰ (Cintrón *et al*. 1978). Very few mangroves survive above a soil salinity of about 70-80 ‰. The biomass, mean canopy height, and basal area generally increase in the direction riverine> basin, and fringe > dwarf within any latitudinal zone (Table 1). This is due to a number of factors including lower salinity and sulfide stress and higher nutrient input. These will be addressed in more detail in subsequent sections.

Another important constraint on the development of biomass in mangroves, particularly in areas such as the Caribbean, is the frequency of hurricanes. It is interesting that of those sites from the Gulf coast and Caribbean islands in Fig. 8a (25° latitude), those with the highest biomass are located on west coast of Yucatan peninsula where hurricanes seldom occur (Ruffner, 1978). The basin mangrove forest in Rookery Bay was apparently damaged by a hurricane in 1965, and the regeneration of this forest is demonstrated by high density and low biomass of trees in 1971 compared to 1987 (Fig. 7). A decline in density and increase in basal area is typical of a developing forest. Biomass was stable by 1987, indicating that a mature forest had developed within 25 yrs following the hurricane disturbance. Flores-Verdugo *et al*. (1986) attributed the poorly developed forest structure in el Verde Lagoon on the Pacific coast of Mexico to frequent hurricanes. Most mangroves in the tropics that are susceptible to damage from high winds and hurricanes are considered young successional forests.

The time scale for a mangrove forest to reach maturity based on steady state levels of biomass is dependant on the regional and local attributes of the environmental setting. Forests in lower latitudes with no natural or human disturbance may reach biomass levels over 250 ton/ha (Fig. 8a). In the protected areas of Malaysia, biomass of mature forests is considered 350-400 ton/ha (Putz and Chan, 1986). Yet forests in higher latitudes do obtain the levels of biomass as observed in lower latitude forests (Fig. 8a). These mangroves may reach mature levels of biomass in less time than in the lower latitudes, given similar rates in wood production. In the Caribbean and Gulf of Mexico, 25 -30 years may be enough time for forests to reach maturity given the potential biomass that can be supported in these areas (Figs. 3 and 8a). The constraints of solar energy (temperature) and microtopographic factors that establish upper limits of biomass and the frequency of disturbance of forest structure are important forcing functions that determine the level of maturity of mangrove forests in a region.

Productivity

A variety of factors influence the productivity of coastal wetland plants. Most factors are associated with changes in the physical or chemical environment, including solar radiation, temperature, tides, nutrient concentrations, soil type, drainage, oxygen concentration, and pH (Fig. 5). The individual plant species present in the intertidal zone can also affect patterns of productivity, because some plants have growth rates that are intrinsically higher than others. Some of these factors cause a difference in productivity over a latitudinal range within wetlands, while others operate at the local level. The primary productivity of mangroves is most often evaluated by measuring the rate of litterfall, as recorded for other forest ecosystems (see Brown and Lugo, 1982; Odum *et al*., 1982, and Twilley *et al*., 1986 for reviews of mangrove productivity). Litter productivity values for mangrove forests worldwide range from about 2 to 16 ton ha^{-1} yr^{-1} and also decrease with increase in latitude (Fig. 8b). Based on the mangrove sites represented in Fig. 8, the maximum level of litterfall is about 14 ton ha^{-1} yr^{-1} from 0 to 20 latitude. Above this latitude, litterfall decreases to less than 10 ton ha^{-1} yr^{-1}. The lower limit of productivity is 8 ton ha^{-1} yr^{-1} in the lower latitudes, compared to less than 2 ton ha^{-1} yr^{-1} in the subtropical zones. This trend indicates that litter productivity is less sensitive to changes in latitude than observed for biomass. The ratio of litter productivity to biomass (%) ranges from 5

Table 1. Structural characteristics, primary productivity, respiration, and litter fall for different types of mangrove wetlands in the New World Tropics (modified from Day *et al*., 1989)

Mangrove Wetland Type				
Parameter	**riverine**	**basin**	**fringe**	**dwarf**
Structral Characteristics[1]				
Mean canopy height (m)	17.7	9.0	8.2	1.0
Stem density (No./ha)	1760	3580	5930	25032
Basal area (m^2/ha)	41.3	18.5	17.9	0.6
Primary Productivity (g organic matter $m^{-2}d^{-1}$)				
Gross primary productivity [2]	24.0	10.0	-	2.8
Total plant respiration [2]	11.4	12.4	-	4.0
Net primary productivity [2]	12.6	5.6	-	0
Litterfall (g m^{-2} yr^{-1}) [3]	1170	730	906	120

[1] From Pool *et al*. (1977) and Brown and Lugo (1982). [2] From Brown and Lugo (1982), based on CO_2 gas exchange methods. [3] From Brown and Lugo (1982), Twilley *et al*. (1986), and Day *et al*. (1987)

Figure 9. Ratios of litter production to biomass for mangrove forests based on data in Figure 8.

to 10 % from 0 to 20 ^{o}, but increases exponentially to 35% from 20 to 35° (Figure 9; Y= 2.65 e $^{(0.058\ X)}$, R = 0.91). Although both biomass and litter productivity decrease from tropical to subtropical regions, the allocation of productivity to biomass also changes with latitude with less going to wood production in the cooler climates. Wood production to biomass ratios also shows this latitudinal shift in allocation of mangrove productivity away from biomass accumulation in the subtropics (Warner, 1990).

The range of productivity with latitude is about 8 ton/ha/yr, indicating the local effects of topography and hydrology on mangrove productivity (Fig. 5). Pool *et al*. (1975) suggested that regional rates in litter production in mangroves are a function of water turnover within the forest. The rank of the means of litter production in Fig. 10 of riverine> fringe > basin > dwarf (see also Table 1) supports this hypothesis. Fewer tides and lower freshwater input cause higher soil salinity (Cintrón *et al*., 1978) and/or the accumulation of toxic substances (eg. hydrogen sulfide Carlson *et al*., 1983; Nickerson and Thibodeau, 1985; McKee *et al*., 1988), which can result in increased stress on these inland mangrove forests (Hicks and Burns, 1975; Lugo, 1978). The mechanisms by which higher water turnover stimulates litter productivity are complex (Fig. 5) and may include a combination of factors including increased fertility, control of toxic substances in pore waters, aeration of soil matrix, and supply of silts and clays (Wharton and Brinson, 1979). These factors are described in more detail in the following sections. Turnover rate of mangrove biomass ranged from 0.041 to 0.126 (Table 2). There was no apparent relationship of turnover rate with latitude. Shifts in ratio of litterfall to biomass indicate less allocation of net productivity to wood production in higher latitudes (Warner, 1990). Average wood production based on eleven estimates is 12.08 ton ha^1 yr^1 (Table 2). Wood production decreased with latitude and a curve was fit to the data (Y = -0.449 X + 19.88, R= 0.60). Most of the wood production occurs in the 0° to 10° zone at about 0.1 Pg C/yr. Total wood production for mangroves is estimated at 0.16 Pg C/yr.

Hydrology in mangroves. Hydrology in mangroves is affected by tides, river input, and rainfall. Fringe mangroves usually are inundated by each tide that occurs, compared to more inland mangroves that are infrequently flooded by tides. For example, fringe mangroves in Rookery Bay, Fla., are inundated twice daily by tides for an annual total of about 750 tides. In the basin mangroves, there are about 175 tides annually with nearly 30 tides during September compared to only 2 tides in February (Twilley, 1985a, see Fig. 12).

Table 2. Wood production (growth) of mangroves relative to biomass and latitude and the turnover rate of mangrove biomass at each location

Site	Latitude	Biomass (ton/ha)	Growth ton/ha/yr	G:B (yr-1)	Reference
Malaysia	4° 50' N	286.8	11.8	0.041	Ong *et al*., 1979
Malaysia		257.4	24.1	0.094	Ong *et al*., 1979
Phuket, Thailand	8° N	159	20	0.126	Christensen, 1976
Puerto Rico	18° N	62.8	3.07	0.049	Golley *et al*., 1962
Estero Pargo. Mexico	18° 35' N	120	7.72	0.064	Day *et al*., 1987
Boca Chica, Mexico	18° 35' N	135	12.06	0.089	Day *et al*., 1987
Florida, USA			7.31		Sell, 1977
Florida, USA			13.33		Sell, 1977
Hainan, China	19° 53' N	248.5	11.5	0.046	Link *et al*., 1990
Fujian, China	24° 24' N	9304	8.69	0.093	Kin *et al*., 1985
Hong Kong	23° N	129.1	13.3	0.103	Lee, 1990

The flooding frequency in dwarf mangroves is very low and these areas have the lowest reported productivity. Gradients in tidal flooding frequency related to mangrove productivity follows the idea of tidal subsidy in these forested wetlands as developed for salt marshes (see Day *et al*., 1989). The hydrology of riverine mangroves is influenced by both river flooding and tide. These tidal low salinity to fresh areas have the highest reported mangrove productivity (Table 1).

Several observations have correlated the occurrence of higher biomass and productivity of mangroves with the presence of high river discharge (Fig. 10, Table 1). For example, Day *et al*. (1987) reported total aboveground productivity values of 2458 and 1607 g m^{-2} yr^{-1} for riverine and fringe forest, respectively, in Laguna de Terminos, Mexico. High productivity can develop with high river input even when there is poorly developed forest structure. Flores-Verdugo *et al*. (1987) reported very high litterfall (1,100 g m^{-2} yr^{-1}) in a small coastal lagoon in Mexico with high river input. The forest structure was poorly developed (basal area 11.9 m^2 ha^{-1}, monospecific stand of *Laguncularia*, mean height 7m) due to frequent hurricanes.

Limiting nutrients and hydroperiod: Nitrogen and phosphorus have been implicated as the nutrients most likely limiting primary productivity of mangrove ecosystems. Onuf *et al*. (1977) found greater leaf production in guano enriched overwash mangrove islands as well as significantly higher foliar nitrogen concentrations. Enhanced productivity of these islands along the Florida coast was not associated with a particular nutrient. However, leaf tissue analysis indicates that guano is enriched with more P than N and

Figure 10. Mean values (and one standard deviation) of litterfall for types of mangrove forests from Twilley *et al*. (1986) and estimates of organic carbon net export from riverine (Boto and Bunt 1984), fringe (Heald 1971), and basin (Twilley 1985) mangrove forests. (Mx is mixed basin mangrove forest and Mo is monospecific basin forest)

these naturally enriched sites indicate that nutrients are important to the primary productivity of mangroves. Boto and Wellington (1984) found a significant increase in productivity of mangroves forests in north Queensland after nitrogen and phosphorus enrichment. Growth of dwarf mangroves in a reef ecosystem off the coast of Belize was stimulated when fertilized with mixtures of nitrogen and phosphorus (Fig. 11). Highest growth rates in both leaf production, increased stem length, and tree height occurred in 5m x 5m plots fertilized with tree spikes annually from 1986 to 1988 (Twilley *et al*. unpublished). Two types of fertilizer spikes were preferentially enriched with nitrogen and phosphorus. A more marked response in tree growth was observed in the higher P relative to N enrichments. In addition, replicated plots of each treatment exhibited different rates of growth. Topographic surveys of the plots showed that the duplicate plot for each treatment was located in area with 10 cm greater water depth. Thus the productivity of mangroves is influenced by a combination of fertility and hydroperiod.

Hydrogen sulfide: Nickerson and Thibodeau (1985) reported that the distributions of *Avicennia* and *Rhizophora* were closely correlated with the amount of hydrogen sulfide in the soil (McKee *et al*., 1988; Carlson *et al*., 1983) They found that when compared with vegetation distant from the streamside, vegetation fringing streams was taller, more robust and grew in soils with lower hydrogen sulfide. This suggests that the concentration of hydrogen sulfide is an important factor regulating both primary productivity and forest structure in mangroves. McKee and Mendolssohn also found zonation of fringe and basin mangroves in Rookery Bay associated with H_2S and redox concentrations (unpublished). Greenhouse studies on seedlings have shown that *Rhizophora* is more tolerant that *Avicennia* and there is differential ability to oxidize soils. Scholander *et al*. (1955) demonstrated the mechanisms whereby gases can be transported in both species with release of oxygen from rhizosphere. Oxygen pumping can occur in both species, but it is not clear how this mechanism controls relative productivity and distribution of both species in adult root systems.

Salinity: At high salinities, osmotic stress (resulting in reduced water uptake) or cell membrane damage are likely to limit growth. Membrane permeability changes can reduce the influx of necessary nutrients and/or cause leakage of nutrients from the roots to the surrounding substrate. Increased permeability may also decrease the effectiveness of any selective ion uptake mechanisms in addition to increasing the potential for losses of needed oxygen from the roots (Linthurst 1980). Cintrón *et al*. (1978) found that with increasing salinity the structural values of mangroves decreased (Fig. 6). Above a soil salinity of about 70-80 ‰ very few mangroves survive. In Rookery Bay there was an apparent inverse relation of litter production among five basin mangrove sites and average soil salinity (Twilley *et al*., 1986). Soil salinity integrates the relative contribution of precipitation, river inundation, and tides as forcing functions to mangroves (Fig. 5). Where salt accumulates above normal sea water, stress to the development of biomass and productivity occurs and limits the function of mangrove ecosystems. Inland mangroves, such as basin and dwarf mangroves, are particularly susceptible to these conditions due to the infrequent inundation patterns associated with micro-topographic factors.

Figure 11. Results of fertilization studies of dwarf mangrove forests in Twin Cays, Belize. Three treatments with duplicate 5 x 5 m plots of mangroves in West Pond as follows: C is control, N is nitrogen enriched fertilizer (11% N, 5% P), and P is phosphorus enriched fertilizer (5% N and 13% P). Mean and one standard deviation are based on 3 systems tagged on each of five trees in each plot

Litter Dynamics

Litter produced in the canopy of mangrove forests represents a major source of organic matter and nutrients for outwelling to adjacent coastal waters (Odum and Heald, 1972). Thus the dynamics of mangrove litter including productivity (discussed above), decomposition, and export influence the coupling of mangroves to coastal ecosystems (Twilley, 1988). There are now ten estimates of carbon export from mangrove ecosystems that range form 1.86 to 401 gC m^{-2} yr^{-1} (Table 3). The average rate of carbon export from mangroves is about 210 gC m^{-2} yr^{-1}. This is nearly double the rate suggested by Nixon (1980) for carbon export from salt marshes (100 gC m^{-2} yr^{-1}). Greater carbon export from mangroves may be associated with the more buoyant mangrove leaf litter, higher precipitation in tropical wetlands, and greater tidal amplitude in mangrove systems studied (Twilley, 1988).

Export of detritus from mangroves is linked to the hydrology of mangrove forests. Rates of organic carbon export from basin mangroves are dependent on the volume of tidal water inundating the forest each month, and accordingly export rates are seasonal in response to the seasonal fluctuation in sea level (Fig. 12). Rainfall events may also increase organic carbon export from mangroves (Twilley, 1985a), especially dissolved organic carbon (DOC). Total organic carbon (TOC) from infrequently flooded basin mangroves in southwest Florida is 64 gC m^2 yr^1, and nearly 75% of this material is DOC (Twilley, 1985a). Particulate detritus export from fringe mangroves in south Florida was estimated at 186 gC m^2 yr^1 (Heald, 1971), compared to 420 gC m^2 yr^1 for a riverine mangrove forest in Australia (Boto and Bunt, 1981). Estimates of average tidal amplitude in these three forests types are 0.08 m, 0.5 m and 3 m, respectively. Accordingly, as tidal amplitude increased, the magnitude of organic material exchanged at the boundary of the forests increased (Twilley, 1985a; 1995).

The production of litter from the canopy and subsequent storage on the forest floor describes the dynamics of litter in different types of mangrove ecosystems (Fig. 13). Turnover rates of the litter compartment can be evaluated using the model $K = L/X_{ss}$, where L is litterfall, X_{ss} is the steady state value of litter on the forest floor and K is the litter turnover rate (Nye, 1961). This assumes that the litter compartment is in steady state, with litter production equal to litter losses. Litter turnover rates in temperate forest are less than 1 yr^{-1} compared to between 1 and 2 yr^{-1} for tropical forests (Olson, 1963). Differences are associated with the influence of temperature and soil moisture on the decomposition and consumption of litter on the forest floor. In mangroves, an additional fate of litter is transport by tides to adjacent coastal waters. Litter turnover rates for mangroves are generally higher than 2 yr^{-1} with some rates at 10 yr^{-1} indicating the potential significance of export on litter dynamics (Fig. 13). The range in litter production in fringe, overwash, and basin forests is less than three-fold (Lugo and Snedaker, 1974, Pool *et al*., 1975; Twilley *et al*., 1986), however the range of leaf litter turnover on the forest floor is almost twelve-fold. This suggests that processes on the forest floor such as decomposition and export are important factors regulating litter turnover in mangroves.

Figure 12. Hydrology and organic carbon export of a basin mangrove forest at Rookery Bay, Florida. (a) The monthly number of tides (solid line) and runoff (dashed line) in the forest (mean and standard error of tides based on 7 years of data). (b) Number of days each month that the forest floor was submersed in 1979. (c). Net export of total organic carbon from the two basin mangrove forests. (from Twilley 1985a)

Table 3. Export of organic carbon from mangrove forests (gC m^{-2} yr^{-1})

Site	export	Reference
Florida, USA	9.1	Lugo and Snedaker, 1974
Florida, USA	292	Odum and Heald, 1972
Florida, USA	186	Heald, 1969
Florida, USA	64	Twilley, 1985
Puerto Rico	401	Golley *et al*., 1962
Hichinbrook, Australia	340	Robertson, 1986
Hichinbrook, Australia	420	Boto and Brunt, 1981
Matang, Malaysia	193.5	Gong *et al*., 1990
New Zealand	109.5	Woodroffe, 1985
Hong Kong	1.9	Lee, 1989
average	**210**	

According to Twilley *et al*. (1986), the turnover rate of litter in fringe forests would be higher than basin forests because of the increased frequency of tides. Fringe and overwash sites in Rookery Bay have turnover rates of 6.4 and 8.3 yr^{1}, respectively (Fig. 4; Steyer, 1988). These rates are similar to those studied by Pool *et al*. (1975) for fringe and riverine sites in the Caribbean. The riverine, fringe, and overwash sites compared in Fig. 4 are frequently flooded sites located in south Florida and dominated by *R. mangle*. This group of mangroves has litter turnover rates greater than 5 yr^{-1}. An exception is a fringe forest with a turnover rate of 1.5 yr^{-1} due to accumulation of leaf wrack along the shore. Generally, frequently flooded mangrove forests such as riverine and fringe forests can be characterized as having elevated rates of litter turnover.

Leaf litter productivity in mixed basin forests is similar to fringe and riverine sites, yet leaf litter standing crop is much higher than in the frequently flooded sites. Litter turnover rates in these mixed basin forests are about 2 yr^{-1}, more than half the rates observed for fringe and riverine forests. Basin mangroves are located in areas with fewer tides and lower rates of litter export compared to fringe and riverine forests (Twilley, 1982). Leaf litter productivity by *R. mangle* and *A. germinans* is equal among the infrequently flooded basin mangroves in group 2 (Fig. 4). Yet rates of leaf decomposition of the latter species is much higher (Twilley *et al*., 1986), and the lower turnover rates reflect the slower decomposition rate of *R. mangle* on leaf litter dynamics. Since export is less in basin forests, decomposition of leaf litter has more influence on rates of leaf litter turnover.

Figure 13. Leaf litter of mangrove forest versus the productivity of leaf litter for different types of mangrove forests. Data are from the following: scrub and riverine II (Pool *et al*., 1975), basin III (Twilley *et al*., 1986, Steyer, 1988), fringe III and overwash III (Steyer 1988), riverine I (Twilley *et al*., 1990). Roman numerals refer to environmental setting as described in Table 1

Leaf litter productivity in the monospecific basin forest is from *A. germinans* and is lower than the fringe and mixed basin sites. The leaf litter standing crop is proportionately lower in the monospecific basin forest compared to mixed basin sites. Leaf litter turnover rates in these infrequently flooded forests are from 2 to 4 yr^{-1}, between the rates for fringe and mixed basin forests. Decomposition rates for *Avicennia* leaves, based on incubation of leaf litter in bags on the forest floor, range from 2.6 to 5.7 yr^{-1}. The frequency of tides in basin forests dominated by *A. germinans* in group 3 is similar to the mixed

basin mangroves in group 2 (Twilley, 1982). The higher rates of leaf litter turnover are associated with the higher decomposition rate of *Avicennia* leaf litter. Among the infrequently flooded basin forests in this study (group 2 and 3), the characteristics of leaf litter dynamics on the forests floor follow the pattern of leaf litter decomposition.

Trends for litter productivity and export suggest that as geophysical energy increase, the exchange of organic matter between mangroves and adjacent estuarine waters also increase. Litter productivity in a riverine forest in Ecuador is similar to a riverine forest in south Florida at about 10 Mg ha^{-1} yr^{-1}. However, the riverine forest in Ecuador has a 3 m tidal amplitude, while the tides in the riverine forests in south Florida are 0.5 m. Leaf litter on the forest floor in Ecuador is absent except for three months of the year (Twilley *et al*., 1990). This may be expected to be associated with greater export owing to the effect of tides on the transport of leaf litter from the forest. Yet observations in the mangroves in Ecuador suggest that most of the leaf litter on the forest floor is harvested by the mangrove crab, *Ucides occidentalis*, and transported to sediment burrows (Twilley *et al*., 1990). During September and October, when the crab aestivates, the standing crop of leaf litter increases on the forest floor. The levels of leaf litter during these two months are still much lower than expected based on daily rates of leaf fall suggesting that leaf export is significant. The influence of mangrove crabs on litter dynamics has been described in other mangrove ecosystems with high geophysical energies and rates of litter turnover above 5 yr^{1} (Malley, 1978, Leh and Sasekumar, 1985; Robertson and Daniel, 1989). Thus, the use of geophysical forcing functions such as tides to predict export of leaf litter is limited by consideration of biological factors within the ecosystem. In these examples, high rates of litter turnover do not reflect the coupling of mangrove to coastal waters, but the conservation of organic matter within the forest.

Nutrient Cycling

Nutrient Recycling

It has been argued for other ecosystems that nutrient recycling may be of greater significance than inputs to maintaining productivity. In mangroves, recycling processes include reabsorption or retranslocation of nutrients prior to leaf fall (Ryan and Bormann, 1982; Vitousek, 1982), and the immobilization of nutrients in leaf litter during decomposition (Brinson, 1977). There may also be mechanisms of nutrient regeneration associated with animal communities that colonize aerial root systems of mangroves, yet these mechanisms have received little investigation. The patterns in nutrient recycling may influence the productivity of mangrove communities, as well as the exchange of nutrients at the boundary of mangroves. Depending on the nature of nutrient recycling within the forest, mangroves may serve as either a nutrient source or sink to adjacent coastal waters.

Retranslocation of nutrients from senescing leaves to stems prior to leaf fall is an intrasystem nutrient recycling mechanism that may reduce the loss of nutrients to export (Switzer and Nelson, 1972; Turner, 1977; Ryan and Bormann, 1982). Steyer (1988) found that nitrogen storage and retranslocation are associated with litter dynamics in fringe and basin forests in Rookery Bay (Fig. 14). Fringe forests are inundated daily by tides, and the accumulation of leaf litter is small compared to basin forests (see Fig. 13). Accordingly, the content of nitrogen in the soil of each forest differs from about 200 g/m^2 in the fringe to 475 g/m^2 in the basin forest (Fig. 14). The retranslocation of nitrogen in *R. mangle* in these forests is significantly lower in the site with higher nitrogen fertility (Steyer, 1988). Thus the canopy may be a site of nitrogen conservation in mangroves and, together with leaf longevity, could influence the nitrogen demand of these ecosystems. It is not clear if the relative amounts of nitrogen conserved in the canopy via retranslocation responds to amount of soil fertility.

The concentration of nitrogen in leaf litter usually increases during decomposition on the forest floor (Heald, 1969, Rice and Tenore 1981, Twilley *et al*., 1986; Day *et al*., 1987). If this increase of nitrogen is proportionately greater than the loss of leaf mass during decomposition, then there will be a net input of nitrogen to the forest floor. The source of this nitrogen may be absorption and adsorption processes by bacterial and fungal communities (Fell and Master, 1973; Rice and Tenore, 1981; Rice, 1982), and nitrogen fixation (Gotto and Taylor, 1976; Zuberer and Silver, 1978; Potts, 1979; Gotto *et al*., 1981; van der Valk and Attiwill, 1984). Twilley *et al*. (1986) found that this process of nitrogen immobilization occurs in decomposing *R. mangle* leaf litter in a basin mangrove forest. Given the accumulation of leaf litter in this type of forest, this net input of nitrogen may be important to the nitrogen economy of these mangroves. However, in the fringe and riverine forest where the residence time of *R. mangle* leaves is very short, these processes are unimportant to nitrogen cycling on the forest floor (Twilley, 1988).

Figure 14. Nitrogen retranslocation associated with soil fertility in fringe, overwash, basin forest with mixed vegetation and basin forest with monospecific vegetation in Rookery Bay, Florida (Steyer 1988)

In riverine and fringe mangrove forests where leaf export is high, the reabsorption of nutrients by trees from leaves prior to leaf fall increases nutrient conservation. Inland mangrove forests have higher decomposition and mineralization rates of leaf litter, and along with infrequent tides, have lower rates of detritus export. Thus high litter turnover may increase the availability of nutrients for reabsorption by roots and prevent the loss of nitrogen from the forest. These results suggest that different mechanisms to conserve nitrogen may have evolved at different levels of fertility found along a tidal continuum. In areas of high tidal frequency, higher recycling efficiency occurs in the canopy via retranslocation. Whereas in sites with lower tidal activity, nutrient recycling is enhanced on the forest floor via leaf decomposition. These mechanisms are based on only limited data for basin mangrove sites in Rookery Bay and Estero Bay, with even less information for riverine or fringe mangrove forests. Also, fluxes associated with denitrification and nitrogen fixation must be accounted for before the complete significance of these recycling processes can be evaluated (Vitousek 1984; Twilley *et al*., 1986).

Gaseous exchange

Determining whether mangroves are a nutrient source or sink, and defining processes associated with this function, is clearly one of the most understood properties of mangrove ecosystems. The exchange of nitrogen, together with the accumulation of nutrients in mangrove sediments (see below), are two of the key processes associated with the function of mangroves as a nutrient sink. The net exchange of nitrogen gas in mangrove ecosystems depends on the relative rates of nitrogen fixation and denitrificaiton. Nitrogenase activity has been observed in decomposing leaves, root surfaces (prop roots and pneumatophores) and sediment, but few of these studies have interpreted these rates relative to the nitrogen budget of mangrove forests (Kimball and Teas, 1975; Gotto and Taylor, 1976; Zuberer and Silver, 1978, Potts 1979; Gotto *et al*., 1981). Results from mangrove sediments in south Florida indicate that nitrogen fixation rates range from 0.4 to 3.2 g N m^{-2} yr^{-1} (Kimball and Teas, 1975; Zuberer and Silver, 1978). Nitrogen fixation rates of specific components of a mangrove ecosystem are more commonly normalized to dry mass basis.

These studies have shown that decaying mangrove leaves are sites of particularly high rates of fixation, and thus may account for some of the nitrogen immobilization in leaf litter on the forest floor (Gotto *et al*., 1981; van der Valk and Attiwill, 1984). For example, Gotto *et al*. found that nitrogen fixation ranged from 4 nmol gdw^{-1} h^{-1} (nmol of ethylene produced from acetylene) in beach sediments to 875 nmol gdw^{-1} h^{-1} in decaying *Avicennia* mangrove leaves. Nitrogen fixation in *Avicennia* leaves of this study was nearly twice that of *Rhizophora* leaves. Rates of nitrogen fixation in decaying mangrove leaves may also depend inversely on the ammonium concentration or fertility of mangrove sediments (van der Valk and Attiwell, 1984). Thus the contribution of this ecological process to the fertility of mangrove ecosystems may depend on the nutrient status of litter among different types of mangrove ecosystems as discussed above.

Direct estimates using nitrogen gas evolution and acetylene blockage techniques from temperate zones in the Northern Hemisphere indicate that denitrification may account for 2050% loss of nitrogen from estuarine systems (Seitzinger *et al*., 1980). While denitrification estimates are fundamental to developing annual budgets of nitrogen in mangroves, there are few estimates of denitrification in tropical estuaries. Walsh (1967) noticed that nitrogen concentrations decreased in waters moving through a mangrove in Hawaii. Nedwell (1975) using enclosures to measure nutrient uptake in mangrove sediments noticed they had a great capacity to dissimilate nitrate, particularly in areas of nutrient enrichment from sewage discharge. These and other observations on the fate of nitrate in waters exchanged with mangroves suggest that this process is potentially significant in mangrove ecosystems.

The coupling of nitrification and denitrification has been investigated in some wetlands, but not in mangroves. Sediment redox conditions that enhance the coupling of these two processes in mangroves may be maintained by frequency of

tidal inundation and plant roots (Smith and Patrick, 1983). Reddy and Patrick (1986, 1984) showed how the frequency of inundation in flooded soils maximized the coupling of denitrification reactions in the root zone of plants. Since oxygen from the atmosphere is neccesary for nitrification (the oxidation of NH_4 to NO_3) to occur within sediments, frequency of flooding becomes an important factor controlling nitrogen cycling in wetlands. Denitrification (the reduction of NO_3 to N_2) occurs under anaerobic conditions and is influenced by the concentration of nitrate and organic matter (Payne, 1973). Under appropriate redox conditions and sources of NO_3, denitrification represents a major loss of N loss from aquatic sediments to the atmosphere. Since supply of nitrate is often limiting in sediments, rates of nitrification are one of the most important processes controlling denitrification (Jenkins and Kemp, 1984). In vegetated sediments NH_4 in deeper anaerobic zone of the sediment diffuses to the root zone where it is either absorbed by aquatic plants or oxidized to NO_3 near the vicinity of roots. The rhizosphere provides an oxidized interface in an otherwise anaerobic environment, thus providing a mechanism for the supply of NO_3. This NO_3 is either used by plants or diffuses into adjacent anaerobic zones where it is denitrified (Reedy *et al*., 1989).

Nishio *et al*. (1983) estimated that the rate of denitrification coupled to nitrification was 2.5 times higher than denitrification using NO_3 from the overlying water. Thus the NO_3 produced by nitrification was a major source for denitrification. The biological control of nitrification and denitrification in sediments and wetland soils by plants has recently been addressed by Reddy *et al*. (1989) and Caffrey (1989). Christiansen and Sorensen (1986) measured higher denitrification rates in lake sediments covered with *Littorella* sp than in nonvegetated areas. They concluded that higher denitrification rates in vegetated sediments were due to O_2 transport into the root zone that stimulated nitrification.

Denitrification depends on a number of environmental factors (Knowles, 1982; Seitzinger, 1988) which fluctuate and cause temporal and spatial variability in rates (Law *et al*., 1991). The ecological importance of these redox interfaces is that the coupling of anaerobic and aerobic processes may promote the loss of nitrogen from wetland ecosystems. These interfaces enhance the coupling of nitrification and denitrification spacially by forming microsites caused by plant irrigation of sediments. Interfaces may also form temporally from hydrology causing wet and dry cycles that promote oxygen diffusion to sediments. There are few studies in the field to test the spatial and temporal scales of these processes in wetland ecosystems. In tidal coastal wetlands both the effects of plants and tides may be important in understanding denitrification. Thus the combination of zonation and hydrology in different types of mangrove forests may be important to the exchange of nitrogen gas in these coastal forested ecosystems.

Nutrient Accumulation

Sediments suspended in the water column are deposited in mangroves during flooding and this material enriches mangrove soils. The extensive root system of mangroves enhances this trapping process and retards the forces of erosion along the shoreline (Scoffin, 1970). Although this function has been overstated to the extent of calling mangroves “walking trees”, roots do contribute to sedimentation in estuaries (Lynch *et al*., 1989). The accumulation of organic matter in the five sites investigated in Florida and Mexico by Lynch *et al*. (1989) ranged from 130 to 409 g m^{-2} yr^{-1} (Fig. 15a). Levels of organic matter accumulation were not correlated with amount of litter production. In Boca Chica the average accumulation of organic matter was 272 g m^{-2} yr^{-1}. Based on litter productivity (dry mass) of 12.6 Mg ha-1 yr-1, there was approximately 21.6 g m^{-2} yr^{-1} accumulated per Mg ha^{-1} yr^{-1} produced.

In Estero Pargo, the ratio of accumulation (organic matter) to production (dry mass) was 24.1, whereas in the basin forest in Rookery Bay the ratio was 26.7 (based on seven year average of litter productivity, Twilley *et al*., 1986). The higher ratio associated with the basin forests may be due to the increased residence time of leaf litter, although the role of belowground productivity to the accumulation of organic matter in mangrove forests is unclear.

The contribution of inorganic material varied greatly among the five sites and ranged from 133 to 1404 g m^{-2} yr^{-1} (Fig. 15a). The higher values occurred in the riverine mangrove forest in Terminos Lagoon in Mexico where the Candelaria, Chumpan, and Palizada rivers discharge more than 190 m^3/s of freshwater. The ratio of inorganic to organic material in the sedimentation process was 0.70 and 1.9 for the basin forests in Estero Pargo and Rookery Bay, compared to 4.5 for the riverine forest in Boca Chica. These ratios indicate the relative contribution of allocthonous and autochthonous sources of materials to sedimentation in different types of mangrove ecosystems. Riverine mangroves have higher sedimentation rates due to the higher input of inorganic materials to these ecosystems.

Figure 15. The accumulation of inorganic and organic matter associated with the sedimentation in different types of mangrove forests based on accretion rates estimated from lead-210 analysis and the nutrient accumulation associated with these estimates of sedimentation (Lynch 1989)

Associated with processes of sedimentation is the accumulation of nutrients in mangrove soils (Lynch, 1989). Within site variation in accumulation of nitrogen was greater than the among site variation (Fig. 15b). As observed for organic matter accumulation, the accumulation of nitrogen among the riverine and basin forests was similar at about 5.5 g m^{-2} yr^{-1}. Phosphorus accumulation, on the other hand, varied considerably among the five mangrove sites studied by Lynch (1989). For example, phosphorus accumulation was 0.78 g m^{-2} yr^{-1} in riverine mangroves at Terminos Lagoon, compared to only 0.18 g m^{-2} yr^{-1} in the basin forest at Rookery Bay. The accumulation of phosphorus is related to the input of inorganic sediment. This phosphorus is apparently adsorbed onto sediment particles and trapped in mangrove forests. The selective nature of this mechanism for phosphorus relative to nitrogen is reflected in nitrogen:phosphorus ratios (atom weight) that are less than 20 for riverine forests, compared to a range of 50 to 70 for basin mangroves influenced by tides (Lynch, 1989). Thus, an ecologically significant difference in fertility among the riverine, fringe, and basin sites in the study by Lynch was the accumulation of phosphorus associated with river discharge.

Conclusions

The ecosystem approach to the management of coastal resources integrates both the ecological processes of environmental systems together with the socioeconomic characteristics of human systems (Fig. 16.). Many of the ecosystem models of coastal systems, such as mangroves, presently lack quantitative analysis. Thus in many cases, site specific management plans have to be applied to a variety of systems and issues. This review suggests that the geomorphological and ecological characteristics of a coastal region can be used to understand the structure and function of mangrove ecosystems. The influence of these external energies on the productivity and nutrient cycling will determine the role of mangroves in habitat and water quality in the coastal zone.

There are many intrasystem processes that are linked to hydrology of coastal regions that influence the productivity and nutrient dynamics of mangroves. It is evident that the function of mangroves, as determined by productivity and nutrient cycling, are constrained by the forcing functions in an environmental setting by establishing certain patterns of intrasystem processes. Better understanding of whether mangroves serve as a nutrient source or sink, or in the outwelling of organic matter, will occur as we increase our knowledge of the mechanisms that link hydrology with ecosystem processes

Some quantitative examples of this concept are presented, such as effects of latitude, soil salinity, and phosphorus content in rivers on the biomass and productivity of mangroves. In addition, the outwelling of organic matter will vary according to amplitude and frequency of tides. Other functions such as nitrogen fixation and denitrification are less understood, leading to continued confusion as whether mangroves are nutrient sources or sinks to coastal waters.

Figure 16. Diagram of linkages among energy signature and the ecological function, atributes, and uses of mangrove ecosystems

Sediment accumulation has been quantified and is greater in riverine mangroves compared to basin forests. Quantifying sedimentation in mangroves has implications to global sediment budgets in tropical regions (particularly in coastal river systems such as the Amazon and in Asia, Twilley *et al*., 1992). This process may also be important to the mass balance of nutrients and trace elements in these land margin ecosystems. Succession is still poorly understood, even though we've had models to test since 1940. This review suggest that the regeneration rates of natural forests will vary with latitude, ranging from 25 years at 20 to 30° compared to 100 years at latitudes less than 10°. This is because the potential biomass that can develop at the lower latitudes requires longer time constants for forests to reach maturity. As we discover more of these relationships between environmental conditions and ecosystem properties, we will vastly improve our ability to manage these natural resources

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Productividad Secundaria, Utilización del Hábitat y Estructura Trófica

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Resumen

Los organismos marinos, en el transcurso de su ciclo de vida, pasan por distintas etapas biológicas, desde huevo hasta adultos reproductores, acoplando cada etapa con características físico-ambientales que son propias para los diferentes ambientes y hábitats. Cada uno de estos momentos son críticos para el óptimo desarrollo de las distintas etapas biológicas. En escalas espaciales y temporales, esto se traduce en una clara separación de ambientes físicos acoplados con cada una de las etapas biológicas de las especies. Dentro de la complejidad de la zona costera, ésta se caracterizada por diferentes subsistemas entre los que se incluyen lagunas costeras y estuarios, bocas de conexión entre aguas protegidas y el mar, plataforma continental adyacente. En latitudes tropicales, estos subsistemas están caracterizados por una gran diversidad de ambientes entre los que se pueden mencionar a los manglares, pastos marinos y zonas palustres entre otros, los cuales son áreas idóneas de reproducción, crianza y alimentación de diferentes organismos. En éste capitulo se describe a los manglares como hábitat critico que contribuye significativamente a la producción secundaria. Se destacan dos importantes funciones ecológicas del ecosistema: **1.** Como una área de protección, debido la estructura de sus raíces especializadas y adaptadas a periodos de inundación, lo cual le permite al ecosistema mantener una importante biodiversidad, y sostener poblaciones de importancia ecológica y comercial; **2.** Como fuente de carbono (a través del detritus) para muchos de los organismos que residen en los manglares a través de la trama trófica. Esto hace que el ecosistema de manglar funcione como un área de alimentación para juveniles y adultos, crianza para larvas y juveniles de diferentes especies.

Abstract

The marine organisms, in the course of their life cycle, go through different biological stages from egg adult reproductive, coupling each stage with environmental characteristics for different ambient and habitats. Each one is critical for the optimum development of the different biological stages. In spatial and temporary scales, this is observed as a clear physical environment coupled with each one of the biological stages of the fish species. The coastal zone is a complex environment characterized by different subsystems which are coastal lagoons, estuaries, connection inlets protected waters and the sea, adjacent continental shelf. In tropical latitudes, these subsystems are characterized by a great diversity of environments such mangroves, sea grass, swamp zones. They are suitable reproduction areas, feeding and nursery areas of different organisms. In this chapter we are described the mangroves as critical habitat that contributes significantly to the secondary

production. This point of view emphasized In two Important ecological functions of the ecosystem: **1.** As a protection area, due to the structure of their specialized and adapted roots to flood periods. This function permits to maintain an important biodiversity and support important commercial and ecological populations; **2.** As source of carbon (detritus) for many animal species that live in the mangroves, through the trophic chain. The above causes make that the mangrove ecosystems operate as a feeding area for juveniles and adults, as a nursery area for larvae and juveniles, protection for eggs, larvae and juveniles of different species.

Introducción

Se ha discutido ampliamente que los ecosistemas de manglar en la zona costera tropical, conforman un hábitat crítico para numerosas especies de Invertebrados (moluscos y crustáceos), y de vertebrados como aves, mamíferos y particularmente peces que utilizan sus recursos en alguna etapa de su ciclo de vida. Considerando a los ecosistemas de manglar como un hábitat particular, Day y Yáñez-Arancibia (1988) establecen, desde el punto de vista teórico, que un hábitat representa una unidad morfofuncional de un todo mayor. Es decir, es el mínimo nivel de información que define un paquete de elementos comunes, normalmente Identificados como una "región" especifica dentro de un ecosistema.

Este componente del sistema costero en la banda subtropical y tropical es de suma importancia por las diferentes funciones que desempeña, que van desde el mantenimiento de las características físicas de la costa, ya que prevén la erosión de la línea de costa por su ubicación y estructura. Así como importantes áreas de alta diversidad biológica por sus funciones de alta productividad y protección de diferentes especies (Szelistowski, 1990; Yáñez-Arancibia *et al.,* 1988; 1991; 1993).

Los estudios sobre los ecosistemas de manglar y su ¡interacción con las comunidades de animales se enfatizan desde que Odum (1970) y Odum y Heald (1972, 1975) establecen la hipótesis de que el carbón de los manglares (hojas, propágulos, y tejidos de la madera) pueden contribuir a la trama trófica basada en el detritus, de las aguas costeras adyacentes. Sin embargo, las diferentes Investigaciones que se han llevado a cabos desde entonces aún no han podido clarificar esta relación y aun permanece mucha Incertidumbre en relación con la Importancia de este material en la producción secundaria de invertebrados, peces, pájaros entre otros.

El presente capitulo, tiene por objetivo sintetizar diferentes investigaciones sobre el papel ecológico de los bosques de manglar en cuanto a su función como hábitat critico que proporciona refugio y protección a las especies animales de importancia ecológica y comercial. Como fuente de alimento a través de la trama trófica y finalmente en la producción secundaria relacionada con las pesquerías comerciales. Este enfoque se enfatiza en los estudios realizados en el sur del Golfo de México.

Utilización del Hábitat

Los ecosistemas de manglar en la zona costera por la forma de las raíces aéreas de sostén y los neumatóforos, se consideran que proporcionan un hábitat critico que puede ser particularmente propicio para ser usado por los juveniles y adultos de especies nectónicas como áreas de protección y alimentación, así como áreas de crianza y desove (Jeyaseelan y Krishnamurthy, 1980; Odum *et al.,* 1982; Bell *et al.,* 1984; Thayer *et al.,* 1987; Robertson y Duke, 1987; Yáñez-Arancibia *et al*., 1988,1991, 1993; Vega-Cendejas *et al.,* 1994*).*

En el sur del Golfo de México Yáñez-Arancibia et *al.* (1988, 1991) evalúan la estacionalidad de la biomasa y diversidad de los peces estuarinos vinculados a la heterogeneidad espacial de la Laguna de Términos. Para lo cual, estudian los patrones de biomasa, densidad, número de especies y talla de la comunidad de peces.

Para establecer el patrón de utilización secuencial de los hábitats de la laguna por las comunidades de peces, se tomaron en cuenta las siguientes consideraciones: **1)** el patrón de comportamiento individual de ciertas especies que son definidas como especies dominantes con base a tres parámetros **a)** por su alta frecuencia de aparición en las capturas y sus valores altos de **b)** biomasa y **c)** densidad. **2)** Para determinar el uso secuencial de los diferentes hábitats de la laguna se consideró la acoplación de las estrategias biológicas del ciclo de vida de las especies (juvenil, adulto madurando, adulto en reproducción, adulto en descanso) con la estacionalidad ambiental (época de secas, lluvias y nortes), cuantificado por el índice de Abundancia de Rogers y Herke (1985). Con ésta información se infiere el uso programado estacional de las especies.

Figura 1. Localización de los sitios experimentales analizados en la Laguna de Términos. SFL ubicado en el Río Palizada se refiere a los manglares con influencia fluvial; SMS, EP, SM y MP corresponden al área de interacción pastos marinos y manglar; PR, P ubicado en Puerto Real se refiere al hábitat de pastos marinos (modificado de Yáñez-Arancibla *et a*/., 1993)

Los diferentes ambientes de la Laguna de Términos que Yáñez-Arancibia *et al. (1988,* 1991, 1993) analizan, son los hábitats de manglar y de pastos marinos, que generalmente son componentes importantes en los sistemas costeros (Fig. 1). El hábitat de manglar, como área de estudio, se localiza en los sistemas fluvio-lagunares (SFL) que corresponde a los ríos asociados a la laguna, presentando manglares ribereños; mientras que el hábitat de pastos marinos se ubica tanto en un canal de marea de la Isla del Carmen denominado Estero pargo (SMS. EP, SM. MP) con la presencia de praderas de *Thalassia testudinum* y asociados a manglares de franja; y en la Boca de Puerto Real, que es un ambiente típicamente marino con la presencia de pastos marinos (PR, P) -[las iniciales dentro de los paréntesis corresponden a la nomenclatura utilizada en las figuras para identificar a cada hábitat]-.

Este último hábitat, también constituye una de las dos bocas que conecta a la Laguna de Términos con el Golfo de México, que comprende la principal ruta de inmigración de peces a la laguna. Dentro de la laguna, los movimientos migratorios de los peces son favorecidos por las corrientes hacia el canal de marea o Estero pargo siguiendo hacia la Boca del Carmen. Esta última boca en un ambiente de agua salobre y turbia que funciona como una ruta de migración de algunas especies de peces que se dirigen a la Sonda de Campeche (Fig. 1). No obstante, esta boca también constituye una ruta de inmigración de los individuos a la laguna por la capa inferior del agua, distribuyéndose principalmente en áreas de baja salinidad y alta turbidez (Yáñez-Arancibia *et al.,* 1991).

Esta inmigración de individuos a la laguna es constante a lo largo de año (Yáñez-Arancibia y Day 1982; Yáñez-Arancibia *et al.,* 1991). Sin embargo, en septiembre y octubre se registra la mayor inmigración de Juveniles relacionada con los cambios climáticos entre las épocas de lluvias y nortes, cuando se manifiesta la mayor descarga de ríos, con valores altos de productividad primaria en las aguas abiertas de la laguna, principalmente cerca de las bocas de los nos. Asimismo, durante este interperiodo, se asocia un incremento de la diversidad de peces y de tallas pequeñas. Similarmente, Febrero constituye el interperiodo entre la época de nortes y la de secas. Durante éste, se registra baja diversidad de especies, individuos de tallas grandes y alta biomasa.

Para el análisis de las especies de peces entre los hábitat SFL y SMS de la Laguna de Términos, Yáñez-Arancibia *et al.* (1988) comparan la abundancia relativa de las especies dominantes a largo del año (Fig. 2). El comportamiento de esta sucesión de curvas, sugiere el uso secuencial del estuario por las diferentes especies. No obstante que en latitudes tropicales, no se registran fuertes fluctuaciones de biomasa total a través del año, como es común en estuarios de latitudes altas. Estos pulsos presentaron una tendencia a ser mayores en época de nortes en el hábitat SFL, mientras que en el hábitat SMS se presentan los mayores pulsos en época de nortes-secas.

De esta forma las especies dominantes actúan como controladores de la estructura y función de toda la comunidad. Puesto que la amplia distribución espacial de estas especies en ambos hábitats (SFL, SMS) optimiza sus ciclos de vida, esto es, diferentes etapas biológicas se presentan en hábitats diferentes, reflejando el comportamiento general de la comunidad. Por ejemplo, en el hábitat SMS *Sphoeroides testudineus, Diapterus rhombeus* y *Eucinostomus gula* presentan una talla promedio de los individuos más pequeña que en FLS. Lo opuesto es cierto para *Bairdiella chrysoura* y *Arius melanopus* (Yáñez-Arancibia *et al*., 1985a).

Figura 2. Variación temporal de la abundancia de siete especies dominantes de peces. Los ejemplos calculados en los hábitats FLS y SMS muestran una clara programación estacional de especies de peces y una utilización secuencial del hábitat. Otras dos importantes especies exclusivas de cada hábitat estudiado son *Orthopristis chrysoptera* (SMS) y *Petenla splendida* (FLS).

Figura 3. Variación temporal en abundancia de ocho especies de peces dominantes. Sistema de pastos marinos (S) y Sistema pastos marinos/manglares (S/M) muestra Ob= *Opsanus beta,* Oc= *Orthopristis chrysoptera,* Bc= *Bairdiella chrysoura,* Cs= *Corvula sacta-luciae,* Ar= *Archasargus rhomboidalis,* Ap= *A. probatocephalus.* Am= *Arius melanopus,* Af= *A. felis.*

Por lo tanto, se establece que los peces de un hábitat son significativamente más pesados en relación a su longitud que los peces del otro hábitat. El predominio de tallas pequeñas de una especie en un hábitat determinado establecerla que es un área de alimentación y protección para los juveniles de la misma; mientras que las tallas grandes en el otro hábitat representaría un área de alimentación y maduración o descanso gonádico de la especie.

Similarmente, al comparar las comunidades de peces y el uso secuencial en las bocas de conexión en la laguna de Términos, se establece que la comunidad de peces en el canal de mareas (EP, MP) ubicado entre las dos bocas de conexión de la laguna, esta constituida de individuos de talla pequeña en promedio. Este mismo hábitat, presentó la mayor densidad de peces en comparación con los otros dos hábitats estudiados (PR, P y Boca del Carmen), donde los peces fueron de tamaño grande y pocos numerosos. la predominancia de peces juveniles y preadultos en manglares / pastos marinos (EP, MP) comparado principalmente con los adultos de la misma especie en pastos marinos (PR, P), constituye una evidencia del uso secuencial de los hábítats (Yáñez-Arancibia *et al.,* 1991).

De acuerdo a la tendencia de las curvas establecidas por el Índice de Abundancia de Rogers y Herke (1985) de las especies dominantes, se observa que estas son más abundantes en la Boca de Puerto Real (PR, P) a fines de la época de lluvias y durante toda la época de nortes (Fig. 3). Mientras que en el sistema manglares / pastos marinos (EP, MP), la mayor parte de las especies analizadas presentan un máximo a fines de la época de nortes y durante toda la época de secas.

Por lo tanto, las praderas de pastos marinos en la boca de conexión (PR, P) constituye un área de tránsito. El movimiento de inmigración a través de la boca durante la época de nortes, es facilitado por el fuerte flujo neto de agua, que se presenta particularmente durante los eventos meteorológicos denominados nortes. Mientras que para el sistema de manglar / pastos marinos (EP, MP) ubicado a lo largo del litoral interno de la Isla del Carmen constituye un área de crianza caracterizada por la presencia de aguas tranquilas, alto contenido de materia orgánica y altas densidades de invertebrados (Fig. 4; Yáñez-Arancibia *et al.,* 1991, 1993).

Los individuos que penetran por la Boca de Puerto Real en época de nortes, se localizarán en el canal de marea (EP) durante la época de secas, sincronizándose a los pulsos de productividad primaria acuática. El papel ecológico de este hábitat como un área de alimentación esta representado por *Arlus melanopus* y *Lutjanus sinagris,* que son principalmente reportadas como adultos y como área de crianza para *Eucinostomus gula* y *Orthopristis chrysoptera* que se reportan como juveniles. Finalmente, es un área de reproducción de *Cichlasoma urophthalmus, Chilomycterus schoepi* y *Opsanus beta,* las cuales se registran tanto como individuos juveniles como de adultos (Caso Chávez *et al.,* 1988; Lara-Domínguez y Yáñez-Arancibia, 1988; Yáñez-Arancibia *et al.,* 1985a).

La figura 5, muestra algunos ejemplos de ciclos de vida de diferentes especies de peces dominantes para ambos hábitats. las interacciones entre los hábitats con las especies define patrones de migración y colonización que se relaciona con las estrategias de reproducción, protección contra predadores y áreas de crianza, hábitos alimenticios y reclutamiento. De esta manera, se detectaron que especies que son reproductores marino-estuarinos usan el hábitat de pastos marinos y manglares (SMS, ER, MP), los reproductores estuarinos usan tanto hábitats de manglares (FLS) como de pastos marinos y manglares (SMS, EA, MP), mientras que otros exclusiva-mente usan hábitats de pastos marinos (PR, P).

Figura 4. Variación de diferentes parámetros ambientales en función de las bocas de conexión (BP= Puerto Real; BC= Boca del Carmen) y del canal de marea ubicado en la Isla del Carmen (EP= Estero Pargo)

El uso de diferentes hábitats por las diferentes estrategias de vida, optimiza las tasas de reclutamiento, por ejemplo, los Juveniles de los reproductores marinos e.g., *Archosargus rhomboidalis* y *Haemulon plumieri* migran del hábitat de pastos marinos y manglar (SMS EP. MP) en la época de secas cuando la productividad es alta en este hábitat. Mientras que los reproductores dulceacuicolas-estuarinos como *Arius melanopus* y *Bairdiella chrysoura* se alimentan como subadultos en el hábitat de pastos marinos y manglar (SMS EP. MP) durante la época de secas y regresan a FLS para reproducirse durante la época de lluvias, usando ambos hábitats durante los periodos de mayor productividad. Finalmente, *Cichlasoma urophthalmus* y *Urolophus jamaicensis* usan exclusivamente SMS durante diferentes etapas de su ciclo de vida, principalmente cuando se registra la productividad más alta en el área (Yáñez-Arancibia *et al.,* 1985a).

Por otro lado, muchas de las especies analizadas son de importancia comercial y el separar sus ambientes de alimentación, reproducción y crianza favorece su permanencia en el ecosistema. De manera que los diferentes mecanismos de reclutamiento de los peces costeros dependientes estuarinos o relacionados a estuarios pueden estar controlados por dos principales tipos de procesos: **1)** los procesos físicos que tiene su principal influencia durante las etapas de huevos y larvas sobre la plataforma continental, las bocas estuarinas y parte del estuario; y **2)** procesos biológicos que tiene su principal influencia durante la distribución y abundancia de juveniles dentro del estuario. En el sur del Golfo de México, las especies de peces analizadas ya han sido transportadas, por procesos físicos, desde los ambientes marinos a las aguas costeras de diferentes ambientes como manglares, pastos marinos, lagunas costeras entre otros. Mientras que dentro de las áreas costeras predominan los procesos biológicos determinando el uso secuencial del hábitat acoplado a las estrategias biológicas.

Comparativamente en la costa del Pacifico Tropical Este, Szelistowsky (1990) establece que existen tres variables ecológicas que probablemente son importantes en la constitución de la estructura de las comunidades de peces en los manglares. Estas incluyen la proximidad de los manglares con respecto a otros hábitats, la mejor ruta del flujo de energía y las limitaciones físicas impuestas por el mismo sistema. Para este autor los hábitats de arrecifes de coral y pastos marinos en Punta Morales, Costa Rica, se encuentran pobremente desarrollados y es aquí donde los manglares

Figure 5. Ciclo de vida de seis especies de peces selectas: desovadores marino - estuarinos *A. rhomboidalis* y *H. plumieri;* dosovadores estuarinos *C. urophthalmus* y *U. jamaicencis;* desovadores agua dulce - estuarlnos *A. melanopus* y *B. chrysoura.* Los peces migratorlos usan los hábitats SMS y FLS en los periodos de mayor productividad para alimentación, desove o crianza.

tienen un papel ecológico fuertemente vinculado a los estuarios, bahías y/o grandes sistemas deltáicos (e.g., Golfo de Nicoya, Golfo Dulce). Donde las comunidades de peces están fuertemente dominadas por fauna estuarina típica, siendo abundantes el grupo de los bagres (Ariidae), de las corvinas (Sciaenidae), mojarras (Gerreidae) y lisas (Mugilidae).

Otro aspecto de los ecosistemas de manglar que aún no se discute a fondo, es que sus parámetros físicos son altamente variables tanto dentro como entre el sistema de raíces, y los estudios ecológicos se han limitado a observaciones de peces pasajeros más que dentro de las raíces (Thayer *et al*., 1987). En general entre las raíces, se pueden registrar amplios .rangos de salinidad, temperatura, fuerza de la marea y turbidez, que pueden limitar la distribución de los peces. Únicamente Thayer *et al.* (1987) ,en el sur de Florida, Zárate Lomeli (1996), y Yáñez-Arancibia *et al.,* (1994) en Laguna de Términos y Vega Cendejas (1998) en Ría Celestún, México, han caracterizado y cuantificado las comunidad peces en el sistema de raíces adyacente a los hábitats de manglar.

Este último autor encuentra que, los factores más importantes de producción natural que proporcionan las raíces de manglar para las poblaciones de peces fueron la turbidez que les ofrece protección, la materia orgánica como resultado de la dinámica del detritus que asegura la disponibilidad de alimento, y las relaciones biogeográficas de las especies.

Finalmente, son pocos los estudios sobre los primeros estados de vida de los peces (huevos y larvas) en los manglares, y la supuesta importancia de los manglares como sitios de desove y áreas de crianza de larvas esta basada más sobre especulación que sobre una fuerte base de datos. Ramírez *et al.* (1989) examinaron localidades de desove y distribución de larvas de anchoas en el sistema de manglar así como adyacente al mismo en Punta Morales (Golfo de Nicoya). Los resultados obtenidos muestran que, las anchoas parecen desovar próximas pero no dentro de los manglares reclutándose dentro del sistema a una longitud de 12 mm.

Ramírez *et al.* (1990) conducen una evaluación de ictioplancton en la misma área encontrando que las densidades de huevos planctónicos fueron menores dentro de los manglares que en las localidades adyacentes, pero que la densidad y diversidad de larvas no difiere significativamente entre las estaciones de muestreo. Sin embargo, son necesarias más Investigaciones antes de formular generalizaciones acerca del uso de los sistemas de manglar por los primeros estados de vida de los peces.

Estructura Trófica

En relación de como las principales rutas del flujo de energía pueden influir en la estructura de las comunidades de peces, Odum y Heald (1972, 1975) concluyen que la hojarasca del manglar, vía ruta del detritus, es la principal fuente de energía para los consumidores de la trama trófica, siempre que la biomasa de las algas y del plancton fueran bajas. Consecuentemente, dominarían la comunidad los peces capaces de utilizar directamente el detritus del manglar y los otros que predan sobre los detritívoros y hacen notar que algunas zonas costeras de importancia comercial se localizan próximas a los bosques de manglar y pastos marinos. (Heald y Odum, 1970; Odum, 1971; Heald, 1971; Odum y Heald, 1972, 1975).

Esto ha conducido a generalizaciones acerca de la estructura de la trama trófica en los estuarios con manglares. Por ejemplo, se estableció que en la mayoría de los estuarios la fuente primaria de alimento proviene del detritus del manglar. Esto condujo a estudiar cuantitativamente la hojarasca, así como a estudiar experimentalmente la dinámica de la descomposición de las hoja (Pool *et al.,* 1975; Fell *et al., 1975;* Malley, 1978; Fell y Master, 1980; Bunt, 1982; Twilley *et al.,* 1986; Flores-Verdugo *et al., 1987;* González-Farías y Mee, 1988; Woodroffe *et al.,* 1988). No obstante las múltiples investigaciones sobre el tópico, esta afirmación continúa relativamente sin respuesta.

Una forma de establecer el vínculo del detritus en la trama trófica es a través del estudio del contenido estomacal de las especies que conforman la comunidad estuarina asociada a ecosistemas de manglar. Sobre este tópico, se llevó a cabo un estudio sobre dinámica alimenticia del contenido estomacal de los peces en la Ría Celestún, al norte de la Península de Yucatán. Los resultados obtenidos, muestran que los micro-crustéceos son la presa más Importante al constituir el 51% de la biomasa total (Vega Cendejas, 1998). Estos autores concluyen que, el consumo de este grupo es característico en la estructura trófica de los peces asociados a las raíces de manglar y representa, través de la dieta del cangrejo, la incorporación indirecta de detritus a su alimentación así como de otros tipos de alimento, tales como el fitoplancton. De tal forma que, la fauna que mantiene a las poblaciones de peces en este ecosistema costero, dependen directa e indirectamente del detritus proveniente del manglar.

Estos estudios han conducido a realizar análisis más complejos como son las caracterizaciones isotópicas de los organismos en pantanos salobres y de pastos marinos de latitudes templadas Esta técnica consiste en identificar la relación de isótopos estables ($\delta\ ^{13}C/^{12}C$, $\delta^{15}N/^{14}N$) al marcar al detritus en la trama trófica. Diferentes autores concluyen que detritus vascular en los pantanos salobres y de pastos marinos en estas latitudes, puede no ser tan importante como se pensaba previamente (Thayer *et al.,* 1978; Haines y Montague, 1979; Mc Connaughey y McRoy, 1979; Huges y Sherr, 1983).

Rodelli *et al.* (1984) implementan esta metodología para determinar la proporción de isótopos estables en la biota de los pantanos de manglar, bocas costeras yaguas costeras en Malasia y concluye que los manglares constituyen una significativa fuente de carbón para muchos animales que residen en los manglares y en las bocas, pero no en aguas costeras. Por otra parte, Stoner y Zimmerman (1988) encontraron en una laguna rodeada de manglar en Puerto Rico que; los camarones se alimenten principalmente de organismos detritívoros, la proporción de isótopos de carbón

tanto del camarón como en sus presas sugiere que la mayoría del origen de su carbón proviene de algas bénticas más que de los manglares.

Para la Laguna de Términos, en Campeche Raz Guzmán y de la Lanza (1993) establecen la proporción isotópica del carbono orgánico en camarones, sedimento y vegetación. Determinan que el δ13C de *Rhizophora mangle* es de -25.6 a -30.2 ‰ registrándose entre los valores más ligeros de la vegetación del sur y centro de la laguna Dicho carbono es posible que se incorpore a las redes tróficas locales e influya en la proporción isotópica de los consumidores. Puesto que su estudio se enfoca principalmente a las praderas de pastos marinos *(Thalassia testudinum* y *Dictyota* sp) como fuente de carbono para los macrocrustáceos, principalmente camarones. Los resultados del análisis de δ13C coincide con el patrón de migración de *Peneus setiferus* dentro de la Laguna de Términos. Existiendo una relación aparente entre el δ13C, la talla de los Juveniles y la localidad de colecta.

Otra forma de determinar el papel ecológico del detritus proveniente de los manglares en la zona costera es a través del uso de modelos ecológicos que constituyen una herramienta útil para el análisis, la integración, la síntesis y consecuentemente la predicción del sistema y sus recursos bióticos. En esta línea. Soberón-Chávez *et al.* (1988) desarrollaron un modelo ecológico para explicar los cambios en dirección e intensidad de las interacciones entre las aguas protegidas de la Laguna de Términos y la plataforma continental de la Sonda de Campeche y cuales son los factores que producen alteraciones en la diversidad, distribución, abundancia y persistencia de los recursos. En este modelo un compartimiento lo constituye la biomasa de los desechos foliares de los manglares, que dentro de la laguna se clasificó en dos tipos diferentes, que a continuación se describen.

Manglar de *Influencia marina,* se refiere a los desechos foliares que se localizan en la Isla del Carmen. La principal característica de este manglar es que no presenta influencia fluvial. Por lo cual, se considera que la producción de los desechos foliares en esta área, están relacionados con la precipitación y la iluminación. *Manglar de influencia fluvial,* que son los desechos foliares de los manglares que se localizan en la desembocadura del Río Palizada. Los procesos que controlan la producción en esta zona son únicamente con la iluminación.

Adicionalmente, en el detritus convergen los flujos de material proveniente de todos los componentes del sistema en estudio. En promedio, el 5.3% del detritus total en la laguna proviene de los manglares, teniendo su máximo impacto en el sistema fluvio lagunar este (Subsitema III) donde equivale al 14%. Asimismo, se determina el flujo del detritus a través de los diferentes hábitats de la Laguna de Términos. Esto es, la cantidad de detritus proveniente de los manglares de influencia marina presenta una tasa de exportación de 0.083 g/mes (g de desecho). En cuanto a la cantidad de detritus proveniente de los manglares de influencia fluvial, representa una tasa de exportación de 0.04 g/mes (g de desecho) (Soberón-Chávez *et al.,* 1988).

El modelo establece que la exportación del detritus a otros ecosistemas esta en función de los vientos, descarga fluvial y una constante. De tal manera que, el flujo de exportación del detritus de la plataforma carbonatada de la Sonda de Campeche (Subsistema B) se divide en dos partes: alrededor del 90% se dirige a la plataforma terrlgena (subsistema A), y el resto entra a la laguna acarreado principalmente por los vientos del norte a través de la Boca de Puerto Real (Subsistema 1). Ya dentro de la laguna, el detritus que se exporta de la Cuenca Central (Subsistema 11) se divide en dos partes, la primera es acarreada por los vientos del norte al sistema fluvio lagunar del Este (Subsistema III), y el resto se dirige al sistema fluvio-lagunar Oeste y Boca del Carmen (Subsistema IV). Finalmente, la laguna de Términos exporta detritus a través de la Boca del Carmen hacia la plataforma terrígena impulsado por la circulación de la laguna y por la descarga fluvial del Río Palizada. Este flujo es 6.594 veces mayor que el que entra a la laguna por la Boca de Puerto Real (Soberón-Chávez *et al.,* 1988*).*

Este intercambio de detritus entre los diferentes hábitats, esta vinculado al patrón de migración de los organismos nectónicos y el modelo define 3 pulsos migratorios:

1. Peces básicamente subadultos y adultos, provenientes del Subsistema B que entran a la laguna hacia las praderas de pastos marinos (subsistema 1) en época de secas con fines de alimentación. Regresan al Subsistema B en época de lluvias, moviendo en esta forma entre 60 y 85 ton/año de materia entre los diferentes ambientes.

2. Organismos que entran en lluvias a la laguna como larvas y juveniles a través del Subsistema 1. Se dirigen al Subsistema III a través del Subsistema ll y salen de la Laguna en secas pasando por el Subsistema IV. Estos organismos regresan al Subsistema B a través del Subsistema A. Causando un movimiento de aproximadamente 200 ton/año.

3. Organismos provenientes del Subsistema A que entran en lluvias a la laguna por el Subsistema IV y salen por ésta misma ruta Asimismo existen organismos que salen por el Subsistema IV y que no forman exclusivamente parte del Patrón de Migración 2 y que constituyen parte de este tercer patrón. Este pulso migratorio mueve casi 160 ton/año.

Con este mismo enfoque se llevó a cabo un análisis sobre la ecología trofodinámica de dos hábitat críticos (pastos marinos y manglares) en la Laguna de Términos. Se empleo el Programa ECOPATH que está diseñado para la construcción de modelos del ecosistema a través de las interacciones tróficas y flujos de nutrientes (Christensen y Pauly, 1996). El modelo tiene una entrada total de 9.474 g peso seco/m^2/año, con 18.7% de respiración. El detritus proveniente del manglar, es un Importante aporte "extra" al detritus de la laguna, cuyo suministro es de 5797.68 g peso seco/m^2/año. En este modelo el detritus constituye el 82% del flujo total, tal como un sistema maduro trabaja. Asimismo, el porcentaje de eficiencia de transferencia de los productores fluctuó de 6.4 a 0.7%.

De acuerdo a los resultados obtenidos se determinó que existen cuatro niveles tróficos para estas comunidades, esto significa casi el 90% de los consumidores de estos hábitat corresponden al segundo y tercer nivel trófico con un amplio espectro y dependientes del aporte de detritus. Subrayando que muchas de las especies de importancia comercial, por ejemplo los camarones, presentan un uso muy Intenso de estas áreas durante alguna etapa de su ciclo de vida (Rivera *et al.,* 1997).

Similarmente, Vega Cendejas (1994, 1998) determina que del total de los flujos del sistema de manglar analizado, el 22.7% se utiliza para los procesos respiratorios, 0.01 % para exportación y 35% se canaliza a detritus. Los niveles tróficos de los consumidores son relativamente bajos, lo que refleja por una parte, que la mayoría de los grupos de peces que lo utilizan son juveniles y por otra, la dependencia directa e indirecta para su producción de los productores primarios como las macrofitas, fitoplancton y el detritus.

Productividad Pesquera

Numerosas investigaciones se han realizado en torno a las variables que controlan la diversidad y abundancia de los recursos pesqueros. Destacan por su Importancia las áreas vegetadas costeras puesto que funcionan como zonas de protección de juveniles de especies de importancia comercial. Así como por la gran disponibilidad de alimento que representan a través del detritus, o bien como fertilizadores de las áreas costeras adyacentes que estimulan la producción primaria en aguas costeras.

No obstante, éstas funciones están controlados por procesos físico-ambientales de la zona costera como son: **1)** las condiciones físico-químicas del agua (transparencia, nutrientes, salinidad, temperatura), **2)** Latitud geográfica, **3)** batimetría y tipos de sedimentos, **4)** meteorología y clima, **5)** descarga de los ríos, **6)** rangos de marea y variación del nivel del mar, **7)** lagunas costeras y estuarios adyacentes, **8)** dinámica de interacción entre los estuarios y el mar. Que en su conjunto se han denominado mecanismos de producción natural (Soberón Chávez y Yáñez-Arancibia, 1985).

La relevancia pesquera del Estado de Campeche en el sur del Golfo de México, depende de la interacción entre laguna de Términos y la Sonda de Campeche. Por lo que se ha sugerido que ambos sistemas ecológicos tienen interdependencia reciproca. Por lo tanto en los últimos 20 años se ha manejado la hipótesis de que la productividad pesquera de la plataforma marina de Campeche depende, en parte, de diversos efectos ecológicos de la Laguna de Términos hacia el mar (Sánchez *et al.,* 1981*).*

Esto hace a la región de la Laguna de Términos particularmente crítica para la Sonda de Campeche por las extensas áreas costeras vegetadas que presenta, con diferentes asociaciones como son manglares, pastos marinos, pantanos fluvio-deltáicos. También, por sus sistemas lagunares-estuarinos y los aportes de agua dulce, sedimentos, nutrientes y materia orgánica que descargan en la Sonda de Campeche. Asimismo, existe un gran intercambio de fauna marina y estuarina entre ambas áreas y los peces consumidores secundarios pueden ser importantes en este flujo de energía y nutrientes (Robertson y Duke, 1990; Twilley *et al.,* 1996*).*

Como resultado el vinculo de la Laguna de Términos junto con la Sonda de Campeche ha sido importantes por las capturas de ostión, peces, pero principalmente de camarones peneidos. Las pesquerías de peneidos en México -por volumen de captura y por divisas- en la Sonda de Campeche (más del 50 % de la captura de camarón del Golfo de México), comprenden para cada una de las tres especies: *Peneus duorarum* (camaron rosado) contribuye con el volumen de 90.0%, *Peneus setiferus* (camarón blanco) con 5.2% y *Peneus aztecus* (camarón café) con 3.9% (Schultz y Chávez, 1976).

De igual forma, la Sonda de Campeche aporta más del 40% de la captura demersal del Golfo de México. Esta es una pesquería multiespecífica estrechamente vinculada a la pesquería del camarón. Su estabilidad, aumento o disminución es el reflejo de la variabilidad natural de los procesos físico-ambientales y biológicos como consecuencia de interacciones ecológicas en la zona costera.

Las características ambientales de mayor implicación ecológica para los peces demersales de la plataforma continental adyacente a la Laguna de Términos dependen fuertemente, del flujo de los ríos Grijalva y San Pedro en el extremo occidental, del río Champotón en el oriente y de la descarga de la Laguna de Términos, a través de su boca occidental (Boca del Carmen), siendo la influencia de dicha laguna determinante en la dinámica ictiológica de la plataforma adyacente (Sánchez *et al.,* 1981 ; Yáñez-Arancibia *et al*., 1985b A. Yáñez-Arancibia y Sánchez, 1986).

Otro factor determinante en la composición y abundancia de la fauna de la plataforma continental es la influencia de la vegetación costera. El Estado de Campeche presenta la cobertura de manglar más importante en relación con los otros estados del Golfo de México (aproximadamente 40 %), de aquí su relevancia en la producción pesquera en la Sonda de Campeche. En éste sentido, Turner (1977) ha señalado una correlación positiva entre el cociente de la captura de camarones peneidos entre las áreas de vegetación intermareal, con la latitud para las costas de Texas y Florida. Deegan *et al.* (1986) concluyen que las capturas pesqueras del Golfo de México se correlacionan con áreas estuarinas y descargas de ríos, fisiografía y vegetación litoral.

La relación de los recursos pesqueros con los sistemas estuarinos, es bien conocida puesto que éstos son fundamentales en el sostenimiento de alguna etapa del ciclo de vida de más del 90% de las especies marinas que tienen valor comercial. En el sur del Golfo de México, más del 75% de las poblaciones de peces dominantes en la plataforma continental son dependientes estuarinas (Yáñez-Arancibia y Sánchez-Gil, 1988). De acuerdo a la producción pesquera de la región y la infraestructura disponible, una extrapolación del valor de los recursos pesqueros que dependen de la Laguna de Términos tiene un "valor intrínseco" de alrededor de 60 x 10^6 de dólares anuales (en 1988). Esto puede relacionarse con las áreas de manglar y pastos marinos, lo cual plantea el valor económico que representan los hábitats lagunares-estuarinos como consecuencia de su valor ecológico (Yáñez-Arancibia y Aguirre León, 1988).

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Fish and Aquatic Invertebrate Use of the Mangrove Prop-root Habitat in Florida: A Review

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Abstract

While the red mangrove prop-root habitat has been recognized as a fishery habitat for a considerable period of time, few quantitative studies have been conducted to assess their use by fauna. Techniques have been developed and tested recently in Florida that allow hypothesis testing and evaluation of the functional value of this habitat to fishery organisms. Preferred techniques include block nets and drop samplers, and in most instances even these techniques require some minor modification of the habitat before sampling can be initiated. The limited quantitative sampling that has occurred indicates that commercial, recreational and forage fish and crustaceans are important users of the prop-root habitat and that there are temporal and spatial differences in community structure among these habitats in Florida. This chapter provides a brief summary of the data available for Florida.

Resumen

Mientras que los habitas de las raíces de sostén del manglar rojo han sido reconocidos como un hábitat de pesca por un periodo de tiempo considerable, pocos estudios han sido realizados para evaluar su uso por la fauna. Las técnicas que han sido desarrolladas y probadas recientemente en Florida que permite probar la hipótesis y evaluar de su valor funcional de este hábitat para organismos con importancia pesquera. Las técnicas preferidas incluyen redes de bloque (block nets) y muestreadores de caída (drop samplers), y en la mayoría de los casos aún estas técnicas requieren alguna pequeña modificación del hábitat antes del muestreo pueda ser iniciado. El muestreo cuantitativamente limitado indica que los peces y crustáceos de importancia comercial, recreativa y de forraje son usuarios importantes de los hábitats de sostén, y que existen diferencias temporales y espaciales en la estructura de la comunidad entre estos hábitats en Florida. Éste capítulo proporciona un breve resumen de los datos disponibles para Florida.

Introduction

Mangroves represent a major coastal wetland habitat in the southeastern United States, occupying about 202,000 hectares of estuarine and coastal shoreline (Odum *et al*., 1982). As noted by Thayer *et al*. (this volume), the functional roles these systems play in supporting primary and secondary productions of coastal waters are poorly understood. It is critical to understand these roles because mangroves continue to be replaced by housing developments, mariculture facilities, canals and other forms of human development. We believe that a significant portion of this habitat loss results from the lack of quantitative data available to resource managers on the value of mangrove systems: spatial and temporal use by fishes and invertebrates, and their food and refuge potentials for aquatic species.

While it has long been recognized that red mangrove habitats in the southeastern United States are important to fishery resources (see Odum *et al*., 1982), there have been few quantitative studies dealing with the use of these habitat types and their functional value to fishery organisms (see Thayer *et al*., 1987; 1988; Sheridan, 1991). This general paucity of quantitative information stems largely from the lack of techniques to address the contribution of mangroves to fishery organisms. Recently, however, several techniques have been developed and tested, with results published in the open scientific literature or in abstracts for scientific meetings, agency annual reports or funding reports. It is the purpose of our paper to review several of the published manuscripts and available information from other sources, and by necessity this requires direct use of some of the information and data from these sources. The authors (GWT and PFS) have published the papers upon which much of this chapter is based, and we have attempted to include information yet to be published or not easily obtained for the Florida mangrove habitat that we were aware existed. In-so-doing, we inadvertently may have omitted some papers and reports, for which we apologize to those scientists.

Techniques

The red mangrove canopy and prop-root structure have presented formidable obstacles to evaluating the temporal and spatial distribution and abundance of fishes and decapods crustaceans utilizing this habitat type. This is a major area that has been recommended for investigation by a recent scientific workshop held in St. Petersburg, Florida (Thayer *et al*. this volume). Visual censes have been used frequently, and are advantageous in determining use of prop-root habitats by large predators; can be used to quickly survey areas; require little equipment and no habitat destruction; and can be used in deep areas where nets and rotenone may be difficult to use (J. Ley, Univ. Florida, pers. comm.). This approach does not work well under turbid conditions characteristic of many mangrove habitats. Techniques that have evolved recently to sample fish and macroinvertebrates of the red mangrove prop-root habitat fall into three major categories: block sampling, drop sampling and traps.

In western Florida Bay, where tidal amplitude is small, Thayer *et al*. (1987, 1988) used a block net procedure. The block net was 32 x 2 m in size with 3 mm mesh. The bottom of the net was fitted with 6 mm galvanized chain and the top with a cork line. Wooden staffs were fixed to each end of the net. Prior to any sampling, 2.8 m long pipes were driven into the sediment 4-8 m apart at the seaward corners of each mangrove site to be sampled. Then, a 0.5 m wide path was cleared to the shoreline from each stake perpendicular to the shoreline to allow the net to be moved up along the sides of the site.

The blocking procedure involved 2 individuals who approached to within about 5 m of the site by boat, and then deployed the net at about peak high tide. The net was carried rolled up to the center of the stakes which had been set at the seaward edge of the site. The net was unfurled and spread out by passing it around the outside of the stakes. Each individual then moved the net up a cut path between mangroves onto the shore, pulling the net tight as they moved. The chain line was checked immediately and pushed into the sediment to prevent escape of organisms. Therefore, the net blocked the front and sides of each sample area with the shoreline forming the interior border.

Sampling was conducted after application of 5% rotenone (w/w), diluted about 1:4 that was dispensed below the surface of the water. Four individuals then positioned themselves adjacent to the net or within the blocked area and used dip nets to capture surfacing organisms over the next 30 minutes. The chain line was then lifted and fish settling on the net were removed. Fin-clipped fish of a variety of species were added as a check for collection efficiency, which averaged about 75% during every month but January.

Ley (1990; 1991, pers. comm.) and Ley and Montague (1991) also have used this block net and rotenone technique to sample fish in northeastern of Florida Bay near the Buttonwood Sound-Long Sound-Joe Bay complex. Ley (1990) carried out capture efficiency analyses using fin-clipped fishes of a variety of species with recoveries of l2 - 72 % and a mean recovery of 36%; larger species were collected more efficiently than smaller species. These efficiencies are considerably lower than those recorded by Thayer *et al*. (1987).

Florida Department of Natural Resources is employing a passive block net technique to sample fish use of mangrove habitats in Tampa Bay and currently is contemplating conducting similar work in Charlotte Harbor (McLaughlin pers. comm.). This technique requires a tidal prism to drive organisms out of the habitat in question, and modifications of this technique have been receiving increasing use in studies of other tidal wetland systems (e.g. Hettler, 1989). They have been employing a 63 m long net that is 2.5 deep and has a 2.5 × 2.5 × 2.5 m tail bag. The net is brought up onto the shore to the high tide mark on each side of the sample area at high tide and allowed to fish during the ebb tide, after which the catch is removed from the tail bag (McLaughlin pers. comm.). Sampling began in November 1990 and data are not available at this time; however, capture efficiencies using marked fish of several species and size classes appear to be 60-70%.

Very recently, portable and stationary drop samplers have been employed in mangrove systems to assess the use of the prop-root habitat by fish and invertebrates. Sheridan (1991) sampled using a 1.8 m (diameter) circular drop sampler developed by Zimmerman *et al*. (1984). Fixed mangrove sites were used in this study with a maximum depth of 1 m. In each instance a 0.5 m path was cleared around each site by cutting prop-roots to the sediment surface, and in some instances overhanging limbs were removed.

Sampling was carried out by hoisting the sampler on a boom mounted on the bow of a sampling boat (see Zimmerman *et al*., 1984) and maneuvering the boat quietly to the sampling site. The sampler was dropped to the substrate and subsequently pushed into the sediment 15-20 cm to seal off the sample. Water enclosed by the sampler then was pumped out through a 1 mm mesh plankton net, and the organisms remaining on the substrate were picked up. Previous testing by the author (PFS) indicated an overall recapture rate of 82-94% for fish, shrimp and crabs in a variety of habitats.

Lorenz (1991; pers. comm.), working in brackish water areas in the northern side of Florida Bay, is using a stationary drop net sampling approach, similar to that commonly used in seagrass habitats (Fonseca et al. 1990). The 9 m^2 nets are hung on permanently mounted frames of # 3 reinforcement bar crossbeams and 1 inch PVC uprights at each corner. The crossbeams rest on 15 cm long cotter pins inserted through each PVC corner pole so that the crossbeams are supported approximately 1 m above the water surface. The end of each crossbeam encircles the corner poles and each has five 20 cm-long V-shaped wire staples attached at equal distances long its length with the open end of the V-staple turned upwards.

The nets are 1.5 m wide with 1.6 mm mesh. A float line of each net is attached to the top of each PVC pole and the lower end of the net is slipped under the inside of each crossbeam and fitted over the outside upright of each of the V-staples.

The nets are allowed to stand overnight, and are triggered the following day from a distance of about 10 m by lines attached to each of the four cotter pins. The weight of the crossbeams makes the net sink to the bottom and forces the bottom of the net into the sediment. Rotenone and dip nets are used to collect the dead fish from within the net over a 24 h period. Efficiency tests indicate recoveries of between 63-92%.

Traps have been used in several studies to survey the fishery organisms utilizing mangrove prop-root habitats (Gilmore *et al*., 1987; Ley, 1990, 1991), but there is no way to quantify the area fished by a trap. Gilmore and coauthors used heart traps (a small minnow trap with one entrance and shaped like a heart) that were net for 24 h at two locations on the east-central coast of Florida under the red mangrove canopy. On several occasions, throw traps adjacent to mangrove root habitats have been used to provide quantitative measures of fish abundance (Gilmore *et al*., l987).

Each of the methods noted above has its advantages and disadvantages. The block net approach requires some modification of the habitat and can be used in both low and high tidal amplitude areas; in low tidal amplitude areas, fish poisons must be used. The drop sampling approaches also require some modification of the habitat and are limited to shallow depths for sampling. Never-the-less, these are quantitative approaches to addressing the problem of temporal and spatial use of the prop-root habitat that have provided critical information for habitat managers on the value of these habitats to fisheries. These approaches also have begun to address functional issues that are described by Thayer *et al*. (this volume).

Summary of Faunal Use Data

In reviewing some of the literature on fish use of mangrove swamps, particularly those on the Atlantic coast of Florida, Gilmore and Snedaker (In press) indicated that there are both resident and transient species, and that the numerically abundant mangrove swamp resident fish species also are common in peripheral high marsh habitats of Florida. They noted that mosquitofish (*Gambusia affinis*), sailfin molly (*Poecilia latipinna*) and sheeps head minnow (*Cyprinodon variegatus*) are numerical dominants. They pointed out further that tide water silverside (*Menidia beryllina*), fat sleeper (*Dormitator maculatus*), and rivulus (*Rivulus marmoratus*) also are common residents. Transient species are more diverse in this system than are the residents, and appear to be dominated by striped mullet (*Mugil cephalus*), white mullet (*M. curema*), snook (*Centropomus undecimalis*), ladyfish (*Elops saurus*), Irish pompano (*Diapterus auratus*), yellowfin mojarra (*Gerres cinereus*), tidewater mojarra (*Eucinostomus harengulus*), sheepshead (*Archosargus probatocephalus*), and gray snapper (*Lutjanus griseus*). These observations are based primarily on heart and throw trap collections. Most of these transients are commercially or recreationally important species.

Quantitative studies by Thayer *et al*. (1987, 1988) and Sheridan (1991) with block nets and drop samplers have demonstrated that there appear to be different complexes of fish in mangrove habitats of Florida and Rookery Bay (Gulf of Mexico coast), and the mangrove habitats on the Atlantic coast evaluated by Gilmore *et al*., 1987). These studies indicate that there appears to be a fish community in the mangroves that is distinct from that of the adjacent seagrass habitat; some of the species are similar between the two habitats but they comprise a different fraction of each community.

Thayer *et al*. (1987) collected 64 species and 32 families of fish from among the mangrove prop roots during seven surveys in 1984-1985 in western Florida Bay, Coot Bay and White water Bay, Everglades National Park, Florida. The mean density of fish was 8/m^2. Fishes of the families Atherinidae, Cyprinodontidae, Gerreidae, Engraulidae and Gobiidae were represented most abundantly among the red mangrove prop-roots. The predominant fishes collected were forage species: hardhead silverside (*Atherinomorus stipes*), silver jenny (*E. gula*), goldspotted killifish (*Floridichthys carpio*), spotfin mojarra (*E. argenteus*), code goby (*Gobiosoma robustum*), rough silverside (*Membras martinica*), striped anchovy (*Anchoa hepsetus*), and clown goby (*Microgobius gulosus*). These forage species are common dietary items for several species of piscivorous birds and fish.

Thayer *et al*. (1987, 1988) also collected juveniles of several commercial and recreational species that in the mangrove prop/root community: snook, gray snapper, spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), striped and white mullets (*M. cephalus, M. curema*), sheepshead, and great barracuda (*Sphyraena barracuda*). Although these fishes were present in the lock net collections on a routine basis, they never were as abundant as forage fish species.

Ley (1990, 1991) and Ley and Montague (1991), also used a block net system, worked in areas of eastern Florida Bay having harsh environmental conditions, with salinity ranging from 0-50 ppt and temperatures ranging from 4-37 degrees C. The fish community appeared to be dominated by small species and juveniles of larger species, and during 6 months of sampling 48 species of fish had an average density of 3.3 fish/m^2. The dominant organisms were euryhaline species that frequently serve as forage food for fishes and birds: silversides, anchovies and killifish. Ley (1990) supplemented these block net samplings with minnow trap collections and visual observations, and has noted recreational species such as blue-striped grunt (*Haemulon sciurus*) and gray snapper among the prop-roots. The composition of the community did not appear to differ greatly from that observed by Thayer *et al*. (1987, 1988) in the western Florida Bay complex.

Ley (1990) also has been investigating temporal and spatial distribution of fishes. She has observed that average fish density appeared to be lower in upstream areas of the study sites that were subject to more variable salinities, and higher in down stream areas where salinities tended to be more stable. Subsequent sampling showed similar trends, but statistical analyses are showing it to be a trend and not significant (Ley, pers. comm.). Species composition also appeared to follow a similar trend with more variability in the upstream areas and less in the mangrove prop-root areas located downstream near or in Florida Bay. At the time of this writing, Ley is in the process of analyzing these data for her Ph.D. degree at the University of Florida, and the authors thank her for use of her data.

Lorenz (1991 and in Powell and Bjork, 1990) is sampling red mangrove habitats in interior portions of the northern Florida Bay area which have salinities between 10 and 50 ppt. Similar to observations by Ley (1991) and Thayer *et al*. (1988), he is finding that sheepshead minnow, marsh killifish and sailfin molly are the predominant species collected by the drop net approach. Total fish densities have ranged between less than 1 and in excess of 8 fish/m^2, with the majority of fish collected being less than 5 cm in total length. This investigator has noted that these small fish are pre-dominant food sources for the roseate spoonbill (*Ajaia jaja*).

Lorenz currently is conducting research for an advanced degree at the University of Florida and is a Cooperative Research assistant for the National Audubon Society Research Unit and the Department of Wildlife and Range Sciences at the University. The authors thank him for the use of his preliminary data on techniques and fisheries in mangrove habitats.

Northwest of Florida Bay, Sheridan (1991) conducted quantitative sampling of the mangrove prop-root habitat in Rookery Bay, using a drop sampler, and demonstrated a somewhat different and less diverse fish community than was noted for Florida Bay. The community of fish in this area contained only 13 species, dominated by the spotfin mojarra which represented 75% of the fish collected. Fish densities averaged 5.8/m^2. Goldspotted killifish, marsh killifish (*Fundulus confluentus*), and sailfin molly also were contributors to the population and were primarily present in this habitat relative to other habitats sampled (i.e. open water and seagrass meadows nearby). Organisms such as spotfin mojarra, pinfish (*Lagodon rhomboides*), and gray snapper were able to exploit flooded mangroves along with other habitats in Rookery Bay, but species such as scaled sardine and anchovies that were present in mangrove habitats in Florida Bay rarely moved into the Rookery Bay mangrove habitat.

Both Sheridan (1991) and Thayer *et al*. (1987, 1988) recognized that there could be diel differences in species composition of these mangrove habitats (sampling was carried out primarily during daylight hours). Thayer *et al*. (1988) conducted a few comparative day-night samplings in Florida Bay. The small database suggested juvenile great barracuda, goldspotted killifish, spotfin mojarra, tidewater silverside (*M. peninsulae*), and timucu (*Strongylura timucu*), were taken more frequently from the mangrove habitat during the day while redfin needlefish (*S. notata*) and gray snapper were encountered more frequently at night. Whether these movements are directed as feeding migrations or refuge are unknown, but night sampling might provide additional information as to fishery use of this habitat type as well as linkages among habitats.

Sheridan (1991) also investigated on the invertebrate use of mangrove habitats. This study appears to be the only one in Florida to address aquatic invertebrate use of mangrove prop-root habitats quantitatively. Florida grass shrimp (*Palaemon floridanus*) was the dominant shrimp collected among the prop-roots followed by daggerblade grass shrimp (*Palaemonetes pugio*). Five shrimp species averaged 3.9 individuals/m^2. Among 9 species of crabs, the broadback mud crab (*Eurytium limosum*), green porcelain crab (*Petrolisthes armatus*), and mangrove tree crab (*Aratus pisonii*) were the most prevalent. Crab densities averaged 3.6/m^2 in the Rookery Bay mangrove system. Both Sheridan (1991) and Thayer *et al*. (1987, 1988) noted that the mangrove prop root did not appear to be an important habitat for commercial blue crab (*Callinectes sapidus*), stone crab (*Menippe mercenaria*), rock shrimp (*Sicyonia* spp) or pink shrimp (*Penaeus duorarum*) in the areas they sampled.

Conclusions

The development and testing of quantitative sampling approaches for use in the mangrove prop-root habitat have allowed testing of scientific hypotheses and gathering of data that are important to habitat managers in their quest to conserve and protect valuable natural resources. Until recently, these techniques have not been available and the information base on importance of this habitat has been limited to visual census in clear water environments. The preferred gear at this time is block nets and drop samplers, and recently these techniques have been used successfully in a variety of mangrove prop-root habitats in Florida to assess fish and invertebrate use.

Quantitative sampling has shown that this habitat is utilized by transient and resident fishes and invertebrates representing forage, commercial and recreational species. Data

suggest that the majority of the species are adults of small individuals or juveniles of many species including piscivorous fish. Densities appear to range between 38 fish and 7-8 decapods/m^2 for those studies reporting densities. There also are temporal and spatial differences in species composition and diversity that appear to be a function of geographic location (e.g., Florida Bay *vs* Rookery Bay) or as extremes of conditions along a salinity gradient (e.g., within the Florida Bay complex). There are limited indications that diel differences exist in the composition of the community. Where data are available (e.g., Rookery Bay), they suggest that invertebrates are more diverse than the fish community and are dominated by caridean shrimp and xanthid crabs.

These few studies have just scratched the surface, but they have demonstrated that the prop-root habitat is an important one for fish and invertebrates of food web, commercial, and recreational value. There also are indications of linkages among this habitat type and adjacent seagrass, open water and marsh habitats. Efforts need to be increased to evaluate this and more extensively flooded mangrove habitats for their relative value to fish and crustaceans. The techniques developed provide the avenue to address spatial and temporal variation in habitat use in relation to water level and to compare feeding and refuge potentials among mangrove habitats and among other vegetated and unvegetated coastal and estuarine habitat types.

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Environmental Impact in Mangrove Ecosystems: Sâo Paulo, Brazil

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Abstract

The Baixada Santista is at the moment an intensely occupied area by urban and industrial processes and harbor activities. The physiognomic features of Baixada Santista were constituted by a natural environment with different topographic aspects which had important plant communities as the Mata Atlantica in Serra do Mar cliffs, the resting and the mangrove in the coastal plaines. This environment was seriously altered by economic growth. Today, the environment quality of the region is precarious, and still under several kinds of pressures.

Due to the industrialization of Baixada Santista in the mid 1950 there was a great contamination of the region by heavy metals, affecting mainly the Santos estuary. One can still find high concentration of heavy metals in the sediments, mainly the mercury, zinc and plumb.

As for the contamination of heavy metals in the mangrove, the three species (*R. mangle*, *L. racemosa* and *A. schaueriana*) presented an accumulation of these substances in their leaves, mainly in the latter. Furthermore, a correlation between the most contaminated areas and the mangroves with the most degraded forest structures was observed.

The mangroves in the region suffered all kinds of pressures such as: fillings, solid waste, changes in the water bodies, industrial and domestic effluents causing chemical and organic contamination. One of the most harmfully and frequent impacts is caused by oil pollution.

A long-term survey has being carried out in the coast of Sâo Paulo State since 1984 after a spill of 2500 tons of crude oil reached the mangrove following a pipeline burst. The study is in progress and monitoring continues. Results so far show that the forest was seriously damaged. Reduction of the basal area was 40% and 20% of the forest density. Loss of basal area was greatest for *Avicennia*, thus this appears to be the more vulnerable species of the tree present in the area. The three species showed a continuous increase of leaf area after the event that caused an initial high rate of defoliation; increase of leaf area was (*R. mangle*: 18.5%, *L. racemosa*: 17.7% and *A. schaueriana*: 27.2%). There was a reduction of herbivore on the three species.

Leaves showed chronic effects such as withering, necrosis, discoloration malformation. Fissured epidermis, dissecation and necrosis of the stem were frequent. Anomalously shaped prop roots were formed and died off before reaching the sediment's surface.

Propagule density was reduced and was accompanied by atrophy and malformation of the remaining propagules. The impacted area was rapidly colonized by new seedlings that grew up to about 1m high; 100% mortality followed when the nutrient reserves of the propagules were exhausted. The growth of seedling into sapling could not take probably because of the presence of toxic residues in the water and soil of the impacted area.

These observations may be used to develop an impact assessment methodology in events of oil pollution in mangrove areas. First, environmental quality. Second, high density of seedlings does not necessarily represent recovery. A better criterion to this is the presence of rooted saplings.

Furthermore, structural responses of mangrove forest to oil are slower than functional responses and can be divided in four post spill phases as follows:

1. Initial effect: no significant structural alteration

2. Structural damage: high mortality

3. Stabilization: few or none alterations in the studied parameters,

4. Recovery: observations indicate that the mangrove area under study is at the beginning of the recovery stage.

Based on this study it was possible to determine the effects of oil spill on the mangrove ecosystems; to develop an impact evaluation methodology; to develop rehabilitation techniques under the environmental conditions prevailing in the study area.

Resumen

La Baixada Santista es actualmente un área intensamente ocupada por procesos urbanos e industriales, así como actividades portuarias. Los rasgos fisonómicos de la Baixada Santista estuvieron constituidos por un ambiente natural con diferentes aspectos topográficos los cuales tienen importantes comunidades vegetales como la Mata Atlántica en los acantilados de la Sierra del Mar, la restinga y los manglares en las planicies costeras. Este ambiente fue seriamente alterado por el crecimiento económico. Actualmente, la calidad del ambiente de la región es precaria, y continua bajo diversas clases de presiones.

Debido a la industrialización de Baixada Santista a mediados de la d,cada de 1950, existió una gran contaminación en la región por metales pesados, afectando principalmente el Estuario de Santos. Aún pueden encontrarse concentraciones altas de metales pesados en los sedimentos, principalmente mercurio, zinc y plomo.

La contaminación de metales pesados en las tres especies de manglar (*R. mangle*, *L. racemosa* y *A. schaueriana*) presentó una acumulación de estas substancias en sus hojas principalmente en la última especie. Además, una correlación entre la mayoría de las áreas contaminadas y los manglares se observó con la mayoría de las estructuras del bosque degradadas.

Los manglares en la región están afectados por toda clase de presiones tales como: rellenos, desechos sólidos, cambios en los cuerpos de agua, afluentes industriales y domésticos causando contaminación química y orgánica. Uno de los impactos más perjudicial y frecuente es el causado por la contaminación por petróleo.

Un estudio de largo plazo llevado a cabo en la costa del Estado de Sâo Paulo desde 1984 después de un derrame de 2,500 ton de petróleo crudo alcanzo los manglares seguidos de una ruptura de cañería. El estudio está en progreso y el monitoreo continua. Los resultados así por mucho muestran que el bosque fue seriamente dañado. La reducción del área basal fue 40% y 20 % de la densidad del bosque. La pérdida del área basal fue más grande para *Avicennia*, de este modo, parece ser la especie más vulnerable de las tres presentes en el área. Las tres especies muestran un incremento continuo del área foliar después del evento que causo inicialmente una alta tasa de desfoliación; el incremento de el área foliar fue (*R. mangle*: 18.5%, *L. racemosa*: 17.7% y *A. schaueriana*: 27.2%). Existió una reducción de la herbivoria de las tres especies.

Las hojas muestran efectos crónicos tales como marchitamiento, necrosis, malformaciones de decoloración. Epidermis fisuraza, disecación y necrosis del tallo fueron frecuentes. Anómalamente, la forma de las raíces de sostén fueron formadas y murieron antes de alcanzar la superficie de los sedimentos.

La densidad de propágulos fue reducida y estuvo acompañada por atropía y malformaciones de los propágulos restantes. El área impactada fue rápidamente colonizada por nuevas semillas que crecieron hasta casi 1m de altura; seguida del 100% de mortalidad cuando las reservas de nutrientes de los propágulos fue agotada. El crecimiento de la semilla en el vástago no podía tener lugar probablemente debido a la presencia de residuos tóxicos en el agua y suelo del área impactada.

Estas observaciones pueden ser utilizadas para desarrollar una metodología de evaluación del impacto en eventos de contaminación por petróleo en reas de manglar. Primero, el área basal y la densidad del bosque son los indicadores m s reales de la calidad del ambiente. Segundo, la alta densidad de semillas no necesariamente representa una recuperación. Un mejor criterio de esto es la presencia de vástagos enraizados.

Además de la respuesta estructural de los bosques de manglar al petróleo es más lenta que la respuesta funcional y pueden dividirse en cuatro fases post-derrame como sigue:

1. Efecto inmediato: sin alteraciones estructurales significativas

2. Daño estructural real: alta mortalidad

3. Estabilización: pocas o ninguna alteración en los parámetros analizados

4. Recuperación: las observaciones indican que el área de manglar en estudio esta en un inicio del estado de recuperación.

Basado en este estudio fue posible determinar los efectos del derrame petrolero en los ecosistemas de manglar; para desarrollar una metodología de evaluación de impacto; para desarrollar técnicas de rehabilitación bajo las condiciones ambientales prevalecientes en el área de estudio.

Introduction

Throughout the Brazilian coast there is a great variety of wetland ecosystems, however, most of them are suffering a fast and intense process of environmental degradation caused by the urban and industrial settlements. Out of the 25 metropolitan areas in Brazil 14 are situated in estuaries in which the main petrochemical centers and portuary systems of the country and industries lie, causing a major damage to those important ecosystems (Diegues 1987). It is worth pointing out that ecosystem such as the estuaries, lagoons and closed bays where the mangrove dominates, are the most sensitive to environmental impact.

The mangrove area in the coast of the state of Sâo Paulo is 231 km^2 and 42.5 % of them are located in the Baixada Santista (Herz, 1987). Despite their degradation level and their ecological importance (Rodrigues et al., 1987), there is still a great pressure to convert those wetlands to human uses as agriculture, urban expansion and other activities that cause different environmental impacts.

This region is within the most degraded Brazilian coastal areas because of the presence of a major industrial and portuary center as a result of a fast growth due to economic demands. Although these mangrove areas still present some structural and functional alternations provoked by human activities they do perform an important role in the retention of sediments and toxic substances. Actually, this region benefits from their location for not only does the mangrove retain part of the pollutants released in the rivers but also in the estuary, preventing them from reaching the coastal waters.

According to Lugo (1987), the study of degraded regions is as important as the one preserved ecosystems, once they enable one to understand the ecosystem responses to different kind of stresses. Thus, this knowledge might be applied to prevent, minimize, and evaluate other impacts and even to correct previous ones.

In view of this, the aim of this chapter is present an updated picture of the degradation of the mangrove areas in Baixada Santista in the central coast of Sâo Paulo state, as well as the results of a long-term study of environmental impact.

A summary of the physiognomy of Baixada Santista will be made together with an analysis of the historical development of the land use. In addition, the environmental alterations related to heavy metal and oil contamination will be described. To conclude the chapter a study case is presented describing the long term effects of oil spill on a mangrove ecosystem and discussing an impact evaluation methodology.

The Coast of Sâo Paulo: Features of the Region

Location of Baixada Santista

The Baixada Santista is located on the coast of Sâo Paulo state in the southeast of Brazil, under the Tropic of Capricorn (between 24° 50'S, 46° 45'W and 23° 45'S, 45° 50'W). The so-called Baixada Santista is the region that goes from Bertioga, in the northeast, to Mongaguá, in the southwest and from Santos, on the coast, to the interior, until the cliff of Serra do Mar (Goldenstein, 1972).

The Baixada Santista is a well-defined unit in the central area of the coast for it divides the north and the south coasts, each one with its different features. In the North coast the Serra do Mar cliffs are close to the sea whereas in the south coast their distance to the sea gets bigger as we go to the south. Thus, its peculiar position makes it differ from the other two regions (North and South coasts) marked by the existence of two important sedimentary islands very close to the continent, namely Santo Amaro and Sâo Vicente (Azevedo, 1965) (Fig. 1).

Figure 1. Study area, Baixada Santista - São Paulo, Brazil

Climate Features

The region presents hot and wet coastal climate as indicate the yearly average temperature of 22°C, and the high rainfall rates between 2,000 and 2,500 mm. The temperature ranges from 38°C to below 10°C.

The relative humidity of air is high, reaching more than 80% during the year. The rainfall is higher in the summer (January-March) decreasing in the winter (from July- August), but without a real dry season (Santos, 1965) (Fig. 2).

Geological and Topographic Features

The Santos Coastal plain forms a crescent 40 km long and up about 15 km wide that is limited by the Mongaguá mountains to the south and the rocky portion of the Santo Amaro island to the North. In the central and northeastern parts, the coastal plain drained by lagoonal and tidal channel systems that isolate Sâo Vicente and Santo Amaro Island (Suguio and Martin, 1978).

Practically in all the extension of this part of the Brazilian coastline there are uncontestable records of ancient sea levels higher than the present. These records can be correlated to two different transgressives episodes: the Cananéia transgression (120,000 years BP) and the Santos transgression (8,000 years BP).

During the first regression the sea reached as far as the foot of the Precambrian crystalline rocks along the entire coastline. Shallow marine sands were deposited within extensive bays located at the present sites of Santos and other coastal plains. During the following regression, hydrographic systems established on these deposits eroded deep valleys. When the last transgressive phase occured, the sea initially penetrated into these lower-lying zone thereby

Figura 2. Baixada Santista climate diagram (Instituto Nacional de Meteorologia, INEMET (data from 1977-1986)

creating lagoonal systems. Simultaneously, the higher portions were eroded by the transgressive sea and the products of this erosion contributed to the Holocene marine deposits (Suguio and Martin, 1978).

The combination of these events gives to the Baixada Santista two different kinds of geomorphological compartments. There is a sharply contrasting topography which is composed by high cliffs together with coastal plains (Fig. 3). The first one is constituted by crystalline basement and the second one is a result of recent marine and riverine sedimentation processes. These quaternary deposits receive the fresh water input of the rivers that run down from the Serra do Mar (Goldenstein, 1972).

Hydrology

The proximity to the Serra do Mar makes the rivers flow fast and intensely, losing this energy when reaching the coastal plains which have little or no declivity, slowing down the flow. As a result, streams and creeks are formed making a complex hydrological network, transforming vast regions in wetlands. That is where mangrove lies (Goldenstein, 1972).

Vegetation

There are three main plant communities in the coastal area which occupy adjacent environmental areas with different features: the Mata Atlantica, the restinga and the mangroves (Fig. 4). The Mata Atlantica occurs in the Serra cliffs that overlook the sea, whose topography acts as a climate barrier where the high relative humidity and rainfall remain. The main feature of this rain forest is the fact of being exposed directly to the maritime influence. In this forest the covering is dense and continuous. Most of the trees are 20 to 30 m high. The other strata are less representative. There is also a great number and variety of epiphytes and vines.

As a result of the devastation for land uses in State of Sâo Paulo approximately 5% of the original rainforest remains due to its location on the steeper cliffs. There are also some remaining areas in the inland sectors. The Mata Atlantica in Sâo Paulo State occupied originally 753 km^2, occurring in 55% of the Baixada Santista area. There is still 43% (319 km^2) which has preserved its original characteristics, and 232 km^2 of them are located in the Bertioga region representing 73 % of all the remaining

Figure 3. Topography of the Baixada Santista showing the contrast between Serra do Mar and the coastal plane of Santos (Drawned by F.R. Holmes)

original Mata Atlantica in the Baixada Santista. Besides, 31% (226 km^2) of the original forest is now replaced by secondary forest in an advanced state of succession, mainly in the areas where there were banana crops, 142 km^2 of which are located in Santos and 74 km^2 are very degraded. Furthermore, 116 km^2 which correspond to 16% of the original Mata Atlantica area are occupied by urban, industrial and other human activities. Generally speaking, the areas of Mata Atlantica which remain preserved are located mainly in the mid and high cliffs of the Serra do Mar an the secondary forests and degraded areas are located in the low cliffs and the isolated hills in the coastal plain (CETESB, 1991). As a result of the devastation for land uses approximately 5% of the original rainforest remains due to its location on the steeper cliffs. There are also some remaining areas in the inland sectors.

As for the restinga, the plant communities are varied, sharing the same sandy soil, poor in organic matter and clay and located close to the beaches, beach-ridges, dunes or lagoon banks. There are restinga forests mainly in the larges plains such as Juréia and Itanhaém, on the south coast.

The restinga forests are from 6 to 15 m high without a defined stratification. Near the sheltered beaches the trees are smaller and shaped by the marine spray effects, whereas near the larger beaches there is a dense transitional shrub strip, and close to the sea there is an herbaceous vegetation which colonizes the dunes.

There is still (90 km^2) 22% of the original restinga forest of Baixada Santista that remain with the same physiognomic structure and species composition. From these, 88 km^2 are located in the Bertioga Coastal plain. The remaining 78% (232 km^2) are very degraded and 78 km^2 are at the secondary succession stage with arboreal size; 83 km^2 are very degraded mainly due to deforestation, sand extraction and to the industrial pollution, presenting only shrubs and herbaceous vegetation. The other 162 km^2 are occupied by urban, industrial and rural activities (CETESB, 1991).

The constantly flooded lands, mainly by the tides and also by the rivers, constitute an appropriate area for the development of mangroves. This condition occurs due to the great amount of rivers on the coastal plain under the influence of the tides and the high rainfall which increases the input of sediments and nutrients, besides reducing the salinity. The location of the region close to the south limits of the Brazilian mangrove distribution (Laguna 28° 30' S in Santa Catarina, Cintron and Schaeffer Novelli, 1983) has to be taken into account once it makes the mangrove structure less developed, probably related to lowest temperatures.

Figure 4. Alterations in the plant communities of the Baixada Santista (modified after CETESB, 1991)

The total extension of Baixada Santista is 1329 km^2 and 10% of this area was tidal plains originally occupied by mangrove forests. At the present moment 40% of these forests are well preserved and they are mainly located in Bertioga's region, and some in Sâo Vicente's region (CETESB, 1991). The degraded mangroves totalize 31% (42 km2), mainly in Santos region. The most degraded mangrove forests whose alteration is clearly related to industrial pollution are concentrated in the region of Santos estuary. The degradation of this region is mainly due to oil spills and the influence of the Cubatao and Mogi rivers whose waters receive a great load of industrial and urban effluents and the waters of the Billings, coming from the power plant of Henry Borden (CETESB, 1990a).

Mangrove Features

A study carried out from 1982 to 1986 in 33 different mangrove sites has shown that forest height ranges from 4.50 m to 13.20 m, the average being 8 m. The forest density varied according to the degradation of areas, ranging from 600 to 3,800 trees per hectare and from 900 to 5,800 number of stems per hectare. As for the average diameter, a variation of 3.60 cm to 12.75 cm was observed together with a total basal area of 3.593 to 31.126 m^2 per hectare. The large range of variation was observed among the seedlings and saplings density, being from 0 to 23,200 and from 0 to 5,200 per hectare respectively (CETESB, 1988).

As for the leaves size, the average lengths in the different sites ranged from 7.6 to 11.38 cm for *R. mangle*, 5.91 to 10.66 for *L. racemosa* and 6.20 to 8.83 for *A. schaueriana*. The average widths for each species were 3.48 to 5.26 cm for *R. mangle*, 2.91 to 4.35 cm to *L. racemosa* and 2.86 to 4.24 to *A. schaueriana*. The average leaf areas were 20.65 to 36.46 cm^2 for *R. mangle*, 12.54 to 27.94 cm^2 for *L. racemosa* and 10.49 to 18.75 cm^2 *A. schaueriana*. (CETESB, 1988)

The cluster analysis of the different mangrove sites of Baixada Santista, according to these structural features showed groups of mangrove forest with different degrees of degradation. The analysis of the distribution of these groups indicated that elements of the same group are not found necessarily close to each other although there is a concentration of them in some places in particular.

It followed from this observation the delimiting of a transverse area (direction northeast-southwest) between the region of Sâo Vicente and Santos estuary (Fig. 5), which presents a higher concentration of highly degraded mangrove areas, whereas the south of the Sâo Vicente estuary and to east, near Bertioga, there is less degraded areas. It is hard to tell to what extent the human activities affect this distribution once this region is exposed to several impacts. It is worth mentioning that Cubatao is in the very heart of the area where the most degraded mangroves are. Beside that, the rivers that cross the main industrial complex situated in the north of this area flow directly into it.

Figure 5. Distribution of less degraded mangrove forest (groups 1 and 4) and the highly degraded mangrove area (groups 2 and 3) with the industrial complex of Cubatão

Taking this into account one could assume that the precarious state of conservation of the mangroves situated in this area is a consequence mainly of the environmental changes caused by the existence of this industrial complex.

The plant community in this region is thus highly altered by human activities. To have a clearer view of the causes of these alterations in natural ecosystems, mainly the mangroves, a brief historical background of the human occupation in this area will be described in the next item.

Land Conversion to Human Uses

In the last century the Baixada Santista has been going through deep changes, with marked influence in the economic and social picture, not to mention alterations in the landscape and environmental quality. A brief description of this process is made below, based mainly on the information given by Goldenstein (1972) and Branco (1984).

In this region the indian has always made a living from fishing, shellfish harvest as shown by the "sambaquis" or shell-midden (archaeological site where shells and skeletons were found) hunting and some roots crops (mandioca). The Portuguese brought the cattle, cane and cereals cultivation and sugar mills.

Later with the development of cattle raising to slaughter, tanning spots started to crop up, specially in the region of Cubatao, close to the mangroves, particularly on the grounds of the tannin organic compound, found in the leaves and bark of the mangrove and still largely used in leather preservation due to its bactericidal properties although recently substituted by synthetic products.

In spite of the inadequate soil, the large extension of lands available and the low demographic density favored the installation of fruit crops mainly the banana. The banana turned out to be the most important product of the region, occupying large extensions of lands and the local labor force and being the raw material in the manufacturing of sweets. These factories belonged to a first industrial period of the region together with the tannin, aniline, fertilizers and paper factories.

In the early 60s, the urban and industrial boom together with the building of new roadways gradually took over the banana crops (Franca, 1965). The Santos port played an important role to the development of the region acting as a compulsory way to all the goods to be commercialized, enhancing the area as a whole.

Through the port the export of sugar started to flourish being the main product until the 1850's. Later there was an expansion of coffee crops in Sâo Paulo State, becoming this a main export product in Santos port until 40's, this situation being changed by the industrial development.

In 1949, the government decided to build a large oil refinery, with capacity of 45,000 barrels per day. The Baixada Santista was chosen for a number of reasons. The existence of roadways, railways and sea, the proximity to the biggest consumers spot of the country, the electrical facilities and finally the political reasons.

Twenty years later the refinery of President Bernards doubled its capacity, reaching the production rate of 115,000 barrels per day. Needless to say it brought together the establishment of chemical industries, constituted by a group 20 factories, most of which had as its raw material products or subproducts of the refinery and some being located there only because of the proximity to the port.

In 1959, the COSIPA works (Companhia Siderurgica Paulista), i.e. steelworks, were launched. This huge establishment was located in a plot of 5 million square meters, between the Serra do Mar, the estuary (Largo do Can,u) and the mangrove. Part of this area was constituted by dry soil, most of which was used to grow banana and palm trees, the main activity in Piaçaguera region. As for the mangrove areas, there was an expensive and harmful process of filling, due to the technical difficulties.

Much in the same way as all the previous big enterprises in the area, non attention was given to the environmental and social impacts that might have happened. As a result, there was a great migration, with a great influence on local customs, society and on the landscape itself.

By the end of the building works, the area was left with a great number of unemployed, homeless and poor people and environmental problems. Therefore, the Baixada Santista was loaded by social problems, mainly habitational ones. It all started in the late 40's, with the building of the first modern roadway which linked Sâo Paulo to Santos, being increased by another roadway in the 70's. It followed from that an increasing process of inappropriate occupation starting in the Serra do Mar cliffs with most of the people living in slums and spreading to unhealthy spots in the mangrove, frequently flooded.

The Baixada Santista has shown an intense urbanization as a result of the industrial, the portuary and the tourism development. Cubatao has 84 industrial spots at the moment, 30 of which are regarded as highly pollution by CETESB. In Santos and Sâo Vicente the most important urban concentrations of the Baixada are found, with no primary industries besides the

traditional ones concerned with food production. Guarujá, located in Santo Amaro Island, has the tourism as its main activity. However, the industrial complex of Dow Qu¡mica and Propensa lie there.

Santos and Sâo Vicente bays normally have an increased population at the weekends and on holiday, mainly during the summer. This particular feature of the region brings about serious problems to the basic services and overloads the sanitary infrastructure worsening the organic fecal pollution in the area. (CETESB, 1978a).

One has to consider another important aspect, the atmospheric conditions, extremely unsuitable for the pollutants dispersion. This fact is worsened by the topography that is, the cliffs which surround the valleys, where the city and industries lie. It is clear to see the lack of social and environmental plan in the industrial installation, resulting in a totally altered landscape. There is also a political choice for the sake of a fast development at the expense of the environment and its natural resources.

Heavy Metal Contamination

The inorganic industrial waste composed basically by heavy metals do not degrade and although they can be diluted in the long run they will always be responsible for an environmental damage even if the source has ceased to operate. The intense occupation and industrialization of the region has launched an enormous amount of waste into the environmental, amongst which the heavy metal. If found in high rates they can be harmful to the organisms and bioaccumulation can occur in the several levels of the food web. Thus, a historical background to this contamination will be described in the three regions of the Baixada: Santos and Sâo Vicente estuaries and Santos bay.

Sources of Heavy Metal Pollution

The installation of Presidente Bernades refinery in Cubatao and consequently of other industries in the region in the mid 50's, started a serious problem of environmental contamination. The inorganic industrial waste composed mainly by heavy metals was released in the water bodies of the region, most times without any kind of treatment.

This industrial complex which is composed by several activities the chemical (Hg and Cr), paper (Hg), fertilizers (Cu, Pb, Hg and Cr), chlorine (Hg), styrene (Hg and Cr) and steelworks (Cd, Pb and Zn) constitute the main sources of heavy metals (CETESB, 1978a, b).

The first studies concerning the environmental contamination by heavy metal in the region started in 1974 and showed a high level of contamination (Pereira *et al*. 1975; CETESB, 1978a; Tommasi, 1979; Tables 1 and 2). The metals whose values presented themselves beyond the aquatic organisms' preservation criteria were the Hg and Pb for the water and the Cu, Hg and Zn for the sediment. As for the sediment, it can observe a negative gradient concentration for the three metals from Santos estuary to Sâo Vicente and Santos bay.

Five years later, the mercury concentration in the water was also high (Boldrini and Pereira, 1987) with average values beyond the aquatic organisms preservation criteria for brackish waters which is 0.1 μg/l (CONAMA, 1986; Table 2). As for the sediment, there was a contamination in the region by cooper, zinc and mercury, once for the these metals the values went beyond the aquatic organisms preservation criteria (Tables 1 and 2). One could also observe a gradient of decreasing concentration of metals in the sediment from Santos estuary to Sâo Vicente and Santos bay.

Thus one can observe that for five years, the picture of contamination in Baixada Santista has not been largely altered. It was not before the state government got alarmed by this high level of pollution in the waters of Baixada Santista, that there had to be a better control of industrial waste, maximizing the usual monitoring mainly after 1984. Based on the data from CETESB (1987), as far as the quality of the waters in the watershed of Cubatao river are concerned, there were significant reduction in the amount of waste released in the waters, from 1984 to 1986.

As for the concentration of heavy metals, it was reduced in 97 % in the period analyzed, falling from 4,000 to 120 kg/day. This value remained the same after 2 years (CETESB, 1990b).

Due to the improvement in the quality of the waters in the Cubatao River, fish, shrimps and other aquatic organisms started to flourish which was worrying because of its unsuitable food value (Boldrini *et al*., 1989). Previous studies had already shown the accumulation of these metals in organisms in the Baixada Santista. Concentration beyond the human consumption criteria for Cu, Hg, Zn and Cd (Nauen, 1983 in CETESB, 1990a) were found in the fish muscles and viscera, from 1979 to 1980.

Thus other measurements of heavy metal in Cubatao River and Santos estuary (CETESB, 1990a) were made and values of concentration of Cd, Pb, Cr, Fe and Hg beyond the aquatic organisms preservation criteria were found for the water and as for the sediment some spots were regarded as highly polluted, according to Bowden classification (in Prater and Anderson, 1977) concerning the Ar, Pb, Hg and Zn.

Table 1. Calculated average values in study sites from cited references

AREA		WATER (μg/l)					SEDIMENT (μg/g)					References
	EC	Cu 50(a)	Pb 10(a)	Zn 170(a)	Cr 50(a)	Cd 5(a)	Cu 10(b)	Pb 20(b)	Zn 20(b)	Cr *	Cd 5(b)	
Santos Bay	X	-	-	-	21	-	-	-	-	-	-	1
	s	-	-	-	30	-	-	-	-	-	-	
	X	14	10	30	-	-	3.4	4.6	29.2	-	-	2
	s	13	10	10	-	-	1.5	5.8	7.3	-	-	
	X	20	10	37	7	0.9	4.5	6.0	31.5	12.9	0.2	3
	s	2	4	8	0	0.2	2.4	4.1	8.2	4.4	0.02	
S. Vicente Estuary	X	6	20	30	-	-	7.2	13.5	36.6	-	-	2
	s	5	10	4	-	-	6.9	12.1	23.1	-	-	
	X	21	8	38	7	0.8	6.9	6.1	38.8	15.0	0.2	3
	s	4	1	14	0	0.1	8.1	8.2	38.4	18.9	0.02	
Santos Estuary	X	6	10	30	-	-	15.5	4.5	55.3	-	-	2
	s	2	10	10	-	-	6.0	1.0	17.6	-	-	
	X	17	8	29	17	0.7	17.7	12.9	72.1	25.5	0.2	3
	s	2	2	7	21	0.2	2.5	4.4	24.8	7.8	0.01	
	X	10	#	48	#	#	4.7	11.7	33.1	3.0	0.2	5
	s	4		6			0.1	8.3	39.1	2.2	0.2	

1- Pereira *et al*. (1975) data from 1974; 2- CETESB (1978) data from 1974; 3 - Boldrini and Pereira (1987) data from 1979; 5 - CETESB (1990a) data from 1989. EC - Established criteria for the aquatic life preservation. (a) according to CONAMA (1986). (b) according to Chester (1975 *in* SEMA, 1980). **-** = not made. * = not exist EC for marine or brackish sediment . # = detection limit " EC .

Table 2. Calculated averages values of Hg in study sites from cited references

Local		Water (μg/l)	Sediment (μg/gr)	References
	EC	0.1(a)	0.1(c)	
Santos Bay	X	0.62	-	1
	s	0.66	-	
	X	0.30	0.08	2
	s	0.10	0.09	
	X	0.18	0.07	3
	s	0.07	0.02	
	X	0.49	0.05	4
	s	1.28	0.05	
S. Vicente Estuary	X	0.50	0.73	2
	s	0.30	1.19	
	X	0.12	0.29	3
	s	0.02	0.33	
	X	0.09	0.06+	4
	s	0.01	-	
Santos Estuary	X	0.80	1.07	2
	s	0.20	0.93	
	X	0.21	0.58	3
	s	0.11	0.42	
	X	0.30	1.58	4
	s	0.12	1.41	
	X	ND	1.47	5
	s	-	0.73	

1. Pereira *et al*. (1975) data from 1974; 2. CETESB (1978) data from 1974; 3. Boldrini and Pereira (1987) data from 1979; 4. Tommasi (1979) data from 1974; 5- CETESB (1990a) data from 1989. EC - Established criteria for the aquatic life preservation; ND= not detected; + = only one sample; (a) CONAMA (1986); (c) Vucetic *et al*. (1974 *in* SEMA, 1980)

An analysis of the average data in the concentration of mercury and zinc in the sediment of Santos estuary showed that both have gone beyond the aquatic organisms preservation criteria (Tables 1 and 2). As for the aquatic organisms, values of concentration of Cu, Hg, Zn, Cs and Pb were found in the fish muscles and viscera that have gone beyond the minimum human consumption criteria established by national and international laws.

The metal found in high concentrations in sediments since 1974 as the Cu, the Zn and the Hg, were also high in aquatic organisms. This shows how important it is to consider the concentration of metals in sediments once, generally speaking, the highest concentration is found in Santos estuary, next in Sâo Vicente estuary and Santos bay. This is due to the location of the sources of industrial waste which are placed mainly next to the high Santos estuary, reaching also Sâo Vicente estuary. Santos bay, because of its further location from the pollution sources is least affected region.

Furthermore, one could observe that even after the reduction of the release of heavy metal from industrial sources, this problem, which started decades ago with the industrialization of Baixada Santista is still present in the region and will continue for quite a long time.

Heavy Metals Concentration in Mangroves

The metals reach the mangrove in two main interchangeable forms: diluted fraction and particulate fraction. The physical-chemical features of this environment cause several transfers between the two fractions.

The increase of the water pH and its ionic power and salinity, together with a decrease in the speed of the river flow when reaching the coastal area, causes the precipitation of several diluted metals and accelerate the deposition of particles (Lacerda and Rezende, 1984). Thus, the mangrove can concentrate these metals in the sediment.

Studies carried out by CETESB from 1982 to 1986 (CETESB, 1988) in mangroves of Baixada Santista (Santos estuary, Sâo Vicente and Bertioga regions) show concentrations of heavy metals such as Cr, Cu, Cd, Pb, Hg and Zn, in the sediment (Table 3) and leaves of the mangrove (Table 4).

This study shows that the concentrations of Hg were higher than the criteria established for marine sediment of 0.1 μg/g (Vucetic *et al*., 1974 in SEMA, 1980) in 97% of the sample sites, the highest ones being found in Santos estuary mainly for the sites next to the industrial complex of Cubatao, reaching 1.60 μg/g in Cascalho river.

As for the concentrations of Zn in the sediment it was shown that in 76% of the sites they were higher than the criteria established for marine sediments of 20.0 μg/g (Chester, 1975 apud SEMA, 1980), the highest ones being 188.0 μg/g in Santos estuary.

As for the concentration of Pb in the sediment, it was observed that in 45% of the sites they were higher than the criteria established for marine sediments of 20 μg/g (Chester, 1975 in SEMA, 1980). Although this contamination was found in a larger number of sites in Sâo Vicente, the highest concentrations were found in samples collected next to Cubatao, in Santos estuary, reaching 76.2 μg/g.

The concentrations of chrome in the sediment for the three studied areas varied from 0.62 to 40.60 μg/g, the highest one being found in Onça river in Santos estuary.

In the same site, the highest concentration of Cu (29.6 μg/g) was found and among the sample sites in only 12% of them the criteria established for marine sediment of 10 μg/g (Chester, 1975 in SEMA, 1980) was surpassed.

The concentration of cadmium in the sediment was below the criteria established of 5 μg/g (Chester, 1979 in SEMA, 1980).

The analysis of average concentrations in the three studied areas (Table 3) shows that in Santos estuary, where the industrial complex lies, the highest levels and variability were found.

The mangrove sediments contamination by heavy metals was also observed in other regions of the Brazilian coast as Rio de Janeiro, where some of them presented higher values them the Baixada Santista. In Enseada das Graças for instance the Cd concentration was 0.50 μg/g and as for the Zn in Coroa Grande it was 180 μg/g (Lacerda and Abrao, 1984). As for the Cu and Cr in rio Irajá the values reached 15.4 and 80.5 μg/g respectively (Lacerda, 1982).

As the concentration of heavy metals was high both in the waters and sediments of the mangroves, this also happened to the leaves of the three species. According to table 4 one can observe that the species which presents highest concentration values of heavy metals was *A. schaueriana*. As for the other two species, *L. racemosa* concentrated more Pb, Cr and Zn whereas *R. mangle* presented higher concentrations for Cd, Cur and Hg. It's worth pointing out that cadmium concentration were similar for the three species.

Table 3. Average, highest, and lowest values, and standard deviation of heavy metals in study sites

Metals		Bertioga	Santos Estuary	São Vicente
Cadmium	X	0.13	0.52	0.09
	s	0.14	0.73	0.11
	Max	0.50	2.09	0.49
	Min	0.06	0.06	0.06
Lead	X	13.3	24.7	21.7
	s	9.1	23.0	10.2
	Max	29.8	76.2	40.5
	Min	1.0	3.8	1.2
Copper	X	6.0	8.9	5.9
	s	3.5	7.4	2.5
	Max	12.9	29.6	9.4
	Min	1.5	2.9	1.9
Total Chrome	X	9.8	9.5	5.0
	s	8.9	11.3	3.2
	Max	26.2	40.6	10.0
	Min	1.6	0.6	0.61
Mercury	X	0.42	0.72	0.25
	s	0.24	0.49	0.12
	Max	0.78	1.60	0.46
	Min	0.12	0.11	0.05
Zinc	X	36.4	48.7	32.0
	s	15.3	47.7	18.2
	Max	55.0	188.00	60.0
	Min	5.4	10.80	9.6

Table 4. Heavy metals concentration (µg/g) values in leaves of *Rhizophora mangle* (Rh), *Laguncularia racemosa* (Lg), and *Avicennia schaueriana* (Av) in Baixada Santista

Metals	Species	X	s	Max	Min
Cadmium	Rh	0.2	0.2	0.6	0.025
	Lg	0.2	0.3	0.9	0.004
	Av	0.2	0.4	1.9	0.004
Plumb	Rh	2.4	1.4	4.7	0.470
	Lg	3.3	1.3	5.6	0.480
	Av	4.3	2.8	14.4	0.460
Copper	Rh	21.4	38.4	184.0	1.660
	Lg	12.0	16.8	93.4	2.150
	Av	44.5	111.7	563.0	2.280
Chrome	Rh	0.9	0.6	3.8	0.480
	Lg	1.3	1.4	8.3	0.590
	Av	1.4	0.6	3.4	0.600
Mercury	Rh	0.047	0.073	0.420	0.0002
	Lg	0.039	0.035	0.160	0.0003
	Av	0.079	0.100	0.540	0.0010
Zinc	Rh	13.6	11.8	64.8	4.79
	Lg	28.5	25.8	155.0	1.10
	Av	47.4	30.9	198.0	12.90

Studies about heavy metal concentration in mangrove leaves (Lacerda *et al*., 1986) carried out in southeast coast of the three species when compared to Baixada Santista values showing that the mangroves of this region are very polluted by this metal as for the Zn the concentration were similar for the two regions. On the other hand the Pb values for the Baixada Santista mangrove leaves were lower.

The different heavy metal contents in the leaves of the three species can be accounted by their physiological adaptation to develop in substrates of high salinity, with different mechanisms of osmotic regulation (Mizrachi *et al*., 1980).

The low concentration of metals in *R. mangle* tissues can be related to its capacity of excluding salt other substances in the root absorption. However *A. schaueriana* performs only a partial exclusion in the roots, completing its osmotic regulation by releasing the salt through the leave surface. Thus, this mechanism facilitates the transport of metals to the leaves,

which would account for the high concentration of these substances found in this species.

Analysis of contamination of heavy metals and structural features of mangrove forests showed that the most contaminated forests (Fig 6), (CETESB, 1988) show most degraded structures.

Moreover, highest concentrations of heavy metals of the region were found in the transverse area of the most degraded mangroves delimited through a cluster analysis. This confirms the fact that these areas receive large amounts of industrial waste, which reinforces the hypothesis suggested (in vegetation) that its present state of degradation is mainly a consequence of this situation.

It is worth pointing out that the least degraded sites are located in the mid and low estuaries, which could be related the minor influence of pollution sources and a bigger action of dispersion due to the tides.

Oil Contamination

Due to the great frequency of oil spills on the Brazilian coast its main sources and causes will be described and analyzed in this item together with a study case where the oil effects on mangrove have been registered through a long term monitoring. This analysis is based on data of the forest structure and field observations registered in 7 years.

Sources of Oil Pollution

On the coast of Sâo Paulo state, there are several sources of oil pollution, mainly in the ports and oil terminals. The oil release in the sea can happen in many ways, some through the loading and unloading of the ships which are regarded as ordinary and represent 96% of oil spills. The remaining 4% are caused through accidents (Branco and Rocha, 1980).

It is in Baixada Santista that most of the accidents in Sâo Paulo estate happen, reaching 19% of the total, being Santos and Cubatao the most affected by this kind of pollutant (Awazu, 1985). From January 1980 to February 1990, 71 accidents involving oil and derived were reported in this region (CETESB environmental accident file), from which only 45% had an estimate of quantity of oil released, which amounts to 5,300 m^3.

The ships themselves were responsible for 59% of the accidents whereas the pipelines, the reservoir-ships and industries for 11.5% each. Besides the accidents, which release great amount of oil in the environment, one cannot forget the continuous input of oil and grease from industries.

Once the mangroves are placed near the coast, where the most of the spills happen, they are constantly affected by this pollutant. Based on studies of the oil spill effect in coastal areas. Gundlach and Hayes (1978) classified the main coastal environments according to their vulnerability to oil. This classification is based on the residence time of oil in the environment and takes into account the initial biological impacts. Sheltered coastal areas as mangrove are regarded as the most sensitive to this kind of impact for being seriously affected by oil. This is due to the residence time of oil in mangroves which can be more than 10 years with a estimated recovery time of 20 years. In order to better understand the ecosystem response to the oil impact a long term monitoring in the mangroves in Baixada Santista was carried out and will be described below.

Oil Effect on Mangroves: a Case Study

A long term survey was initiated in the coast of the Sâo Paulo state after a 2,500 ton pipeline crude oil spill in 1983 reached the mangrove. The aim of this study was to determine the effects of oil spill on the mangrove ecosystem. The results presented in this chapter are from the first 6 years monitory (1984-1989).

Bertioga, situated at 23°51'S 46°08' W, where this study is being carried out, has large mangrove area which when compared to Santos, Cubatao and Sâo Vicente (in Sources of heavy metal pollution) are less degraded.

Bertioga Channel is the main water course, around 25 km long. This tidal channel has its west mouth in the Porto Channel, situated in the mid estuary while, next to Bertioga city its east mouth, the tidal, connects with the ocean, making the tidal flow more intense in this area (Fúlfaro and Ponçano, 1976). The border of this channel is dominated by large mixed mangrove forest of three species: *Rhizophora mangle*, *Laguncularia racemosa* and *Avicennia schaueriana*.

In the border of Santo Amaro island (Fig. 6) there is a narrow band and very little is left of the original forest, mainly due to the fillings for the construction of harbors. On the other hand, the continental border which is large, and more difficult to get to, has mangrove areas spreading along the river banks with developed and more conserved forest.

In order to carry out this research, a sample area in the left bank of Iriri river, which was strongly affected by the oil spill which even drained through the land, was chosen. Moreover, as this spill occurred during the high tide, a great amount of oil reached the inner part of the forest.

Figure 6. The study area of Bertioga Channel nd Iriri river in the coast of São Paulo State

Two 10×10 m plot were limited in the fringe one next to the river bank (outer plot) and the other 20m further towards the inner part (inland plot). These plots were permanently tagged in 1986. In order to monitor the seedling growth, 1 × 1 m plots were also limited established.

For the structural and functional findings the methodology described by Schaeffer-Novelli and Cintrón (1986) and was utilized and the sampling started 4 months after the oil spill. Structural analysis of the forest was based on data related to the tree density, diameter of breast height (DBH) and tree height. From these parameters the specific basal area, the average diameter of the forest and the species frequency were worked out (calculated). As for the functional characteristics, 50 green leaves and 50 senescent leaves of the three mangrove species were collected at random, the first measured width and lengthwise and the latter being measured on the leave area and the grazing rate were measured on the latter.

These data sets are time series through which the moving averages were calculated, in order to identify the trends of each parameter at study.

During the field work, the immediate effect of the oil spill that could be noticed was the withering of the leaves and an increased defoliation. At the same time, an overwhelming mortality of seedlings and sapling was observed. These alterations were called initial effect. However, the mortality of seedlings and sapling

could also be observed after the event, thus constituting the long term effects (CETESB, 1989).

After a high initial defoliation followed a milder one for some months. The same phenomenon was reported by Cintrón *et al*. (1981) and Teas *et al*. (1987) in mangrove areas affected by oil.

In the remaining leaves and in the new ones morphological alterations as spots, speckles, perforations, fading, twisting and necrosis were observed. RPI (1984) also mentions these symptoms for leaves under the oil stress.

Changes were also observed in leaf size, measures of leaf area shown an increase of leaf size for all three mangrove species. A two-way ANOVA was used to analyze species and year effects. For this test, we used only the data for a single month. The results showed that there is a significant difference among leaf area of the three species. *A. schaueriana* has a smaller leaves with a leaf area average of $17.2 \pm 6.5 cm^2$ *L. racemosa* leaf area average was 25.2 ± 8.5 cm^2 and *R. mangle* was 31.3 ± 9.2 cm^2.

There were also significant differences among years and a significant interaction between years and species. Leaf area measurements showed different curves for each species. *R. mangle* had a significant increase ($p<0.05$) of 25.9 % of leaf size from 1984 to 1986. *L. racemosa* also showed an increase (43.4 %) from 1985 to 1987 ($p<0.06$). Only *A. schaueriana* continued showing a significant increase (64.5 %) of leaf area from 1984 to 1991 ($p<0.09$).

To test the statistical validity of these increasing trends, we used auto-regressive models, ARIMA (Box and Jenkins *In*: Morettin and Toloi, 1981) adjustment and a *t-student* test for $p<0.05$. *R. mangle* showed a significant increase from September 1984 to December 1986 (Fig. 7a), *L. racemosa* showed a significant increase from December 1984 until the last observation in March 1992 (Fig. 7b). Leaves of both species started to increase approximately one year after the oil spill in October 1983. Only *A. schaueriana* showed a continuous increase of leaf area since the beginning of the monitoring in 1984 (Fig. 7c).

Other studies in the same area also reported an increase in the leaves of the three species, almost doubling its original leaf size in *A. schaueriana* and *L. racemosa* (Ponte *et al*., 1987). On the other hand, the literature reports a reduction of the leaf surface related to stressing chronic factors as oil and others (Cintrón and Schaeffer-Novelli, 1983; Getter *et al*., 1985). To account for this controversy, the reduction in our study occurred in the first months, the increase being then a mere recovery of its original size, as the long term effect was weakening (Rodrigues *et al*., 1989).

Figure 7. The increase of leaf area for *R. mangle*, *L. racemosa* and *A. schaueriana* in nine years after the oil spill

The grazing rates on the leaves decreased for all the species mentioned, lowering to as little as 5% of the total leaf area, which is regarded as a healthy forest value. This findings clash with the hypothesis mentioned by Schaeffer-Novelli and Cintrón (1986), that impacted forests have a higher herbivory.

The reduction of the grazing rate (Rodrigues *et al*., 1989) can be attributed to the migration of herbivores to other places in search of food, due to the leaf fall. Another possibility would be the release of aromatic fractions and the storage of other substances inhibiting their consumption. In addition, oil could also interfere in the development at some stage in the life of some insects and other herbivores, which would decrease its population.

To sum up, the leaves response to the stress was fast, shown by the overwhelming defoliation and the reduction of leaf size in the first months after the impact. Afterwards, there was a continuous increase of leaf size, in some cases stationary, which would show the leaves have already recovered their original size. However, the structural parameters behaved distinctly, requiring a longer period to respond. Therefore a longer period of sampling is needed, one year at least.

The mangrove structure was seriously affected by the oil impact. After three years the forest density was reduced from 2435 trees/ha to 1936 trees/ha, which represents a 20% reduction. This high loss in trees occurred mainly one year after the oil spill (Fig. 8a). The reduction in forest density caused a reduction of the total basal area, from 15.9 m^2/ha to 9.5 m^2/ha, which corresponds to a 40% reduction (Fig. 8b). It is worth pointing out that this reduction was mainly due to the higher mortality of *A. schaueriana*, (Fig. 8c) once its frequency was highly altered (Rodrigues *et al*., 1990). It is thought that this species is the most sensitive to oil, which according to Getter *et al*. (1985) is due to its mechanism of the osmoregulation wich apparently facilitates the oil to reach the leaves.

These reductions are statistically valid according to the results of the regression analysis of these dummy variables (Draper and Smith, 1981), shown in Table 5, which reveals that the findings before the response to the impact are statistically different from the previous level. As for the average diameter, the trend curves did not show great alterations, only a slight decrease. This fact is due to the reduction of both values: the basal area and forest density, resulting in a stable ratio.

Based on the reported alterations, it could be said that the oil impact in the mangrove caused a disruption of the normal structural development pattern. According to Cintrón and Schaeffer-Novelli (1984), in the normal development of a forest, the expected alterations are reduction in the forest density and increase in the basal area and average diameter, as result of room competition.

The tendencies of a continuous decline observed for the structural parameters in Rio Iriri forest, indicate a long term effect, without signs of stabilization or recovery, until the fourth year of sampling. Yet, that analysis of the data of the last two years which corresponds to the 5th and 6th years after the oil spill indicates a tendency of stabilization in all the structural parameters. This behavior suggests that in the 5th year after the oil spill, the effects tend to get weaker. It is believed that from the 7th year, the recovery of the forest might start, which will be confirmed in future sampling if the parameters happen to show signs improvement.

Figure 8a. Alteration in the forest density nine years after the oil spill

Figure 8b. Alteration in the total basal area of the mangrove forest nine years after the oil spill

Until the 6th year after the spill the sites were rapidly colonized by new seedlings which grew approximately up to 1 meter high. Thereafter their mortality rate was 100%, for once depending exclusively on the sediment water and nutrients they were presumably affected by the remaining toxic substances present in it.

Besides, in addition to low propagule density they also exhibited atrophy and deformations. The rapid colonization was probably due to propagules from other places and although the presence of seedlings apparently indicates recovery it was not the case.

Nine years after the oil spill the presence of seedlings and juveniles will suggest the beginning of the ecosystem recovery, indicating that the seedlings are managing the survive and grow.

The analysis of the trend curves of the structural parameters reveals that all of them show a similar behavior with the same sequence of stages, which corresponds to successive phases of the community response to impact (Fig. 9). It is worth pointing out that these phases are related to the community response as a whole.

Table 5. Results of the Regression Analysis of dummy variables

Parameter	Before Level	Effect	Present Level	Statistical Significance	Reduction %
Basal Area *A. schaueriana*	0.70	-0.64	0.076	0.0	-89.28
Total Basal Area	1.59	-0.63	0.96	0.0	-39.78
Relative density *L. racemosa*	70.49	17.31	87.81	0.0	24.55
Relative density *A. schaueriana*	29.50	-17.31	12.19	0.0	-58.67
Tree number.	243.54	-49.91	193.64	0.0	-20.49
number	370	-147.44	222.56	0.0	-39.85

These phases could be called and described as follows:

1. Initial effect. The structural responses of the ecosystem to oil are not immediate, and there is, therefore, the first phase after the impact when no structural alteration can be measured. During this phase, only seedlings and sapling died. This phase lasted one year.

2. Structural damage. High mortality is observed, the oil impact on the ecosystem can be measured in terms of major structural alteration. This phase lasted a little more than three years.

3. Stabilization. After major alterations, a stabilization period starts, with none or few alterations in the structural parameters. During this phase, it is possible to observe saplings. This phase lasted for five years.

4. Recovery. A period of recovery of the ecosystem follows, when it is possible. to measure improving alterations of the structural parameters. However, the ecosystem might not fully recover to its original state. We believe this phase only begins after nine years.

The duration of each phase might vary depending on environmental conditions, the local features of the place where the oil spill occurred, and the amount and kind of oil spilled. Still, it is assumed that this community response pattern, constituted by this succession of phases described above, should occur in other mangroves affected by oil pollution.

Comparing these post-spill phases to the ones described by Snedaker (1985), where he distinguished three phases: mechanical suffocation, chronic chemical toxicity, and recovery, one could say that the author used the oil action on the mangrove as a major criterium and in this study the criterium was the community response to this action.

It is worth pointing out that to each action there is a correspondent effect that characterizes a response phase so that a relationship can be established between the two classifications. Consequently the first and the last phases described by Snedaker (1985) correspond to the initial effect and recovery phases of this study.

However, during the chronic effect phases, or long-term one, two phases were observed: the first showing a significant structural damage and the other of a relatively long stabilization. It follows from that, therefore, that after the initial effect the structural response does not occur slowly and continuously until the recovery. What happened then was a relatively abrupt alteration in a short span followed by a longer period of stabilization before the recovery itself.

In the literature concerning the oil spill effects on mangroves, a different terminology is used. The effects described are generally classified in three ways: **1)** acute and chronic (Davis *et al.*, 1980; Getter *et al*., 1981; Jernelóv and Linden, 1983 and Lewis, 1983); **2)** immediate or initial and chronic (Jackson *et al*., 1989); **3)** short and long term (IUCN, 1982; Krebs and Burns, 1977).

Beside this, these concepts vary from author to another and sometimes they are not clearly defined. In some cases the acute effect is the one which occurs during the first month (Lewis, 1983). To other authors the same phase can lost months (Davis *et al*., 1980). One can also find the term acute effect related to the high mortality of trees which actually happens initially in most cases (Snedaker, 1985). The long term or chronic effect is the one which happens after the acute one.

In this study the major mortality rate does not coincide with the initial or acute effect. Therefore, the alterations observed and measured during the first year after the oil spill will be called initial or short-term effect, whereas the other alterations observed in the following years including the high mortality rate of the second and third years will be called long-term effects.

Figure 9. Post spill phases of the structural response of the mangrove forest

Due to the oil impact on mangrove areas, initial effects in the first months and long-term effects, until the fourth year, were observed. The stabilization of these alterations in the last two years suggested that after six years the effects started to weaken, which might indicate the beginning of recovery. This study confirms that the time residence of oil in mangroves is long and that the ecosystem requires a long period to recover. This calls for an urgent oil pollution control, by preventive action, besides the elaboration of emergency plans to protect these ecosystems effectively.

Conclusions

The mangrove in the region suffered all kinds of pressures such as: fillings, solid waste, changes in the water bodies, industrial and domestic effluents causing chemical and organic contamination, not to mention the successive oil spills.

However, they still perform an important ecological role such as the retention of sediments in the estuary, protection of the coast line, as well as a retention of toxic substances as heavy metals, preventing them from reaching the coastal area. Ecological and environmental impact studies are invaluable for they help to understand the ecosystems responses to the stress factors, which will be extremely useful in other estuary regions in the tropical America which are facing similar problems.

The conclusions drawn from the case study, concerning the oil effects in the ecosystem can be seen in Figure 10 and are described as follows:

- as for leaves the initial effects was the withering and high defoliation. The long-term effect was the alteration of the shape and color of the leaf, besides perforations and necrosis. It was also observed an increase of the leaf area and a decrease in the herbivory for the three species.

- the oil impact caused an interruption of the normal process of development expected for a forest, due to the reduction of the numbers of trees and stems and the total basal area.

Figure 10. Schematic representation of the oil effects on the mangrove forest

- *A. schaueriana* was the most sensitive species to the oil effects.

- the responses of the mangrove to the oil impact can be divided in four successive phases called: initial effect, real structure damage, stabilization and recovery.

- the oil effects on the mangrove were more evident one year after the oil spill, with higher mortality rate as from this period. These effects persisted four years after the oil spill. The stabilization of the structural parameters in the last two years suggests that after six years the weakening of the effects might be a sign of recovery.

- the high density of seedlings does not necessarily indicate a recovery of the ecosystem. A more adequate criterium for this would be the presence of saplings.

- the presence of some saplings in the last year of sampling is a clear signal of recovery of the forest, which confirms the tendencies of structural parameters.

These results enabled one to confirm the importance of long-term studies, making it possible to compare different situations, once it is believed that these four phases of the mangrove responses to oil can occur in other cases. It also reinforces the need to develop researches concerning the functional aspects of the ecosystem once the functional responses occur faster than the structural ones and can be measured in a shorter period of time.

In view of this, long-term studies of productivity are recommended in order to obtain more information about degraded ecosystems through the identification of yearly environmental patterns so as to compare to non degraded ecosystems. The aim of this approach is to implement a methodological standardization and to produce ecological information management oriented.

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The Environmental Quality of Coastal Ecosystems in Ecuador: Implications for the Development of Integrated Mangrove and Shrimp Pond Management

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Abstract

The shrimp farming industry in Ecuador, ranked second only to oil export revenue for the country, has suffered loss of production due to the lack of available post larvae ponds. The problems of the shrimp industry in Ecuador demonstrate the linkage of ecological processes of coastal ecosystems, with a variety of regional economic activities. In this chapter we described the ecological linkages between shrimp farming in Ecuador with the functions of mangroves to illustrate the importance of environmental quality to sustainable management of coastal resources. We present an integrated description of the diverse factors that contribute to environmental quality and how they influence the sustainability of the shrimp farm industry. In addition, we describe the potential negative feedbacks of shrimp ponds management on coastal resources, particularly mangroves and the potential deterioration of water and habitat quality of the coastal zone. Commercial shrimp operations have increased dramatically, rising to over 50,000 metric tons with value of 482 million dollars. By 1991, these were more than 150,000 ha of shrimp ponds.

One of the major limiting factors in the expansion and productivity of the shrimp farm industry is the availability of postlarvae, but data suggest that the optimum carrying capacity is about 60,000 ha of shrimp ponds. The influence of the shrimp farm industry on changes of land use patterns and utilization of estuarine waters had prompted concerns over possible negative impacts of this industry to habitat and water quality of coastal ecosystems. The most controversial issue related to the environmental quality of the coastal resources of Ecuador has been the exploitation of mangrove associated with the construction of shrimp ponds, most of which are located in the southern provinces of Guayas and El Oro. Initially most ponds were constructed in Salinas, but the

construction moved the mangroves. The reduction of mangrove area from 1969 to 1991 was estimate at 42,285 ha or 20.8 % of the original 203,695 ha. While the national average of mangrove loss is about 21 %, the ranger for the four coastal provinces was from 12.8% for the Guayas province to 70.5% for Manabi.

The life cycle of shrimp involves use of the coasts, ocean, nearshore and estuarine areas. Shrimp farms operate by providing an artificial habitat to facilitate the post larvae shrimp development to adults, thus bypassing those stages of the life cycle that normally occur in the estuarine ecosystem. The natural system tends to recycle genetic stock between inshore and offshore waters, as dictated by the shrimp life cycle. Shrimp farming short circuits this process by serving as a sink of genetic resources of shrimp from the coastal zone. Environmental quality of coastal resources is influenced by inputs from upland watersheds, exchanges with the intertidal zone and oceanographic processes. Activities in the watershed include dams, urban expansion, agriculture and industrial discharge. These activities are leading to eutrophication and toxic release. The construction and operation of shrimp ponds leads to a number of environmental impacts because the habitat and water quality of estuaries is linked to a variety of ecological process in mangroves. These include functions that supply wild post larvae to grow out ponds, and water quality conditions that enhance the growth and survival of these juvenile shrimp. Habitat quality of mangroves in the estuary are lost when these forest are destroyed for the ponds constructions. Functions of mangroves such as nutrient sinks are also removed as a contribution to the water quality of the estuary. Mangroves also provide food for estuarine organisms and this function is lost when mangroves are destroyed. Water pumping in shrimp ponds utilizes significant amounts of estuarine water. For example, in the Guayas river estuary, the volume of pumping can be greater than the discharge of the river during low flow. The fishery of post larvae is non-selective and many others species are collected. The long term sustainability of the shrimp farming industry in Ecuador will require integrative approaches to the management of coastal zone resources. These management considerations not only include the interactions of the shrimp farming industry with estuarine and coastal ocean ecosystems, but also the land use activities in the upland watershed and urban centers. The ecosystem approach to the management of natural resources is essential since it integrates both the ecological processes of environmental systems together with the socioeconomic characteristics of regional development. Shrimp ponds management could minimize negative impacts on coastal ecosystems if mangroves are preserved to protect their contribution to the coastal zone environmental quality. The preservation and conservation of mangroves can be implemented either by delineating green belts or buffer strips surrounding waterways, or by establishment of large sanctuaries and conservation areas. The sustainable use of mangroves for production of timber products is also a form of mangrove conservation and utilization that acknowledges the importance of this resource to local economies. The contribution of excess nutrients from shrimp ponds to mangrove ecosystem would most likely enhance that contribution of these forested wetlands to habitat quality of estuaries.

Resumen

La industria del cultivo de camarón en el Ecuador, la segunda más importante del país sólo después del petróleo, ha sufrido de pérdida de producción debido a la carencia de postlavas. En este capítulo se describen los enlaces ecológicos entre el cultivo del camarón y las funciones de los manglares para ilustrar la importancia de la calidad ambiental en el manejo sustentable de recursos costeros. Se presenta una descripción integrada de los factores que contribuyen a la calidad ambiental y cómo influyen en el mantenimiento de la industria. Además, se describen las retroalimentaciones negativas y potenciales del manejo de estanques de camarón sobre los recursos costeros particularmente manglares y el deterioro potencial de la calidad del agua y del hábitat en la zona costera. Las operaciones comerciales de camarón han aumentado dramáticamente, llegando a más de 50,000 ton con un valor de 482 millones de dólares. En 1991 había mas de 150,000 ha de estanques.

Uno de la mayores factores limitantes en la expansión y productividad de la industria camaronícola es la disponibilidad de postlarvas, pero los datos sugieren que la capacidad óptima es alrededor de 60,000 ha de estanques de camarón. La influencia de la industria del camarón sobre cambios en el uso del suelo y utilización de aguas estuarinas ha despertado el interés sobre posibles impactos negativos a la calidad del hábitat y agua del ecosistema costero.

Inicialmente la mayoría de los estanques se construyeron en salinas, pero la construcción se extendió a manglares. La reducción del área de manglar de 1969 a 1991 se estimó en 42,285 ha (20.8%) de las originales 203,695 ha. Mientras el promedio nacional de pérdida de manglar es alrededor de 21%. El ciclo de vida del camarón involucra el uso del océano, costas y áreas estuarinas. Las granjas de camarón proveen un hábitat artificial para facilitar el desarrollo de postlarvas de camarón a adultos, evitando las etapas del ciclo de vida que normalmente ocurren en el ecosistema estuarino, esto tiende a debilitar los recursos genéticos del camarón de la zona costera al limitar el intercambio genético entre comunidades. La calidad ambiental de los recursos costeros es influida por aportes desde tierras altas a la cuenca hidrológica, los intercambios con la

zona intermareal y los procesos oceanográficos. Las actividades en la cuenca hidrológica incluyen diques, expansión urbana, agricultura y descargas industriales. Estas actividades producen eutroficación y liberación de tóxicos. La construcción y operación de estanques impacta al medioambiente porque la calidad del agua y del hábitat se vincula a una gran variedad de procesos ecológicos en los manglares. Estos incluyen funciones que abastecen postlarvas silvestres que crecen fuera de los estanques y condiciones de calidad de agua que mejoran el crecimiento y supervivencia de este camarón juvenil. La calidad del hábitat de los manglares en el estuario se pierde cuando estos bosques son destruidos para la construcción de estanques. La función de los manglares como trampas de nutrientes y la capacidad de proveer alimento a los organismos estuarinos es anulada provocando pérdida de la calidad de agua en el estuario. El bombeo de agua a los estanques puede llegar a utilizar cantidades importantes de agua estuarina, por ejemplo en el estuario fluvial de las Guayas el volumen de bombeo puede ser mayor que la descarga del río en temporada de poco flujo. La pesquería de postlarvas es no-selectiva y se capturan muchas otras especies. El mantenimiento a largo plazo del camarón que cultiva la industria en el Ecuador requerirá enfoques integradores a la gestión de recursos de la zona costera. Estas consideraciones no sólo incluirán las interacciones de la camaronicultura con el estuario, el océano y el ecosistema costero sino también las actividades terrestres en tierras altas, cuenca hidrológica y centros urbanos.

El enfoque del ecosistema para el manejo de recursos naturales es esencial ya que integra tanto los procesos ecológicos como las características socioeconómicas de desarrollo regional. La gestión de estanques para camaronicultura podría minimizar los impactos negativos sobre ecosistemas costeros; si los manglares se conservan para preservar su contribución a la calidad ambiental de la zona costera. La preservación y conservación de manglares puede implementarse tanto por cinturones verdes como por franjas de mitigación que circunden los canales como por el establecimiento de grandes santuarios y áreas de conservación. El uso sustentable de manglares para la explotación maderera es también un tipo de utilización y conservación del manglar que reconoce la importancia de este recurso en las economías locales. El aporte de exceso de nutrientes de los estanques al ecosistema de manglar probablemente mejoraría su productividad y potencialmente la contribución de estos bosques pantanosos a la calidad de hábitat de los estuarios.

Introduction

In August 1986, a workshop was organized in Guayaquil to evaluate the decline of the shrimp farming industry in Ecuador (Olsen and Arriaga 1989). The industry, ranked second only to oil in export revenue for the country, had recently suffered loss of production due to the lack of available post larvae for ponds. Total production and export of shrimp were down in 1984, and during 1985 only half of the 75,000 ha of shrimp ponds constructed in the coastal provinces were in operation. Several factors had been associated with the decline in post larvae in the estuaries along the coast of Ecuador including lower water temperatures (back to normal temperatures following an El Niño event), loss of mangrove habitat, decline in water quality (increased occurrence of red tide, pesticides, and heavy metals), and to indiscriminate over fishing of available wild stocks. From 1980 to 1987 nearly 15,000 ha of ponds were authorized for construction annually increasing the total to 150,000 ha by 1991; and most of these ponds had been constructed in the intertidal zone. There was immediate concern that the unregulated growth of this industry had destroyed the ecological processes of coastal ecosystems, which threatened the sustainability of shrimp farming in Ecuador. Most of the concern was centered around the loss of ecological functions of mangroves, which is attributed to maintaining habitat and water quality of coastal ecosystems. The lack of recruitment and survival of wild post larvae demonstrated the susceptibility of this industry to the environmental quality of the coastal zone of Ecuador.

The problems of the shrimp farm industry in Ecuador demonstrate the ecological linkages of coastal ecosystems with a variety of regional economic activities (Fig. 1). The economic uses and values of mangroves depend on the ecological functions of mangroves. These functions are constrained by the environmental setting or forcing functions of the coastal zone (see Twilley and Day, Chapter 10 this volume). The multiproduct functions of mangrove ecosystems are attributed to the diverse ecological processes that they support in the estuary including primary productivity, detritus export, refugia, sedimentation, and nutrient cycling (Fig. 1). These ecological processes result in the functions of mangroves in providing habitat and water quality, and shoreline stabilization. The uses and values of mangroves in any coastal region depend on the nature of these functions, together with the cultural and economic conditions of the region.

Figure 1. Diagram of the linkages among the environmental setting, ecological processes, functions, and uses of mangrove ecosystems

Economic activities either in the coastal zone or in upland watersheds that are linked by rivers to the coast can also have feedback effects on the ecological processes of coastal ecosystems (Fig. 1). This is an important concept whereby the use of ecosystems by humans can influence the capacity of natural resources to provide ecological functions. Analyses of the ecological and economic linkages of coastal resources must use a multiproduct function approach that requires a holistic perspective of the opportunity costs of different management scenarios (Gottfried, 1992). In this chapter we plan to describe the ecological linkages between shrimp farming industry in Ecuador with the functions of mangroves to illustrate the importance of environmental quality to sustainable management of coastal resources. The multiproduct approach to analysis of coastal ecosystems also must include the impacts of upland and offshore linkages to the coastal zone. The controversy in coastal resource management of Ecuador centers around the relative impacts of pond construction and management as negative feedback to the ecological processes of mangroves and estuarine ecosystems. The success of developing management plans for the coastal zone depends on the ability to identify the properties that determine the environmental quality of coastal ecosystems in Ecuador, and how shrimp pond management influence these linkages (Fig. 1).

The many complex interactions of human and natural resources in the coastal zone of Ecuador underscore the problems with interfacing the shrimp farm industry with coastal ecosystems. Environmental quality of the coastal zone of Ecuador is influenced by unique coastal processes along with a variety of intertidal and upland land uses (Fig. 2). The estuarine resources of Ecuador are strongly influenced by inland watersheds that control freshwater discharge, sediment input, and transport of chemicals from various land use practices in the river basin. The coupling of the estuary with the intertidal zone is enhanced by 3-5 m tides that link the exchange of sediments, nutrients, detritus and organisms with mangrove ecosystems (Fig. 2).

Offshore processes are strongly influenced by El Niño events that control offshore water temperatures and inland precipitation (and thus river discharge). Water temperatures and salinity of the coastal zone are important environmental signals that trigger the recruitment of various biological resources, such as shrimp. This chapter will include discussions of these resources and land uses, and the utilization of offshore and estuarine habitats, to describe the complex nature of environmental quality in the coastal ecosystems of Ecuador. Our objective is to present an integrated description of the diverse factors that contribute to the environmental quality, and how they influence the sustainability of the shrimp farm industry. In addition, we will describe the potential negative feedback of shrimp pond management on coastal resources, particularly mangroves, and the potential deterioration of water and habitat quality of the coastal zone.

Figure 2. The complex interactions of coastal processes and upland land use that determine the environmental quality of coastal resources of Ecuador

Shrimp Farming Industry

The first commercial shrimp operations in Ecuador began in 1969 (Siddall *et al*., 1985), nearly 400 years following the Incas practice of closing off lagoons which were temporarily flooded with seawater and penaeid shrimp larvae. Ecuadorian farmed shrimp production rose dramatically from 1979 to 1984 and by 1989, shrimp ponds produced over 50,000 metric tons while production from the trawl industry remained at 7,500 metric tons (Fig. 3A). The value of production from shrimp ponds increased from $56.9 to $287.9 million US dollars from 1980 to 1986 (Fig. 3A). The export value of the 1991 crop increased to $482 million US dollars, ranked second only to petroleum as an export commodity for Ecuador (Olsen and Arriaga, 1989; Aiken, 1990). The cash generated by this mariculture activity is more important to the economy of Ecuador than bananas and cacao combined, and twice as important as coffee

(Aiken 1990). The tremendous growth of this industry has made Ecuador the second leading farm shrimp producer in the world providing nearly 16% of the world market (McPadden, 1985). Nearly all of this market is consumed in the United States.

The expansion of the shrimp industry in Ecuador is best exhibited by the increase in the construction of shrimp ponds (Fig. 3B). The construction of shrimp ponds averaged nearly 14,000 ha annually from 1980 to 1991 resulting in a total area of over 150,000 ha by 1991 (Fig. 3B). Nearly all of these ponds were constructed in the intertidal zone, with most of the initial sites located in the upper zone or salinas. As these zones disappeared, more of the construction was located in the forested intertidal vegetation, or mangroves. The expansion of the farmed shrimp industry has been largely confined to the two southern coastal provinces of Guayas and El Oro (Fig. 4). A survey from CLIRSEN (1992) cites that the southern provinces of El Oro and Guayas have 127,130 ha or 87% of the total area of shrimp ponds which are constructed in the intertidal zone (Fig. 4). This coastal zone region maintains an extensive area of intertidal communities including nearly 83% of all mangroves in Ecuador (Fig. 4). Thus the rate of pond construction and the impacts of this land use change on estuarine ecosystems in this region became the central focus of concern for the environmental quality of the coastal zone of Ecuador.

One of the major limiting factors in the expansion and productivity of the shrimp farm industry is the availability of post larvae (PL). Although there has been a steady increase in the construction of shrimp ponds, not all of these ponds have been in operation (Fig. 3C). In the initial stages of the development of this industry, nearly all the ponds constructed were in operation up to 1983. From 1983 to 1985, the area of ponds increased from about 60,000 to 100,000 ha, but the area of ponds in operation actually decreased to about 50,000 ha. The abundant supply of post larvae during the El Niño event of 1983, along with available capital, created an excessive demand for construction of shrimp ponds from 1985 to 1987. However, the natural supply of post larvae during the more normal years of recruitment could not supply the existing ponds, resulting in decline in pond operation. The fluctuation in the available PL during other El Niño events suggests that the optimum carrying capacity of the natural system is about 60,000 ha of shrimp ponds (Fig. 3C). The difference between ponds constructed and those in operation has placed a major emphasis to find alternatives to natural post larvae, with major emphasis on production of additional post larvae with hatcheries.

Figure 3.A). Productivity of the shrimp pond industry from 1982 to 1991 based on US dollars and mass of shrimp sold per year. **B)** Index of the rate of shrimp pond construction in Ecuador based on permits issued by the Ministry of Agriculture, compared with direct delineation of shrimp pond area using remote sensing (1983, 1987 and 1991). **C)** Areas of shrimp ponds authorized for operation and estimates of the actual areas of shrimp ponds in production from 1975 to 1988 according to Espinoza (1989)

The influence of the shrimp farm industry on changes in land use patterns and utilization of estuarine waters have prompted concerns over possible negative impacts of this industry to habitat and water quality of coastal ecosystems. Several factors have been associated with the decline in post larvae in the estuaries along the coast of Ecuador including lower water temperatures (back to normal temperatures following an El Niño event), loss of mangrove habitat, decline in water quality (including increased occurrence of red tide, pesticides and heavy metals), and/or to indiscriminate over fishing of available wild stocks. Changes in the environmental quality of coastal ecosystems

may in turn reduce the sustainability of the shrimp farm industry. Existing information suggests that the production in shrimp ponds has decreased from 1,600 to 250 kg of shrimp ha^{-1} yr^{-1} over the last several years, though stocking rates have been maintained at about 65,000 PL ha^{-1} per harvest. Mortality rates in shrimp ponds are estimated at greater than 50 percent, and evidence suggests that maturation rates are also lower. Poorer water quality has contributed to increase occurrence of disease and poor maturation of postlarvae, lower growth rates and higher mortality of wild shrimp. These factors include impacts on both the recruitment or availability of wild post larvae and also the survival of larvae once they are transported to growout ponds. Decrease of wild PL has increased demand for PL from hatcheries. Currently, there are over 100 hatcheries that have been constructed that may produce about 7.7 billion postlarvae annually in 1991 (Armijos 1992). Good water quality is critical to the productivity of hatcheries because larvae are susceptible to disease. These factors demonstrate the susceptibility of this industry to the environmental quality of the coastal zone of Ecuador.

Figure 4. Land use changes in the intertidal zone of the four coastal provinces of Ecuador from 1969 to 1991 including **A)** shrimp ponds, **B)** salinas (high salinity intertidal regions void of vegetation), and **C)** mangroves

Coastal Resources of Ecuador

Oceanographic Resources

Coastal Ecuador is a transition zone, or equatorial front, between southerly flowing tropical water from the Panama Bight and northwardly flowing Humboldt Current from Peru (Fig. 5). Tropical water flows southwards from the Panama Bight along the coast of Panama and Colombia to about 2 ^{o}S supplying warm (>25 ^{o}C) and low salinity (<34‰) waters to the coast of Ecuador (Pesantes and Pérez, 1982). Colder (<22 ^{o}C) and more saline (>35‰) waters flow northward from Peru with the Humboldt current that is strongly influenced by coastal upwelling. The mixing of these two water masses occurs between Manta and Punta Santa Elena along the coast of Ecuador and gradually moves southwards into the Gulf of Guayaquil. The dominance of the Panamanian Current occurs during the summer causing an increase in sea water temperature and initiates the onset of the rainy season (Cucalón 1984, 1989). Years of abnormally warm water temperatures and high rainfall are associated with El Niño climate patterns due to the influx of unusually warm surface water in southeast Pacific Ocean. The warmer offshore waters have resulted in the explosive populations of white shrimp off the coast of Ecuador from enhanced spawning, maturation, and recruitment. In the last century, major El Niño events were recorded in 1925, 1929, 1939, 1941, 1953, 1957-58, 1965, 1972-73, 1976, and 1982-83 (Cucalón, 1989). The high availability of post larvae that supported the expansion of the

Figure 5. Map of Ecuador showing the four coastal provinces of Esmeraldas, Manabi and El Oro, and the coastal offshore currents dominated by the Panamaniam from the north and Humbolt from the south

shrimp industry in 1983 and 1984 has been associated with the latter El Niño event. The unpredictable nature of oceanographic events and their influence on the ecological processes of upland and coastal watersheds contributes to the complex nature of coastal resource management in Ecuador.

Estuarine Resources

The coastal zone of Ecuador (1 ^{o}N to 3 ^{o}S 20'S) consists of four coastal provinces (Esmeraldas, Manabí, Guayas, and El Oro) situated in 284,000 km^2 (of lowlands between the Pacific Ocean and the Andean highlands (Fig. 5). There are three climatic life zones along the coast: a moderately wet climate in the south with abundant fresh water from runoff around Guayaquil; an arid central province with very sparse vegetation; and in the north near Esmeraldas, a more humid, tropical zone with abundant rainfall and runoff. More than 95 percent of the annual precipitation falls during the wet season from January to May (Stevenson, 1981), and varies from less than 500 mm in the central provinces and the coast of the southern provinces, to over 3000 mm at Santo Domingo de los Colorados in the north (Engineer Journal 1972, Schaeffer-Novelli 1983). Annual mean temperatures (from 24.2 to 27 ^{o}C) vary little along the coast, thus potential evapotranspiration is about 1300 mm/yr. Thus the ET/R ratios in the northern provinces are about 0.43, compared to 2.60 in the arid central provinces.

The two major river and estuarine ecosystems of the coast are Esmeraldas River estuary in the north and Guayas River estuary which flows into the Gulf of Guayaquil in the south (Table 1). The Gulf of Guayaquil receives runoff from some 20

Table 1. The principal river systems of coastal Ecuador

Province	River	Annual Mean Discharge (m^3/s)	Watershed Area (km^2)
Esmeraldas		1,932	40,527
	Esmeraldas	990	21,418
	Cayapas	490	5,919
	Mira-San Juan	230	6,329
	Verde	94	1,970
	Mataje	63	821
	Muisne	32	1,600
	Cojimíes	30	1,859
	Carchi	6	341
Manabí		79	9.413
	Chone	41	2,583
	Jama	17	2,205
	Portoviejo	16	2,110
	Jipijapa	5	2,515
Guayas		1,364	48,966
	Guayas	1,160	32,674
	Canar	72	2,110
	Balao	60	2,515
	Taura	57	2,630
	Zapotal	16	7,730
El Oro		80	6,666
	Jubones	58	4,326
	Arebukkas-Zarumilla	22	2,400
Peruvian Rivers	Catamayo-Chira	100	11,012
	Puyango-Túmbez	99	4,965
TOTAL		**3,654**	**121,279**

rivers with a watershed of 51,230 km^2 and is the largest estuarine ecosystem on the western Pacific coast of South America (Cucalón 1984). The major source of freshwater is the Guayas River, which forms 60 km upstream at the confluence of Daule and Babahoyo Rivers. The mean discharge of 1143.7 m^3/s for the Guayas River is the highest among the 30 rivers in the coastal zone of Ecuador representing 39% of the total discharge from this lowland region. Mean precipitation in the Guayas River drainage system north of Guayaquil is 885 mm/yr, which may range from less than 400 to more than 1800 mm during any one year (Fig. 6). Discharge is strongly seasonal ranging from 200 m^3/s during the dry season to 1600 m^3/s in the wet season with an average amount of precipitation (Fig. 6). Tides are semi-diurnal and are of equal amplitude of 1.8 m in the Gulf of Guayaquil, but are amplified to 3-5 m in the Guayas River estuary near the city of Guayaquil (Murray *et al*., 1975).

Figure 6. The iterannual variation of precipitation in the Guayas River estuary watershed (Guayaquil) from 1950 to 1969; and the seasonal nature of discharge of the Guayas River based on average monthly flow from 1962 to 1964 (Stevenson, 1981)

Mangrove Resources

The most controversial issue related to the environmental quality of the coastal resources of Ecuador has been the exploitation of mangroves associated with the construction of shrimp ponds. This controversy is indicative of the need to establish the spatial distribution of natural resources during the initial stages of resolving resource management problems. Along with the growth of the shrimp farming industry during the 1980s was the concern that most of the mangrove ecosystems along the coast of Ecuador were destroyed. This apparent loss was linked to the loss of post larvae due to the loss of habitat and detritus that support the juvenile stages of shrimp in the estuary. The particularly poor recruitment of post larvae in 1984 created concern that the environmental quality of the coastal zone of Ecuador as a nursery of shrimp larvae had been threatened due to the loss of mangroves wetlands.

The government of Ecuador commissioned the Military Geographic Institute, through the Centro de Levantamientos Integrados de Recursos Naturales por Sensores Remotos (CLIRSEN), to determine the distribution of mangrove resources and changes in land use in the intertidal zone due to shrimp farming (Alvarez *et al.*, 1989). Information from a variety of remote sensors including radar images, infrared, black and white, and panchromatic aerial photographs were used to develop a series of thematic charts of land use in the intertidal zone of Ecuador. CLIRSEN performed surveys in 1984, 1987 and 1991 to document the change in mangrove resources due to shrimp farm construction along the coast. They used archived photos from 1969 as a reference point of mangrove resources prior to the expansion of the shrimp pond industry. Land use in the intertidal zone was identified as either mangroves, shrimp ponds, or salinas; in addition other land uses such as upland vegetation (including brush and natural forests), agricultural areas, and urban settlements were also identified along the coast. Mangrove areas were subdivided into three categories depending on tree height; M1 is trees >15m, M2 is trees between 5 and 15m, while M3 is trees <5m. Thematic charts of the scale 1:25,000 were developed from base scale maps of the coastal zone provided by the Military Geographic Institute; these base scale maps were used for transcription of the remotely sensed data (Figs. 7 and 8). Statistics were generated for each of the four coastal provinces from 1969 to 1991, and summed for the entire coastal region. This technical information on the mangrove resources of Ecuador was a very important cooperative effort of the Subsecretaria de Recursos Pesqueros, Directora de la Marina Mercante, CLIRSEN, and Proyecto de Manejo de Recursos Costeras.

The remote sensing surveys of mangrove resources showed that most of the shrimp ponds were constructed in the southern provinces of Guayas (Fig. 7) and El Oro (Fig. 8). The 1991 survey from CLIRSEN (1991) cites that these two southern provinces have 127,130 ha or 87.1% of the total area of shrimp ponds constructed in the intertidal zone (Fig. 4). The intertidal zone is the preferred site because the close proximity of ponds to the shore lowers costs associated with supplying water and larvae to the ponds. Initially shrimp ponds were constructed in more inland intertidal areas called salinas that are basically void of any vegetation. Some of the largest areas of salinas were found in the Guayas and El Oro provinces in 1969, prior to the construction of shrimp ponds (Fig. 4B). These inland intertidal areas were drastically reduced from a total of 51,495 ha in 1969 to only 7,490 ha in 1991, a loss of 85% of these areas. Nearly

61% of the salinas were converted to shrimp ponds from 1969 to 1984, the remainder converted to urban settlements. The shift in land use of shrimp farmers from salinas to mangroves as preferred sites for pond construction was particularly evident in El Oro. From 1966 to 1977 there were 834.2 ha of ponds constructed in the southern coast of El Oro at Piloto Machala and 73% of these were built in salinas (Fig. 8). However, 63% of the shrimp ponds constructed from 1977 to 1982, can be accounted for by the loss of 937 ha of mangroves in this region. The ratio of relative habitat loss of mangroves and salinas (mangrove loss:salina loss) was 0.8 from 1966 to 1977, compared to 3.0 from 1977 to 1982. As the inland areas became scarce, more of the shrimp ponds were constructed in mangrove habitats resulting in the increased loss of this natural resource from the coastal zone (Fig. 4).

These two southern coastal provinces, Guayas (Fig. 7) and El Oro (Fig. 8) also have the most extensive areas of mangroves along the coast of Ecuador (Fig. 4C). In 1969, the total mangrove area in Ecuador was 203,695.1 ha, of which nearly 78% were located in these two southern provinces. By 1991, the total mangrove area declined to 161,410.1 ha, and 81% of this resource remained in Guayas and El Oro provinces (Fig. 4C). The reduction of mangrove area from 1969 to 1991 was estimated at 42,285 ha or 20.8% of the original 203,695 ha (Fig. 9). By 1991 CLIRSEN estimated that 145,940 ha of ponds had been constructed in the coastal zone, suggesting that 29 % of shrimp ponds had reclaimed mangrove areas. During this same interval, nearly 44,005 ha of salinas had been loss, nearly all to shrimp pond construction. Together, reduction in the areas of shrimp ponds and mangroves from 1969 to 1991 can account for only 59% of the area of ponds constructed. Thus there are 86,290 ha of land that has been converted to shrimp ponds that is either not part of the intertidal zone, or some other category other than mangroves and salinas of the coastal zone.

The average annual loss of mangroves between 1969-1984 was 1,434 ha/yr, compared to 2,618 ha/yr from 1984-1987 and 3,362 ha/yr from 1987-1991 (Fig. 9B) (CLIRSEN, 1992). The greatest loss of mangroves has occurred in the Guayas Province at nearly 1,500 ha/yr for both the 1984-1987 and 1987-1991 periods of analysis. Because of the large area of mangroves associated with the Guayas River estuary, this high rate of loss is less than 15% of the existing mangrove resources. The loss of mangroves in the Guayas province represents 38% of the total reduction in mangrove resources from 1969 to 1991. While the national average of mangrove loss is about 21%, the range for the four coastal provinces was from 12.8 % for the Guayas province to 70.5 % for Manabí. In Manabí, the loss of mangroves was nearly 6 % per year from 1984 to 1991. By late 1988 the destruction of mangrove habitat in some estuaries in the province of Manabi was virtually complete, such as in Rio Chone estuary. From 1974 to 1988 mangrove area along this estuary declined from 3,973 to 600 ha, and nearly all of the mangrove loss was associated with construction of shrimp ponds. In the Atacames River estuary, there are only 50 ha of mangroves remaining of the 578 reported in 1970s, representing a loss of 90.1 % of the mangrove resources. In the southern province of El Oro, the Machala-Puerto Bolívar area lost over 50 % of a very productive mangrove system. The perspective of mangrove loss in Ecuador is site specific depending on the intensity of pond management relative to available mangrove resources. This has confused the issue of the national average of mangrove loss along the coast of Ecuador compared to the nearly total elimination in specific estuarine watersheds. Thus the impacts of mangrove loss on the environmental quality of estuarine resources depends on specific regional land use characteristics. However, the cumulative loss of mangroves along the entire coast is also an issue relative to sustaining habitat necessary for continued recruitment of shrimp to the coastal zone (Turner, 1989).

Mangrove exploitation for timber products is less documented, although in the northern coastal province of Esmeraldas mangrove timber is used for the production of charcoal. Mangrove wood produces 4,500 kcal/kg of wood, and is considered an economical supply of energy in the rural coastal areas of Ecuador. This is the only location in Ecuador that extensively uses mangrove wood for charcoal, although much of the woody debris from clear cutting mangrove forests for shrimp pond construction in the southern provinces was also converted to charcoal. Much of the cheap mangrove timber that supplied the charcoal industry in the northern provinces was from clearing the woody debris from initial stages of pond construction. Once pond construction declined, particularly following El Niño periods when post larvae were scarce, wood from pond construction was limited and the charcoal industry lost a cheap and adequate supply of mangrove timber. Now there is a strong demand for mangrove timber to supply an industry that expanded along with the shrimp pond industry. In Esmeraldas, it is estimated that 2,000 m^3/yr of mangrove wood is needed to supply the current demand, which would require 20 ha of mangrove forests per yr. However, mangrove silviculture is not commonly practiced as a form of mangrove management and even the minimum rotation of 20 ha of timber per yr to supply the charcoal industry is a problem.

Figure 7. Map of land use in the coastal zone using remote sensing techniques developed by CLIRSEN. This map represents the Guayas River estuary and Gulf of Guayaquil

Figure 8. Map of land use in the coastal zone using remote sensing techniques developed by CLIRSEN. This map represents the Machala region of El Oro

Figure 9. Loss of mangroves in Ecuador from each of the four coastal provinces and the analysis based on the following indices: **A)** area of mangrove, **B)** change per year, and **C)** percentage of the total mangrove area in each province (from CLIRSEN)

Coupling of Coastal Resources

The life cycle of shrimp demonstrates the important linkages of mangroves with other coastal ecosystems that are required to support the shrimp farm industry (Fig. 10). Adult shrimp reproduce in the coastal ocean and release eggs that develop into initial larval stages while floating in pelagic waters. The microscopic larvae are part of the plankton communities of the coastal ocean and utilize phytoplankton during their development into post larvae. Tides and currents together with their own locomotion provide the transport mechanisms necessary to recruit post larvae into nearshore and estuarine waters, where they receive protection and food in mangrove habitats. It is the combined processes of reproduction, maturation, and recruitment in shelf and coastal ecosystems that supply the estuarine waters with post larvae. Mangroves produce detritus that is utilized as food by shrimp, and prop roots provide refuge for protection from predators, creating a nursery for the critical stages of shrimp life cycle. Juvenile shrimp mature to adults and return to the coastal ocean, again aided by tidal currents. While offshore, adults reproduce and resupply the estuary with a new generation of shrimp. The life cycle of shrimp also represent the patterns of offshore and inshore migrations of other estuarine dependent marine organisms such as crabs and several species of fish. The linkage of post larvae supply to the environmental quality of coastal resources of Ecuador are complex (Fig. 10).

Both the oceanographic processes and mangrove habitat provide excellent conditions for post larvae through optimal spawning, maturation, and recruitment processes. The extreme temporal variation of offshore processes is stochastic, and this limits the ability to asses the relative contribution of oceanic, coastal and estuarine processes to the availability of post larvae during any one year. Thus, the relative role of offshore temperature, rainfall, and mangrove habitat in sustaining post larvae is complicated by the continuous change of each with time. In addition, the coast of Ecuador provides a very diverse set of environmental settings from drowned river estuaries with abundant river discharge, to dry conditions dominated by beach processes.

Figure 10. The life cycle of shrimp from eggs to adults with the approximate duration (in hours or days) of each stage, and the approximate location in the coastal zone where this stage of the life cycle occurs. In addition, the inner diagram describes the stages of the life cycle that are used in the operation of shrimp ponds

Zimmerman and Minello (1986) have found that *P. vannamei* and *P. stylirostris* inhabit areas in the mangroves, but it is not known whether these habitats enhance the survival or growth of these and other marine organisms in the Estero Salado. During periods of warmer temperature of offshore waters, there is a significant increase in frequency of *Penaeus* sp. throughout the mangrove habitats. Zimmerman *et al*. (1991) found that recruits of three species, *P. californiensis, P. vannamei* and *P. stylirostris* were abundant and used the nursery habitats associated with mangroves, while juveniles of *P. occidentalis* and *P. brevirostris* occurred infrequently and were not associated with mangroves. *P. vannamei* was more abundant during years with higher rainfall, particularly during the 1987 El Niño event, while *P. californiensis* was more abundant during drier years. This multi-year study demonstrated that tropical estuaries vary annually in habitat suitability as shrimp nurseries, depending on the temporal pattern of oceanographic processes and available habitat.

The temporal and spatial characteristics of the coastal zone of Ecuador complicate the role of resource utilization, such as shrimp farming, on coastal natural resources. As demonstrated in Fig. 10, shrimp farms operate by providing an artificial habitat to facilitate the development of post larvae shrimp to adults, thus bypassing those stages of the life cycle that normally occur in the estuarine ecosystem. The substitution of natural resources with pond environments relies on the continued feedback of adult shrimp back to shelf ecosystems. Here in offshore waters a new generation of shrimp are produced that resupply the estuaries with new post larvae. Adult shrimp produced in ponds are shipped to foreign markets and thus loss from the ecosystem. Thus while the natural system tends to recycle genetic stock between inshore and offshore waters, as dictated by the shrimp life cylce, shrimp farming short circuits this process by serving as a sink of genetic resources of shrimp from the coastal zone.

The spawning and maturation stages of the shrimp life cycle may also be substituted with hatcheries, thus limiting the dependence of the industry on the either the offshore or estuarine systems to produce post larvae. Hatcheries rely on offshore environments for gravid females to supply eggs from which post larvae are produced. Although artificial insemination of shrimp is a focus of many research areas, this process has yet to replace the natural environment. Even the production of post larvae from wild gravid females is limited in replacing estuarine environments. High rates of mortality of artificially produced post larvae in grow out ponds restrict the the ability of the industry to provide post larvae through hatchery operations. Thus the industry presently remains linked to the sustained secondary productivity of coastal ecosystems.

Impacts of Land Use Changes on Environmental Quality

The coastal resources of Ecuador are impacted by diverse economic activities and land use patterns that may influence the environmental quality of coastal waters. Environmental quality of the Guayas River estuary is influenced by inputs from upland watersheds, exchanges with the intertidal zone, and oceanographic processes in the Gulf of Guayaquil (Fig. 2). Activities in the watershed include a dam project that will influence fresh water discharge, expanding agriculture with associated input of chemicals including nutrients and pesticides, sewage from increased urbanization, and toxic substances from industrial activities (Arriaga 1989, Solórzano 1989). In addition, red tides develop in coastal waters that may be pumped into hatcheries and shrimp ponds. These diverse anthropogenic influences on water quality in the estuary complicate environmental management in this coastal ecosystem. In figure 2, the natural processes that influence the environmental quality of coastal systems are shown with links among river, tides, offshore processes, and mangroves habitat. In the lower section of figure 2, more anthropogenic effects of industry, navigation, urban, agriculture, and tourist activities are linked to environmental quality.

Shrimp Farming

Shrimp ponds represent managed ecosystems that are linked to the ecological processes of several coastal ecosystems (Fig. 10). Methods of shrimp mariculture in the intertidal zone are grouped into three classifications based on the densities of juvenile shrimp stoked in the ponds. Extensive mariculture, using a stocking density of 10,000-20,000 juveniles per ha, relies little on further supplements from seawater exchange via pumping or from artificial fertilization. Predators are present and annual yields are relatively low at 100-400 kg/ha. An increase in stocking rates to 50,000-60,000 juveniles/ha is a semi-extensive system that requires some supplemental feeding for an enriched supply of food, and exchange of seawater to control for

water quality problems such as decreased levels of dissolved oxygen. Production rates more than double with this program. The most highly managed system is semi-intensive operations that stock ponds at 100,000 juveniles/ha. Feed is supplied or ponds are fertilized to increase sources of food. Water exchange with the estuary is higher and annual production rates increase to 1,000-1,800 kg/ha. The shrimp producers association estimates that 60,000 ha, or nearly 60%, of operational shrimp ponds use extensive management (estimate for 1989). Semi-extensive and semi-intensive operations include 25,000 and 15,000 ha, respectively. However, since the semi-intensive operations are much more productive, they produce nearly the same amount of shrimp as the extensive operations.

The impacts of these types of shrimp pond management on the environmental quality of coastal resources is related to the loss of mangroves associated with pond construction, the pumping of water to control pond water quality, and the harvesting of natural post larvae to stock ponds. The evaluation of these interactions of shrimp pond management depends on our understanding of the function of various ecosystems to the habitat and water quality of the coastal zone (Fig. 11). The habitat and water quality of estuaries is linked to a variety of ecological processes in mangroves, as well as other ecosystems in the coastal zone. These ecosystem functions support specific stages of shrimp pond management that is designed to provide a habitat to facilitate the growth of post larvae to adult shrimp. These include functions that supply wild post larvae to grow out ponds, and water quality conditions that enhance the growth and survival of these juvenile shrimp. Habitat quality of mangroves in the estuary is lost when these forests are destroyed for the construction of ponds. Functions of mangroves such as nutrient sinks are also removed as a contribution to the water quality of the estuary. Critical water quality parameters that affect shrimp pond management, and profits, are dissolved oxygen, turbidity, and toxic substance, including red tides. Many of these water quality conditions are managed by the controlled pumping of water from the estuary. Through the recirculation of this water from ponds back to the estuary, pond management also contributes to the water quality of the estuary. This represents a feedback effect of shrimp pond management on estuarine ecosystems. This section will describe the linkages of pond management to the habitat and water quality functions of estuarine ecosystems.

Figure 11. Diagram of the ecological processes of mangroves and their function in maintaining the habitat and water quality of the coastal zone; and how these functions support shrimp farm industry

Loss of Mangroves and Habitat Quality

The loss of mangroves from tropical estuaries may have direct consequence to a variety of food webs by representing a loss of habitat and organic matter. The contribution of mangroves to sustaining secondary productivity of coastal ecosystems is dependent on the fate of leaf litter including production in the forest, transport to the estuary, and utilization by marine food webs (Fig. 11). Production and transport of litter are seasonal within a system, and variation among systems seems to be related to the environmental setting (see Twilley and Day, Chapter 10, this volume). Thus different types of mangroves, such as fringe and basin forests, may contribute different quantities of organic matter to adjacent estuaries. In Rookery Bay, Florida, fringe man-groves export twice as much organic matter per unit area as more inland basin forests. Yet, mass balance calculations of total organic matter contribution of each type of mangrove, taking into account the areal coverage of each habitat, resulted in equal loading rates of detritus to the estuary (Twilley, 1989; Twilley, 1982). In this case, the relative value of mangrove forests cannot be associated with distance from shoreline, but must also account for the relative distribution of each type of mangrove around the estuary.

Three approaches have been used to establish utilization of mangrove detritus in coastal ecosystems including: **1**) correlations of fishery yields with habitat area; **2**) habitat surveys of fauna density and diversity; and **3**) food web analyses. Associations exist between the production rate of shrimp and the extend of mangrove area (Macnae, 1974; Turner, 1977, Jothy, 1984) such that one hectare of mangroves can yield without management more than 600 kg/yr of shrimp and 100 kg/yr of fish (Turner, 1977). Based on an approximate loss of 42,285 ha of mangrove, the reduction on shrimp production from the coastal zone in Ecuador would be 25,400 mt/yr (revised from Turner, 1989 based on 1991 estimate of mangrove loss). This is equivalent to about 33% of the 1991 yield from shrimp ponds. Although these statistics do not bear causal relationships, they do point out that wherever a productive post larvae fishery exists; there is the presence of a mangrove habitat, as has been observed in Malaysia.

Surveys of mangrove habitat utilization and gut content analyses of organisms can be used to determinate the flow of organic matter though food chains. Although these flow diagrams are qualitative, because the relative quantity of food is unknown, they provide insight into the direct utilization of organic matter from mangrove forests. Such analyses of mangrove food webs have been made for south Florida, USA (Odum and Heald, 1972), and Laguna de Terminos, Mexico (Yáñez-Arancibia and Day, 1982, 1988). All of these studies have found a significant portion of the gut contents of detritivores to be material of mangrove origin. Thus in both lagoon and riverine type environmental settings mangroves may provide a significant contribution to detritus food webs.

The abundance of natural isotopes of carbon, nitrogen and sulfur can be used to determine the relative importance of different sources of organic matter to the diet of specific guilds in marine food weds (Peterson and Fry, 1987). One of the few studies using natural isotopes in mangroves food webs in Malaysia found that those shrimp nearshore had a carbon signature similar to decomposing mangrove litter (Rodelli *et al*., 1984). Yet, organisms collected farther offshore were feeding on phytoplankton. In southwest Florida, Macko and Zieman (1983) found that the signal of mangrove detritus in the body tissue of shrimp depended on the relative productivity of mangroves compared to seagrasses and phytoplankton. In Rookery Bay, where mangroves are a dominant habitat, the carbon from mangroves was significant composition of the tissue of shrimp. These studies indicate that the ecological function of mangroves as a source of food may vary among different environmental settings depending on the relative contribution of primary producers to the pool of detritus in the estuary. Isotope analysis of organic matter in the Churute River estuary and Estero Salado indicate that the microbial activity of these tropical estuaries have a strong influence on enriching the nitrogen content of organic carbon in the water column (Cifuentes et al., submitted). Yet, most of the original carbon structure of the suspended pool was of allochthonous origin, indicating the importance of mangroves to the food web of the Guayas River estuary.

Loss of Mangroves and Water Quality: Some preliminary evidence indicates that mangroves may be a sink of nutrients in coastal waters (Fig. 11). This may seem to contradict the outwelling concept of mangroves as a source of detritus to estuarine ecosystems (Odum and Heald, 1972; Twilley, 1985a; Twilley *et al*., 1986). One explanation is that net nutrient uptake may be a balance between inorganic nutrient input and organic nutrient export. However, the net balance of nutrient exchange has seldom been investigated for mangroves although they are generally considered as a sink of nutrients from the estuary. Walsh (1967) noticed that inorganic nutrient concentrations decreased in waters moving through a mangrove in Hawaii. Nedwell (1975) used enclosures to measure nutrient uptake by mangrove sediments and noticed they had a great capacity to remove nitrate, particularly in areas of nutrient enrichment from

sewage discharge. The use of mangroves for treatment of nutrient enriched effluent has received some preliminary investigation (Macnae, 1968), but this function is still poorly understood (Clough *et al*., 1983).

Sediments suspended in the water column are deposited in mangroves during flooding, enriching mangrove soils. The extensive root system of mangroves enhances this trapping process and retards the forces of erosion along the shoreline (Scoffin, 1970). Although this function has been overstated to the extent of calling mangroves "walking trees", they do contribute to the sedimentary processes that exist in estuarine ecosystems (Lynch *et al.*, 1989). Nixon et al. (1984) observed that total suspended sediment load of an estuary in Malaysia, in which mangroves had been reclaimed for agriculture, was an order of magnitude higher than in an adjacent mangrove dominated system. The Guayas River estuary is also a very turbid estuary, and the extensive mangroves along the shoreline contribute to the sedimentary processes of this system (Twilley *et al*., 1992).

Pumping of Water in Shrimp Ponds

In the intertidal zone where ponds have been constructed the natural exchange of estuarine water via tides has been replaced with diesel pumps that link shrimp ponds with the estuary. More intense shrimp farming techniques require strict control of water quality that is maintained by increasing the exchange of water from the estuary. Stocking ponds at higher densities of juveniles necessitates additional fertilization and supplemental feeding to assure an adequate food supply for secondary productivity. This level of pond management requires strict control of water quality since phytoplankton blooms resulting from nutrient additions may deplete dissolved oxygen concentrations to levels that will cause shrimp mortality.

Diesel engines are used to pump water daily from the estuary during high tides to a central aqueduct system that gravity feeds water to individual ponds. This water enters ponds depending on stage of management. Exchange rates vary from 3 to 8% of the pond volume per day under semi-extensive mariculture, and may increase to 10-15% under more intense farming practices. The total volume of water pumped from the Guayas River estuary to shrimp ponds depends on exchange rates (% of ponds volume/day) and area of ponds in operation (using a mean pond depth of 1.5 m) (Fig. 12). At a present operation of 92,000 ha of ponds under semi-extensive management (5% pumping rate), the volume of water exchanged daily with the estuary is approximately 65 $\times 10^6$ m^3 (Fig. 12). This volume is greater than freshwater discharge from the Guayas River during low flow period. At intensive pond management (10% pumping rate), the same area of ponds would exchange more volume than river discharge during high flow periods (Fig. 12). These types of scenarios underscore the importance of the utilization of water by shrimp ponds on the pattern of water quality in this estuary.

A majority of the water that is pumped into ponds is to replace losses associated with seepage and evaporation. Given the potential evaporation rates of this region and the shallow nature of shrimp ponds, this flow of water will increase loss of fresh water from the estuary. The magnitude of this water loss is reflected in elevated salinities of effluent water from ponds compared to influent waters. Snedaker *et al*. (1986) found that water in 22 of 30 ponds surveyed had higher salinities than source water.

Supplemental feeding and fertilization methods are required to meet the demand for food at higher stocking densities of PL in ponds. A main source of nutrition for shrimp in growout ponds are phytoplankton blooms that result from urea and superphosphates added prior to stocking. Supplemental feeding is carried out towards the end of the growth cycle, usually the last four weeks. Much of the nitrogen and phosphate applied to ponds are absorbed by phytoplankton and are thus returned to the estuary in organic form.

Figure 12. Volumes of water exchanged with shrimp ponds per day at different pumping rates (percentage of the volume of a shrimp pond per day) based on the area of ponds (ha) with a mean depth of 1.5 m

These organic nutrients represent biological oxygen demand when this plankton biomass

decomposes in the estuary. The relative change in nutrients and salinity of inflow and outflow waters of shrimp ponds has not been documented. Thus the impact of changes in the use and quality of water associated with shrimp farming is poorly understood.

Indiscriminate Harvest of Fisheries

The dramatic expansion of the farmed shrimp industry and increased levels of pond management simulated the development of a new fishery to provide post larvae and seed shrimp for stocking mariculture ponds. Industry sources estimated that up to 90,000 artisanal fishermen were involved in the 1983 harvest and in 1984 numbers of fishermen working along the coast were even higher (McPadden, 1985). Seed fishing is concentrated in areas of significant fresh water discharge along the coastline, such as El Oro and Esmeraldas, with the highest effort occurring in the Guayas province. The catches of these fishermen are non-selective, with small fish, penaeid post larvae and juvenile shrimp including a mixture of *P. vannamei*, *P. stylirostris, P. occidentalis* and *P. californiensis*, as well as some fresh water Carid species. Since only the former two species survive best in mariculture ponds, owners pay according to the proportion of the stock that is *P. vannamei* and *P. stylirostris* (McPadden, 1985). Selection is a post-harvest process and therefore less-valued species are lost from the estuary. The peak of the seed fishing season is from December to march when fisherman may take up to 40,000 post larvae a day at a size ranging from 7-10 mm. The annual demand for post larvae is estimated at 16.5 billion based on 120,000 ha shrimp ponds using mostly extensive pond management (1989 estimates). Only about half of the post larvae collected along the beaches is *P. vannamei*, requiring a total harvest of 33 billion post larvae. This demand for *P. vannamei* represents a potential impact on the genetic stability of non-targeted organisms that use the coastal environments during their life cycle.

Daule-Peripa River Dam Project

A dam has been constructed at the confluence of the Daule and Peripa rivers for diversion of water supply, control of river flow, and hydroelectric power. Water will be diverted with an aqueduct from the Daule River to the Santa Elena peninsula for potable water, irrigation for agriculture, and industrial use. The dam will also increase the flow of fresh water to the Guayas River estuary during the dry season to prevent salt water intrusion in the lower Daule River and enhance agriculture in this area. The Daule River joins the Babahoyo near Guayaquil to form the Guayas River, and drains one-third of the Guayas River basin. The mean capacity flow of the Daule River is 365 m^3/s, or about 30% of the mean flow of the Guayas River, and supplies most of the potable water for Guayaquil. The total river basin of both the Daule and Peripa Rivers is 13,800 km^2 and a mean precipitation of 1800 mm/yr. A thorough description of the soil characteristics and land use of this watershed are provided in a report by the Guayas River Basin Commission (CEDEGE, 1970)

The dam will create an impoundment with a storage capacity of 6.0 km^3 of water with a surface area of 270 km^2, mean depth of 21m, and volume of 5.4 km^3. The impoundment will supply potable water for 300,000 people at 400 liters per person per day, irrigation water for 42,000 ha of land, and 20 million m^3/yr for industry. Projected industrial use includes a petroleum refinery, nitrogen fertilizer complex, petrochemical complex, and a petrochemical port facility at Monteverde.

The area which drains water into the reservoir comprises 4,025 km^2 (Mendoza 1983). The area of deforestation and removal of vegetation matter will comprise 33,750 ha, and the area to be flooded will cover 27,000 ha (Arriaga, 1989). The annual draw down will be approximately 10 m, and the flooded area will remain at 18,000 ha. The dam will influence the amount of water from the Daule and Peripa Rivers that normally discharge into the Guayas River (Fig. 2). Presently the proposed operation of the dam calls for an average annual flow of from 100 to 175 m^3/s (Jenkins, 1979; Arriaga, 1989). This flow will vary from a high of 321 m^3/s during the wet seasons in April, to a low of 124 m^3/s in August. Compared to the normal flow of the Daule and Peripa Rivers (Fig. 6), this modified flow is such lower than the fresh water discharge of up to 1,000 m^3/s that usually occurs during the wet season. During the dry season, to control salt water intrusion, the dam will provide water above the average discharge of about 50 m^3/s from supplies stored in the impoundment. Based on average monthly flows, the normal discharge of 343 m^3/s for these two rivers will be restricted to 174 m^3/s, a reduction of about 49 % (Fig. 6). This reduction represents a 15% loss of the fresh water to the Guayas River and 13 % from the Guayas River estuary. The loss of fresh water from an estuary in a semiarid zone such as the Guayas province may influence the patterns of salinity in this coastal ecosystem.

The Daule-Peripa dam may influence the distribution and increase the concentration of salinity in the Guayas River estuary (Fig. 2). Mangroves that exist in arid environments such as the coast of Ecuador where evapo-transpiration is greater than precipitation are very susceptible to slight changes in hydrology,

particularly the input of fresh water. For mangrove forests in arid life zones, small shifts in precipitation result in increased soil salinity followed by an increase in tree mortality and a shift in vegetation from forests to tannes or salinas (Davis and Hilsenbeck, 1974; Cintron *et al.*, 1978; Twilley, 1985a). In Ecuador the diversion of fresh water from the Guayas River estuary must be managed with awareness of possible negative effects on mangroves since they exist in a relatively arid environment. Margalef and Crespo (1979) suggested that the loss of fresh water from the dam will probably not affect mangroves, though the researchers did not take into account the climatic influence of mangrove distribution in the southern provinces.

Increases of salinity due to changes in fresh waters supply to the Guayas River estuary may also impact economically important fisheries in this estuarine ecosystem. The Estero Salado, which harbors most of the fishery resources of the inner Gulf of Guayaquil, does not receive fresh water discharges directly form the Guayas River. Therefore, the flushing rate of this section of the inner gulf is less than the more southern sections that are linked directly to the river. As a consequence of the reduced freshwater input, the Estero Salado may be more susceptible to increases in the concentration of materials dissolved in the water column. Precipitation during 1985 was relatively low, and Estero Salado was hypersaline with values up to 30 (Zimmerman and Minello, 1989). This increase in salinity suggests that other materials, such as toxic chemicals and nutrients may also be concentrated (assuming that their behavior is conservative). Organisms, such as shrimp, that inhabit the Estero Salado are very susceptible to changes in water quality, especially salinity and toxicity which may increase their mortality and retard growth rates.

Changes on fresh water supply may also influence seasonal movement or recruitment of organisms into the Guayas River estuary. The recruitment of shrimp into an estuary is important to their life cycle because the estuary provides optimal conditions, such a low predation, during critical stages of maturation. Seasonal timing of recruitment is thought to be dependent on fluctuations in salinity along with influx of offshore water masses. Since the Daule-Peripa dam is designed for a near constant flow of water to Guayas River estuary, the potential impact of this project should be evaluated relative to disturbing seasonal fluctuations of salinity in the estuary. Since the mariculture industry relies on shrimp postlarvae that seasonally utilize the estuary, management plans should strongly consider those factors that influence recruitment of fisheries in the estuarine ecosystem.

Eutrophication

The introduction of chemicals to the coastal zone will be grouped into two categories: those that contribute to nutrient enrichment and water quality parameters such as dissolved oxygen; and those that contribute to the concentration of toxic compounds of the estuary (Fig. 2). The chemicals contributing to the environmental quality of the coastal zone of Ecuador include waste from industry, navigation, agriculture and urban settlements. In this first section, we will describe the contributions of nutrients and chemical water quality of the coastal zone, followed by a section on the ecotoxicology of coastal waters.

Diffuse nutrient inputs include runoff from natural vegetation and from managed landscapes such as agriculture or forestry (Fig. 2). Much research has gone into developing nutrient loading rates for different types of native vegetation and for specific types of crops in watershed in various geographic areas. Most of these loading rates have been developed for watersheds located in temperate climates. Less is known about the loss of nutrients from different types of land use in tropical watersheds.

The five principle crops raised along the coast of Ecuador are bananas, rice, sugar cane, cacao, and coffee (Fig. 13). These agriculture products come primarily from the Guayas lowlands, situated north and east of the city of Guayaquil, and along the eastern shore of the Gulf of Guayaquil. Statistics for the Guayas and Los R!os provinces have been combined to represent agricultural activity in the Guayas River basin. Over 50 percent of the agriculture activity for the coastal zone of Ecuador occurs in the Guayas River basin (Fig. 13).

The Guayas River basin in a major producer of rice, with nearly 95 % of the total rice production along the coast occurring in the Guayas and Los Ríos provinces. Rice in the Guayas River basin is of particular significance to the nutrient economy of the Guayas River estuary because of the large area of production (Fig. 13A), the potential expansion of this crop in the watershed once the Daule-Peripa dam is completed projected at 17,000 ha during the initial phase of the project), and its proximity to waterways. Point source inputs of chemicals to the coastal zone are associated with urban areas and industry (Fig. 2). Loading rates of nutrients from cities are dependent on population density and degree of waste treatment prior to discharge into aquatic system. The population in the coastal provinces of Ecuador has increased over the past 35 years, most dramatically in the Guayas province (Fig. 13B).

Figure 13. A). Distribution of lands under different types of agriculture in the four coastal provinces of Ecuador. The Guayas province includes agriculture activity in Los Ríos province. **B)**. Historical records of population changes in the four provinces of Ecuador

From 1962 to 1982 the population of this province more than double to over 2,000,000 persons. In the last several years, the annual growth rates has been dramatic resulting in a present population of over 2,568,452 (Fig. 3B). Together with the population of Los R!os, there are 3.14 million people in the Guayas River basin, of which 84 percent is considered urban, with 53 percent of the basin population located in the vicinity of Guayaquil. Currently, only 18 percent, or 6,100 ha, of the 34,700 ha city is serviced by an adequate sewer system (Solórzano 1989). In 1979, 450,000 people in Guayaquil did not have sewers and this value has increased annually by 21,000 people. The contaminated waters of the city are emptied, untreated, into the Guayas River (El Guasmo pumping station), Daule River (El Progreso pumping station), and Estero Salado.

From the available statistics, waste from 62 percent of the population is pumped to septic ponds (untreated), however, 86 percent of the 54.83 106 m3 of waste generated annually is discharged to aquatic ecosystems. Based on these population statistics and per capita rates for each treatment, the loading rates for oxygen demand (biological and chemical), solids (total and dissolved), and nutrients total nitrogen and phosphorus) have been calculated. This preliminary analysis indicates that the city of Guayaquil discharges over 90 percent of all domestic wastes that enter the river, and an even greater percentage of the nutrients that enter the Guayas River estuary. Solórzano (1989) claims that domestic and industrial waste has lowered water quality in the Daule and Guayas Rivers by contributing to a high level of bacterial contamination, decreasing dissolved oxygen content, and increasing concentration of nutrients.

Nutrient enrichment of coastal regions has contributed to the continued eutrophication of estuarine ecosystems that has lead to the deterioration of many water quality parameters (Fig. 2). Dissolved oxygen concentrations below 4 mg/L are considered stressful to many estuarine organisms and the negative effects of low dissolved oxygen to environmental quality can also occur by altering basic food chains that support economically important fisheries. The discharge of biological oxygen demand (BOD) and chemical oxygen demand (COD) can cause a decrease in concentrations of dissolved oxygen in the estuary. A balance of processes that contribute (photosynthesis and diffusion) and remove (BOD and COD) dissolved oxygen is necessary for a healthy environment for economically important fisheries. While low dissolved oxygen conditions may be a natural condition in most stratified estuaries (Newcombe and Horne, 1938; Officer *et al*., 1984), a legitimate concern is the recent temporal and spatial increase in anoxia in many coastal ecosystems.

Anoxic waters are apparently uncommon in the Guayas River estuary, occurring only in areas near sewage outfalls (Arriaga, 1989). A survey of five stations in Estero Salado found that dissolved oxygen concentrations at 1 m depth ranged from 2.7 to 4.7 mg/L in the Guayas River, yet concentrations near Guayaquil are usually less than 2.7 mg/L (Solórzano, 1989). Concentrations are normally lower near the bottom; for instance, Solórzano and Viteri (1981) measured concentrations of 3.5 mg/L at 1 m depth compared to 2.0-2.5 mg/L near bottom at two stations adjacent to Guayaquil. Biochemical oxygen demand (BOD) fluctuated from 0.65 to 2.88 mg/L in the Guayas River estuary. Dissolved oxygen concentrations in Estero Salado range from 3.0 to 4.7 mg/L.

Estero Salado receives effluent from 400,000 persons representing BOD of 10,000 mt/yr. Although there are cases of low dissolved

oxygen adjacent to sewage outfalls, there is not the stress of anoxia as expected from the loading to this estuarine ecosystem. The strong tides with amplitudes from 3 to 5 m in the Guayas River estuary and Estero Salado are responsible for the well-mixed aerated water column. However, when this high BOD is pumped into shrimp ponds, together with the in situ biochemical processes in pond waters, there are potential water quality problems. During presence of red tides in the estuary, anoxic problems in ponds are not caused by pumping anoxic water from the estuary; rather anoxia in pond water develops when waters with high BOD potential are pumped into the less well mixed shrimp ponds.

Red tides, phytoplankton blooms that discolor the water, are a common occurrence in the Gulf of Guayaquil and in the inland waters of the Guayas River estuary (DeArcos, 1982; Jiménez, 1980; Jiménez, 1990). There have been 28 reportings of red tides in the coastal zone of Ecuador, and these blooms vary in species composition, density of cells, and duration. The most direct influence of the estuary is fish kills caused by the presence of toxic organisms such as *Gonyaulax catenella* and *Gymnodium breve. Gonyaulax monilata* occurred in the upper portion of the Gulf of Guayaquil in April 1980 and in March 1986 along the coast of Manglaralto. The 1980 bloom resulted in high fish mortality (Jiménez, 1980), while the 1986 bloom caused significant mortality of shrimp postlarvae in eight hatcheries, interrupting operations for 30-45 days (Jiménez, 1986). Other red tides in the Guayas River include *Gyrodinium stratum* in September 1982, *Mesodinium rubrum* in August 1984, *Prorocentrum maximum* from February 1985 to February 1986, and a recent bloom of *Nietzche* sp (Jiménez, 1989).

These blooms caused high mortality in shrimp ponds when phytoplankton contaminated waters were pumped from the estuary. A red tide of *Gyrodinium stratum* (non toxic) in the Guayas River in September 1982 reached concentrations of 93,000,000 cells/L over 50 km of the estuary for over one month. The pumping of this red tide caused anoxia and subsequent shrimp mortality in ponds, representing one of the first occurrence of the negative impacts of red tide on shrimp pond operations. Another incident in Estero Salado in August 1984 resulted in anoxia in shrimp ponds at night associated with the addition BOD of *Mesodinium rubrum* cells. During these events, negative effects of red tides are compensated by increasing the pumping rate and water exchange of ponds. It has also been noted that some of the species associated with red tides, such as filaments of the blue-green algae cause a reduction in the quality of shrimp by changing the flavor and causing a musty odor.

Ecotoxicology

The environmental quality of coastal ecosystem is also influenced by the toxic chemicals introduced by agriculture and industry. Agriculture may contribute toxic substances such as pesticides to rivers and estuaries of the Guayas basin (Fig. 2). Solórzano has expressed concern about the concentrations of pesticides in the estuary, but only traces of pesticides have been detected at the beginning of the rainy season in the Daule River (Solórzano, 1989). A CEDEGE river basin study showed that DDT levels in the rivers flowing into the estuary were low, but little documentation of this problem is available.

The Daule-Peripa Rivers dam project described above will also increase areas of agriculture in the Guayas River watershed. The proposed irrigated area for agriculture is 125,000 ha located in the Daule River basin, the Santa Elena peninsula, and the province of Manabí (Arriaga, 1989). In the lower Daule section, the irrigated area of 50,000 ha is located on both shores of the Daule River between Palesina and Petrillo. The first phase of irrigation is planned for 17,000 ha to be used for plantations of rice, corn, soybeans, beans, onions, tomatoes and castor beans (Herman, 1986). Projected use of pesticides in the irrigated areas includes propanol (herbicide), endrin, and furadan (insecticides). Most of the proposed pesticides are organochlorine and organophosphorus compounds, in addition to carbamates and other urea-based herbicides (Arriaga, 1989). Organochlorine compounds are water insoluble, but are transported in aquatic ecosystems adsorbed to particulate matter.

These compounds are resistant to decomposition and can accumulate in the sediments of estuarine ecosystems. Organophosphorus compounds are water soluble, but susceptible to decomposition and do not accumulate in sediments. However, these compounds are very toxic to aquatic organisms. Crustaceans, especially larvae, are usually more sensitive to low concentrations of pesticide than are other marine organisms (Costlow, 1982). The extensive use of these chemicals in the estuarine watershed creates a potential hazard to the shrimp mariculture industry in Ecuador. Endrin, which is applied at an approximate rate of 145 mt/yr in the rice fields of the Guayas River basin significantly reduced growth rates of rapidly growing juvenile *Mysidopsis bahia* (McKenney, 1986) at concentrations of 60 ug/L. In addition, physiological measurements of metabolic dysfunction in mysids exposed sublethally to pesticides in laboratory and field conditions showed lower growth and reproductive capacity in these organisms during

later stages of their life cycle (McKenney, 1986). Daugherty (1975) noted that decreased shrimp yields in El Salvador probably resulted from the heavy use of pesticides in cotton farming during the 1960's and early 1970's. Pesticides have a tendency to become more concentrated along the food chain and thus may stress predators and higher trophic levels such as fish. Before this problem can be solved, more information is needed on the ambient concentration of these chemicals that are toxic to certain fisheries, and on their fate in the aquatic environment.

There is some mining activity in the Guayas River basin, and several metals have been found concentrated in riverine and estuarine sediments. Solórzano (1989) gives recent measurements of copper, iron, cadmium in the water columns of the Babahoyo, Daule, and Guayas Rivers, and mercury in the sediment of the Guayas. She described the water masses as eutrophic and the concentrations of copper and cadmium over the limit considered as innocuous for aquatic organisms. The concentrations of theses two metals ranged from 36.92-94.52 μg/L and 0.1-14.5 μg/L, respectively, in the Guayas River. These high concentrations of heavy metals in certain areas of the estuarine ecosystem demonstrate the effects of urban development and industry. Solórzano (1986) expressed particular concern for the concentration of copper, cadmium and mercury in the water column and sediments of the Guayas River estuary. Copper concentrations are higher than 10 μg/L which is considered innocuous to aquatic species (Ketchum, 1975), although these concentrations could be due to natural processes. Cadmium is also present in concentrations that could impact aquatic organisms (Ketchum, 1975), and sediments showed significant mercury contamination (Solórzano 1986, 1989).

Environmental Quality and Shrimp Mariculture

The long term sustainability of the shrimp farming industry in Ecuador will require integrative approaches to the management of coastal zone resources. These management considerations not only include the interactions of the shrimp farming industry with estuarine and coastal ocean ecosystems, but also the land use activities in the upland watershed and urban centers. For example, the interactions of shrimp farming activities with the Guayas River estuarine ecosystem indicate the complex nature of how environmental impacts influence the sustainability of this industry (Figs. 2 and 14). The upper panel of Figure 14 describes the present strategy in utilization of coastal resources in Ecuador by the shrimp mariculture industry, including the feedback effect of this enterprise on estuarine environmental quality. Decreases in the environmental quality of estuarine resources affect the productivity of shrimp ponds by influencing the ability of natural resources to supply of PL, and controlling the survival and growth of shrimp in growout ponds. Thus, the secondary productivity of pond ecosystems is constrained by the variety of factors that are linked to water and habitat quality in coastal ecosystems (Figs. 2 and 14).

Changes in the environmental quality of coastal river basins, or ecoregions such as the Guayas River basin, are also associated with land use changes both in upland watersheds and the intertidal zone. For example, it has been shown that the quality of water in the estuary may be influenced by introduction of chemicals such as nutrients and pesticides from agriculture, sewage from large urban areas, and heavy metals from industry (Fig. 2). Rivers provide the conduit that links the ecological processes of the estuary with the land use practices of upland watersheds. Deforestation of natural vegetation followed by replacement with agroecosystems, in addition to urban and industrial activities, can change the chemical composition of riverine inputs to coastal ecosystems. In addition, the distribution and turnover rate of these pollutants in the estuary are influenced by alterations in the quantity and seasonal nature of fresh water discharge from the watershed. Thus the quantity and quality of riverine inputs together are important linkages of the environmental quality of estuaries to the productivity of shrimp pond mariculture.

Tides connect the estuary with intertidal land use practices and with coastal ocean processes, and therefore they also contribute to the environmental quality of estuarine ecosystems. Most of the changes in land use practices of the intertidal zone are associated with the shrimp farming industry itself, caused by the destruction of mangrove ecosystems (Fig. 14). The loss of these ecosystems has a negative feedback on the normal function of tides that couple the function of mangroves with the estuary (Twilley, 1988). As described above, this coupling of mangroves with the estuary influences both the habitat and water quality of estuarine resources (Fig. 14).

Figure 14. Comparison of present practices in coastal zone management (upper panel) with recommended strategies for integrated mangrove management based on the ecological function of mangroves in the coastal zone (lower panel)

The specific ecological processes of mangroves that are lost due to pond construction are illustrated in Fig. 11, along with how they support the productivity of the shrimp ponds. Thus the loss mangroves is linked to the growth and survival of post larvae and chemical ecology of shrimp ponds by decoupling the effect of these forested wetlands on habitat and water quality.

Mangroves have been replaced with shrimp pond ecosystems that have very different ecological functions in the coastal zone. While ponds are designed to enhance the secondary productivity of the estuary, by specifically increasing the yield of adult shrimp, they alter the habitat and water quality of estuarine ecosystems. In pond ecosystems, the use of

tidal energy to exchange estuarine waters with the intertidal zone has been replaced with fossil fuel energy that pumps water periodically during a tide. The ecological processes in pond ecosystems largely determined by the introduction of nutrients and feeds to enhance shrimp production result in the fertilization of estuarine waters. Thus, the functions of pond ecosystems relative to water quality are different compared to the coupling of mangrove ecosystems that may reduce excess nutrients in estuaries. Changes in land use in the intertidal zone by construction of shrimp farms not only is important to the loss of ecological functions, such as mangroves, that may influence environmental quality of the estuary; but also the replacement of natural ecosystems with those that have different ecological functions in the intertidal zone. Therefore, negative feedback of pond construction is not only related to mangrove loss, but also by the negative influence of pond ecosystems on the water quality of estuarine ecosystems (Fig. 14).

The influence of the environmental quality of the coastal zone on the shrimp farming industry is complicated in Ecuador because of the unique oceanographic processes in this region (Fig. 14). For example, elevated water temperatures in the Gulf of Guayaquil may be a dominating factor in the tremendous recruitment of shrimp into the inner estuaries during pacific climatic disturbances know as El Niño. There remains confusion over the relative role of offshore processes and inshore destruction of mangroves to the decline in abundance of post larvae in the last decade. Nationally there has been a loss of about 22% of mangrove resources from the coast. However, in some coastal watersheds such as the Rio Chone estuary the loss of mangroves is greater than 90%. The cumulative impacts of mangrove loss may be site specific, particularly in regions where mangrove loss is high, and other estuaries must provide habitat to sustain the natural genetic stock. During periods of high recruitment, the impacts of habitat loss may not be significant. Yet, during the more normal oceanographic conditions, the negative impacts of habitat loss may be more pronounced along the coast. The life cycle of penaid crustaceans links the physical processes of the coastal oceans with the ecological processses of mangrove estuaries. It is the combination of both that sustain this coastal resource.

The abundant supply of post larvae during El Niño events created n excessive demand for intertidal area for the construction of shrimp ponds from 1985 to 1987. The natural supply of post larvae during the more normal years of recruitment could not stock the existing ponds, such that by 1985 nearly 50 % of the shrimp ponds were not in operation. During this period, there was a major emphasis to produce post larvae with hatcheries, and acclimate these shrimp to growout ponds. In 1986 there were only 12 hatcheries in operation. By 1989 there were 106 laboratories in operation, and another 60 planned for construction. Nearly half of these hatcheries were located in Guayas province and 25 were constructed along the beaches of Manabí. The anticipated production of these hatcheries is nearly 10 billion larvae, yet only less than 25% of these will survive under pond conditions. Most hatcheries produce larvae from wild gravid female, because they have better survival in growout ponds. Thus, the hatchery industry, while quickly responding to the demand for larvae, are presently not replacing the habitat quality of estuarine ecosystems that is needed to sustain the shrimp pond industry.

Although shrimp pond construction has been nearly continuous from 1979 to 1988, there has been a limitation on the acreage of ponds in operation (Fig. 3C). This may be largely due to the availability of post larvae which indicates the importance of habitat and water quality of coastal ecosystems as a constraint on the shrimp pond industry. Thus a carrying capacity of the coastal ecosystems of Ecuador to sustain shrimp pond industry is about 60,000 ha. Without the subsidy of post larvae to the industry from hatcheries, or the periodic supplement from El Niño events, there seems to be a limitation on the amount of ponds that can be supported for operation. According to the linkages described in the upper panel in Fig. 14, the negative feedback of pond construction on mangrove loss and pond effluent on water quality may deteriorate the environmental quality of coastal ecosystems and decrease the carrying capacity of pond operation in Ecuador.

The level of pond management to enhance shrimp production in ponds that are actually under operation will have to be intensified to sustain or increase shrimp yield (Siddall *et al*. 1985). Thus the supply of postlarvae in the estuary has a strong influence on both the number of ponds in operation and the type of pond management practiced in these ponds. The intense utilization of existing ponds would create increased pumping and fertilization of estuarine water which would, in turn, lead to increased loading of nutrients to the estuary. This management alternative may adversely affect water quality of the estuary. The negative impacts of pond construction on the ecosystem are replaced by increased pumping and fertilization associated with more intensive shrimp pond management. These issues demonstrate the importance of considering shrimp pond management in the context of the ecosystem and, particularly, paying close attention to those factors associated with water quality control.

Integrative Mangrove and Shrimp Pond Management

The ecosystem approach to the management of natural resources is essential since it integrates both the ecological processes of environmental systems together with the socioeconomic characteristics of regional development. New techniques that can simultaneously valuate the interactions of environmental and human systems are being developed (Farber and Costanza, 1987; Bell, 1989; Costanza *et al*., 1989; Dixon, 1989; Gottfried, 1992), but many of these models presently lack quantitative relationships. Thus in many cases, a few site specific analyses for particular conflicts in environmental and economic development have to be applied to a variety of systems and issues. Twilley and Day (this volume) suggest that the forcing functions in a coastal region can be used to assess the ecological functions of mangrove ecosystems (Fig. 1). And quantitative ecosystem models for these relationships are being developed (Twilley, 1993). Yet there are fewer quantitative relationships between these ecological processes with the exact nature of ecological functions such as habitat and water quality that these ecosystems provide. Thus, the quantitative links between ecological functions and ecosystem value are still being determined (see discussion below). However, what this description of the shrimp pond industry in Ecuador does provide, is an example of the qualitative linkages of an enterprise that depends on the environmental quality of coastal resources. We can use these linkages to provide a conceptual framework to assess the impacts of human resource management on natural resources. Natural resource management of the coastal zone is accomplished through policy established by human systems. Thus policy actually manages people, rather than the natural resources themselves. But the constraint of ecological processes on the sustainability of human utilization of natural resources requires an awareness of the linkages (both qualitative and quantitative) of ecosystems. We are not describing policy options or specific management plans in this chapter, but are proposing a conceptual model to understand how the ecological linkages of the system are coupled, and how these linkages influence the environmental quality of the coastal zone.

The economics of shrimp farming are linked to the ecological functions of natural resources in the coastal zone. Profit in shrimp farming is the difference between income generated from pond production and costs associated with pond operation. The level of shrimp production and operation costs, such as dredging, construction, pumping, fertilization, and land (authorizations), depend on the quality of water that is pumped from the estuary into the ponds. Mangroves and tides provide the shrimp industry with clean water and important habitat that enhance wild post larvae supply and shrimp production in ponds (Figs. 11 and 14). With the loss of these free services the cost of shrimp production increases such as in the cost of providing post larvae by operating hatcheries, increased dredging to remove sediment, and fuel for pumps to control dissolved oxygen. Thus negative feedbacks of the shrimp industry due to the loss of natural resources will influence profits of the industry since shrimp pond management is so tightly coupled to the natural resources of estuarine ecosystem (Fig. 9a).

Valuation techniques are needed to determine the multiproduct functions of mangroves in order to integrate economics and ecology (Gottfried, 1992). The opportunity costs of different pond management strategies including pond construction and operation must be based on their negative effects on habitat and water quality of coastal ecosystems. In addition, opportunity costs of environmental quality have to be placed on a larger watershed scale to include many complex interactions of the shrimp farming industry with estuarine and river basin ecosystems (Gottfried, 1992). Valuation techniques must use ecological and economic information to identify the negative and positive feedbacks of human systems with the function of natural resources. We are presently developing ecological models of these processes to more specifically predict the response of mangrove ecosystems to both natural and human alterations of coastal environments. The combination of these ecological models together with economic analyses of multiproduct functions of mangroves may provide better techniques that identify the role of ecological information in the valuation and management of mangrove resources.

Shrimp pond management could minimize negative impacts on coastal ecosystems if mangroves are preserved to protect their contribution to the environmental quality of the coastal zone (Fig. 14b). The preservation and conservation of mangroves can be implemented either by delineating greenbelts or buffer strips surrounding waterways, or by establishment of larger scale refuges and sanctuaries. The Australian Marine Science Association (1977) suggests that a terrestrial buffer zone should be at least 200 m wide landward of mangroves. Yet there are many problems in establishing such buffer zones in the intertidal area. In the Philippines, where 60% of the mangroves have been lost since 1960, a presidential decree (705 of the Forestry Reform Code) stipulates a 100 m

wide strip along bay and sea (Velasco, 1980); yet, these greenbelts have not been implemented very well due to corruption (Bailey, 1986). In Indonesia there exist a controversy between the Departments of Forestry and Fishery between the width of greenbelts at 50 and 400 m, respectfully (Bailey, 1986). These institutional conflicts are unique to mangroves since they provide a product to both the forestry and fishery industries.

Another form of preservation is the formation of refuges or national parks. In Malaysia, presidential proclamation 2151 and 2152 declared certain mangrove forests as preserved areas, known as Mangrove Forest Conservation Areas, that exist in Sabah (Malaysia); Indian Sundarbans, Sarawak (Malaysia), Perak (Malaysia), Indonesia. There are also national parks that protect mangrove and marine resources throughout Latin America, particularly in Mexico, Costa Rica, Colombia, and Brazil. In the United States, there are mangrove resources that are protected in estuarine sanctuaries. Preservation of mangroves must not only consider the structure of forests but also the function of these ecosystems in the coastal zone. In some instances mangrove forests have been managed to maintain their presence in the landscape, but alterations in hydrology have uncoupled these ecosystems from estuarine waters. An example of this situation is impoundments in the United States that are used for mosquito control in mangroves. Dikes with water control structures prevent the exchanges of organic and genetic material between mangroves and coastal waters. Thus even though these forests remain in the landscape, they do not contribute to the habitat and water quality of the coastal zone.

The sustainable use of mangroves for production of timber products is also a form of mangrove conservation and utilization that acknowledges the importance of this resource to local economies. The most common description of mangrove management is associated with silviculture of forests based on rates of forest regeneration according to volume of wood produced annually per hectare of forest. Such forest management practices for mangroves has a long and successful history in Asia (Walsh, 1977; Snedaker, 1986) but has not been developed in South America. There have been some recent efforts in Brazil, Panama and Venezuela (Snedaker, 1986), but not of the magnitude as in Malaysia. The sustainable use approach to mangrove management is common in underdeveloped countries where economic activity associated with timber products is important (Snedaker, 1986). There is little management of mangroves in Ecuador for sustainable use for forestry, except in the northern provinces of Esmeraldas for charcoal production.

A similar approach to the sustainable utilization of mangroves as a fishery resource is less common, particularly in Latin America. This is due to the fact that the utility of mangroves as forestry products is directly linked to the harvesting of wood products or production of charcoal. Fishery products of mangroves are less direct, since they are linked to detritus food chains and habitat utilization that are less commonly appreciated, except for by artisanal fisherman. The lower panel in Figure 14 suggests some obvious ways that mangrove processes could be designed and engineered to sustain fishery enterprises such as shrimp farming. There are some indications that mangroves can be used as a nutrient sink and managed to remove excessive nutrients in coastal environments (Nedwell, 1975). This is a particularly important research agenda given the increased eutrophication of coastal waters in the tropics. Mangroves may represent sinks of several primary nutrients used in the fertilization of ponds, particularly phosphates and nitrogen. Mangrove sediments may also have the capacity to absorb some of the BOD associated with pond effluent high in chlorophyll biomass that may shift the balance of dissolved oxygen in the estuary. Effluent from shrimp ponds could be distributed in nearby mangrove forests for nutrient removal prior to the return of water back to the estuary. The use of mangroves as a nutrient filter of pond effluent would limit the negative feedback of shrimp ponds on the water quality of coastal ecosystems (Fig. 14).

The contribution of excess nutrients from shrimp ponds to mangrove ecosystems would most likely enhance mangrove productivity and potentially enhance the contribution of these forested wetlands to habitat quality of estuaries. This scheme to integrative the natural function of mangroves with the management of shrimp ponds would serve as a means of altering what is presently a negative impact of intensive aquaculture to estuarine ecosystems into a positive feedback (Fig. 14). The shift from extensive to intensive mariculture may not necessarily impact the estuarine ecosystem if mangroves could be utilized in the operation of these types of ponds.

Another more direct way that shrimp pond management could be utilized to enhance the habitat quality of the coastal zone is by releasing adult shrimp back into the estuary. As described in Fig. 10, the yield of adult shrimp in ponds is transported to foreign markets and thus lost from the coastal ecosystem. This represents a sink of genetic resources from post larvae in the estuary, which are not allowed to recycle as adults to the offshore environments. Shrimp ponds are managed to increase the yield of adult

shrimp above the capability of natural resources, and some of this enhanced production should be returned to the coastal zone. If managers returned 5% of the annual shrimp pond yield in adults back into the estuary, it would couple shrimp pond management to the natural life cycle of shrimp (Fig. 10). That linkage would represent a positive feedback from ponds to the habitat quality of estuarine resources (Fig. 14). This would essentially serve to replace some of the loss function of mangroves due to pond construction. This could be accomplished by returning some of the pond volume back to the estuary during harvesting without passing the effluent through screens that are used to harvest the adult shrimp.

These recommendations are based principally upon the ecological function of coastal resources and their linkage to shrimp farming in Ecuador. There are many other economic and political considerations important in the development of management alternatives. The point of this chapter is to establish the ecological constraints of human decisions that are associated with the utilization of natural resources. Environmental quality is essential to the long term sustainability of shrimp farming in Ecuador, and it is important to consider the ecological linkages of this type of economic enterprise.

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Recovery of Tropical Mangrove Forest Following a Major Oil Spill: A Study of Recruitment and Growth, and the Benefits of Planting

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Abstract

In April 1986, a large oil spill on the Caribbean coast of Panama killed approximately 75 hectares of tidal mangrove forests dominated by *Rhizophora mangle*. Since then, there has been extensive regeneration in sheltered sites, while those exposed to wind and waves were significantly disadvantaged by the scouring action of mobile wood fragments. The present study, conducted four and five years after the spill, compared annual growth of natural seedlings in both habitats with those in un-oiled natural light gaps nearby. Leaf node production rates, were greater in oiled sites, indicating that remaining oil in the substratum did not depress growth, and it was possibly greater because of higher light levels in more open, oil-deforested light gaps. In both places, advanced seedlings were found that appeared to be older than their respective light gaps. This is an important discovery for oiled sites, implying the need for greater care in post-spill clean-up operations, for example. But, the notion of seedlings previously growing under a shaded canopy has other important implications. Primarily, it means that such pre-established recruits have the better chance in filling gaps. For this reason, *Rhizophora* forests in Panama appear well-prepared for small-scale canopy damage, having this undercanopy community of established recruits in a 'seedling bank'. This bank turns over relatively fast since the plants are essentially shade/intolerant, dying after two or three years where the canopy remains closed. Nevertheless, their numbers are maintained by a seasonal supply of propagules in the second quarter of each year. For the advanced seedlings in light gaps, past growth was followed using the sequence of leaf scar nodes along the main stem, finding height production increased dramatically (4-6 times) after approximately one year following gap creation. This was the case in un-oiled and exposed oil-deforested sites, however, in more sheltered oiled sites; height production was apparently suppressed for two or three years afterwards, depending on the site. The growth of other seedlings in oil-deforested sites were also monitored, comparing natural recruits with those planted soon after the spill in an attempt at large scale habitat restoration. Accordingly, it was found that planted recruits grew faster than natural ones (12-56%), aided by clean soil and fertilizer. However, this apparent benefit was out-weighed by both abundant natural recruitment and a significant negative effect on site recovery where planting took place. These findings bring into question the value of planting in this case. They also serve to emphasis a greater appreciation of natural recruitment and regeneration in future habitat restoration projects which may inadvertently contribute further to the destruction of already disrupted habitats.

Resumen

En abril de 1986, un gran derrame de petróleo en la costa del caribe de Panamá mató aproximadamente 75 hectáreas de bosques de mangle en los que predominaba *Rhizophora mangle*. Desde entonces, ha habido una extensa regeneración en los sitios protegidos, mientras que aquellos expuestos al viento y a las olas fueron significativamente desfavorecidos por la acción arrasadora de los fragmentos de madera. El presente estudio, que cubre el cuarto y quinto año después del derrame, comparó el crecimiento anual de plántulas en ambos hábitat con el de aquellas en sitios no afectados por el petróleo y con claros naturales. La tasa de producción de nudos fue mayor en los sitios afectados por el petróleo, indicando que el petróleo remanente en el substrato no inhibió el crecimiento, y posteriormente ello se deba a los altos niveles de luz en los sitios claros formados por la deforestación consecuente del derrame. En ambos tipos de sitios, todo indicó que las plántulas más viejas se establecieron antes de la formación de los claros. Este importante descubrimiento implica que, por ejemplo, en las operaciones de limpieza posteriores a un derrame se deba tener mayor cuidado. Por otro lado, el hecho de que haya plántulas que crezcan en la sombra genera otras implicaciones importantes. Principalmente, esto significa que esos reclutas preestablecidos tienen mejor oportunidad en la competencia para llenar los claros. Por tal razón, los bosques de *Rhizophora* en Panamá parecen estar bien preparados para daños en pequeña escala en el dosel, teniendo en dicha comunidad de reclutas establecidos un “banco de plántulas”. El mismo se renueva relativamente rápido ya que las plántulas son poco tolerantes a la sombra, muriendo pasados dos o tres años si el dosel permanece cerrado. No obstante, la cantidad se mantiene por el aporte estacional de propágulos dado en los meses de abril a julio. El crecimiento previo en las plántulas más viejas fue medido contando la secuencia de nudos a lo largo del tallo principal, encontrándose que la altura aumentó notablemente (4-6 veces) después de aproximadamente un a o de haberse formado el claro. Este fue el caso en los sitios no afectados por el petróleo y aquellos expuestos deforestados por la acción del derrame, sin embargo, en los sitios protegidos afectados por el petróleo, el incremento en altura fue aparentemente retardado en dos o tres años, dependiendo del caso. También se monitoreó el crecimiento de otras plántulas en sitios deforestados por efectos del derrame comparando las de regeneración natural con las sembradas después del derrame, en un intento de recuperación del hábitat a gran escala. Consecuentemente, se encontró que los reclutas sembrados crecieron más rápido que los naturales (12-56%) ayudados por un suelo fertilizado. Sin embargo, el valor de este beneficio aparente fue superado tanto por la abundancia de reclutas naturales como por un significativo efecto negativo en los sitios donde se llevó a cabo la siembra. Estos hallazgos hacen dudar del valor de la siembra en este caso, también sirven para enfatizar la importancia que debe darse al reclutamiento y regeneración naturales en futuros proyectos de recuperación de hábitat en los que de manera inadvertida pueden contribuir aún más a la destrucción de un hábitat ya perturbado.

Introduction

Mangroves trees, notably species of *Rhizophora*, die when sufficient oil coats their lower trunk and exposed air-breathing roots. This occurs chiefly when oil, perhaps spilled off-shore, floats in on a rising tide driven by wind and waves, and remains as the tide ebbs. Accordingly, when large amounts of oil reach coastal shoreline fringes of mangroves forests, many trees die in groups, leaving various patches of deforestation (Fig 1). The sizes and shapes of these areas are variable, depending largely on the amount and type of oil, the mangrove site, and the prevailing climatic and tidal conditions. In all case, and often before trees die, the animals which depend in them will also perish, leaving desolate oily gaps in the remaining forest.

Nevertheless, forest gaps are not unique to oil spills, or mangroves (Mabberley, 1983), and the recovery processes which act normally, presumably act also in an attempt to repair oil spill damage. Oiled sites, however, are handicapped further since oil often remains in the environment long after a spill (Lee 1980, Cintron *et al*., 1981, personal observations). In these cases, recovery is expected to be retarded, but an assessment of the apparently struggling natural processes needs to be made very carefully, and before attempting to help. This is because the decision to act in projects of habitat restoration is based on the assumption that natural processes are inadequate. But, this may not be the case since so little is known about natural processes and regeneration of these forests. It is obviously important to be aware of natural processes and how they might have been altered, if at all, in oiled areas. Otherwise, the outcome of the good-intentions implicit in projects of habitat restoration, for example by attempting to remove oil or by planting could result in further destruction of this already disrupted and fragile habitat.

Figure 1 (a) In April 1986, oil was lost from a damaged refinery tank in Bahía Las Minas, a large bay on the Caribbean coat Panama. This oil moved into extensive intertidal mangrove forests which surround the bay, killing incalculable numbers of trees and animals. **(b)** After five years, large areas of deforestation are still clearly visible, but now there are extensive stands of new recruits attempting to repair the fragmented canopy. This study provides an assessment of these seedlings, comparing their establishment and growth with the inherent processes observed in natural gap recovery

For this reason, it makes good sense to further investigate the natural functioning of the ecosystem, as well as studying past experiences with restoration, in the hope of developing suitable process-based solutions which do not unwittingly promote further longer term damage. This can be achieved in part, by conducting follow-up studies of earlier efforts of assistance which may, or may not, have be successful. To facilitate this, it would be advantageous also to use a recognized selection of common forest parameters (e.g. Cintrón and Schaeffer-Novelli, 1984), providing a universal measure of health and general condition of the forest. In this way, we might learn to recognize recovery processes and evaluate our efforts in assisting them. And, this would also provide a test of various techniques applied at different sites, like different planting strategies and/or efforts to remove oil. It is also important, however, to understand more about regeneration in natural circumstances.

In all cases, habitat recovery chiefly depends on the establishment and growth of new trees. Clearly, this could take several decades after seedlings become established and until pre-spill conditions are achieved. To help solve this problem it would be invaluable to have some method to age individual trees, but this is apparently not possible (Tomlinson, 1986). Furthermore, this problem is not unique to mangrove forests, applying generally to tropical tress around the world (e.g. Bormann and Berlyn, 1981). Nevertheless, for mangroves, a partial solution was offered recently with the discovery of a method to age *Rhizophora* seedlings and small trees using leaf scar nodes (Duke and Pinzón, 1992). More data on this method are presented in this treatment, and these provide powerful insights into some recovery processes, and the influence of residual oil. In any case, because tree growth is relatively slow, the discovery of such aging techniques and their implementation are critical to our immediate needs of understanding and preserving these threatened forests.

In this chapter, some recent findings of natural recovery processes are presented as part of a larger study taking places in mangrove forests on the Caribbean coast of Panama. This is concerned with the longer-term influence of a massive oil spill in 1986 (Jackson *et al*. 1989) which killed at least 75 hectares of mangrove forests dominated by one tree species, *Rhizophora mangle*. This preliminary assessment also provides an evaluation of the benefits of an extensive planting experiment conducted by the Refineria Panama in 1986 and 1987 (Teas *et al*. 1989). Accordingly, the following discussion is divided into three sections, namely, natural recovery processes, natural recovery following oil spill deforestation, and our evaluation of the benefits of the planting effort.

Methods

This study was conducted chiefly in the vicinity of Bahia Las Minas (9° 25' N, 79° 50' W), on the Caribbean coast of Panama (Fig. 2), but also extended just to the north of Portobelo. Bahia Las Minas is a northward-facing bay, around six kilometers across the mouth, and situated immediately east of the Atlantic entrance to the Panama Canal, and the city of Colón. Its location and physical characteristics are described further by Cubit *et al* (1987, 1989) and Jackson *et al*., (1989). The bay is densely fringed with mangrove forests growing in a variety of habitats from exposed coastal sites behind reef flats, to those bordering tidal channels, and those further upstream alongside freshwater dominated estuarine reaches. Parts of these forests have been altered and removed with some port and industrial development, but apart from this, their chief use includes fishing, scavenging and cutting of saplings at a subsistence level. Cubit *et al*. (1987) and Jackson *et al.* (1989) described a major oil spill in the bay during April 1986, along with some early results of on-going studies of the impact on several habitats, including mangrove forests. This involved extensive deforestation of lower intertidal forests, chiefly dominated by *Rhizophora mangle* L., but with lesser numbers of four other species. *Avicennia germinans* (L.) L., *Laguncularia racemosa* (L.) Gaertn.f., *Pelliciera rhizophorae* Triana and Planchon and *Conocarpus erectus* L.

All studies discussed in this treatment relate to *Rhizophora mangle*, the red mangrove, and particularly to its seedlings. These were monitored chiefly in two ways. First, 252 seedlings were selected in late 1989 from twelve sites, including both exposed and sheltered habitats, and oiled and un-oiled areas. At each site, seedlings were chosen to represent the full range of age classes, determined from leaf scar node counts (Duke and Pinzón, 1992). Each was scored for various physical parameters including: heights for all nodes along the main stem from substratum to the top-most or apical node, stem diameter just above the "zero" hypocotyl node, total number of leaves, and total number of leafy shoots. All were tagged with a

Figure 2. Study sites are located along the northern coastline of Panama, bordering the Caribbean Sea north-east of Colón and the Atlantic entrance to the Panama Canal, and extending north-east to vicinity of Portobelo. Most sites are located in Bahía Las Minas, since the oil spill in 1986 came from the Refinería plant and port, and resulted in patches of deforestation from Punta Galeta to Punta Muerto. All studies were conducted from the Smithsonian Tropical Research Institute facility at Galeta Research Station

stainless steel wire and Dymo label, identifying both the seedling and a known position of an upper node for future reference. The second major study of seedlings in early 1990 involved establishment of three, 12 m^2 quadrats at each 14 sites throughout the bay and including again both exposed and sheltered habitats, and oiled and un-oiled areas. All seedlings in the quadrants were tagged and scored for, total height to the topmost leaf node, hypocotyl height, girth just above the hypocotyl or established prop roots, and the number of nodes along the main stem.

Natural Regeneration in Mangrove Forests
Light Gaps and the Seedling Bank

Deforestation, and the creation of light gaps, are natural and common phenomena in tropical forests (e.g. Mabberley, 1983). And mangrove forests are no exception. In the latter case, however, gaps in mangroves differ chiefly because they result from trees which die standing, instead of treefalls which characterize tropical rainforests, particularly those in the Americas. In mangroves, trees rarely fall green. Furthermore, light gaps in mangroves are rarely created by the death of only old and ancient trees. It is more common to see them comprised of approximately ten dead trees of various age groups and often appearing as roughly circular holes in the continuous canopy (Fig 3). These "pot-hole" impressions from a broad mosaic of regeneration pockets of different depths, reflecting their various ages and stages of healing. Below the canopy, this is also apparent for several reasons, depending on gap age. When a gap is young, there is considerable extra light coming through the gap, illuminating the patch of prolific young plants immediately below, and in an otherwise vacant undercanopy. Later, in older gaps which have refilled, groupings of younger trees are clearly apparent because of their smaller girths. Furthermore, these gaps are common enough that it is believed they are the main process by which mangrove forests naturally regenerate.

The reason for tree death in these gaps is known, but this first observed when a group of trees wilt and drop their leaves. In these, death is usually total, as distinct from other possibilities, such as limb shedding or partial tree death. Potential causes depend on the site, but these range from episodic events such as violent storms, frost damage, plant pathogens, lightning strikes, to slow and progressive changes such as changes in sea level, water courses, and seasonal flooding or drought. The influence of such factors are particularly important for mangrove trees because they live in exposed intertidal environments, where living conditions are relatively harsh for the tropics, and they are subject to constant change. For these reasons, therefore, it is not surprising they would reflect both subtle and episodic changes in local conditions, including those caused by man.

In Panama, the most likely cause of natural light gaps is considered to be lightning strikes. It seems reasonable to assume that a surge of electricity striking a central tree would also reach those in the immediate vicinity, especially as root grafting is very common. This is observed even between different species of the same genera, notably for *Rhizophora*. But, apart from the common occurrence of electrical storms in mangrove areas, there is presently no other data supporting this notion. In fact, few gaps show signs of being created by lightning. Nevertheless, while these gaps probably represent the most common from of tree death of mangroves in Panama, this is not necessarily the case in other locations. For example, in areas of frequent hurricanes, the influence of small light gaps is possibly irrelevant. Especially, considering the putative life span of these trees. In any case, during violent storms, trees are often stripped of leaves and, for *Rhizophora* species, this would result in death, but this is not the case for all mangrove species. In these, notably *Avicennia germinans* and *Laguncularia racemosa*, recovery can be quite rapid as lost leaves are quickly replaced. This difference is expected to profoundly influence the species composition of mangrove forests in these respective regions.

Nevertheless, it appears that *Rhizophora* forests are well-prepared with several recuperative processes, ostensibly for refilling natural light gaps. In this case, regeneration begins long before trees die, and a "seedling bank", reminiscent of the seed bank of terrestrial forests, provides the means for these forests to recuperate more rapidly than previously expected. However, there is an important difference between these forests, since most mangrove do not have seed propagules. And, for those which do, the seed are not long-lived. Instead, many mangroves depend on some degree of viviparous development of seedlings. This was considered to be an attribute developed especially for longevity and long-distance dispersal in the marine habitat, but is possibly more important for other reasons. This is suggested by other non-mangrove plants having successful buoyant seed which are capable of greater long distance dispersal. The importance of vivipary therefore appears to be related to rapid establishment. In this way, our observations further suggest that role of *Rhizophora* propagules is not simply to establish the species in new and distant sites, but it is perhaps more important for them to restock and re-enforce existing populations each season (Fig. 4a). This notion and that of long distance dispersal are each supported by the dominance of *Rhizpohora* species in virtually all tropical mangrove forests around the world. It appears therefore that the survival of these forests is improved by rapid establishment and recovery made possible with viviparous propagules and the seedling bank.

Figure 3. The canopy of the mature mangrove forests around Bahía Las Minas are notably marked by numerous light gap, 'pot-holes'. These light gaps are natural phenomena, and their origin could be the result of lightning strikes. All the same, they represent possibly the most important process of forest regeneration, turnover, and succession in this region. This project assesses recovery in these natural gaps and compares this with recovery in oil-deforested areas

For *Rhizophora* forests on the Caribbean coast of Panama, the undercanopy seedling bank comprises established young plants with one to three pairs of leaves on a single stem, between one half and one meter tall. However, these seedlings are not easily visible since they rarely reach higher than the common tangle of roots. They are also shade-intolerant and usually die before reaching one meter tall when they are between two or three years old (Fig. 4b). Furthermore, their initial response is undoubtedly under endogenous control since they have a rapid burst of growth when first established (Fig. 5a). This is evident as rapid main stem extension for the first one to four leaf nodes. However, after two years, this growth declines from 5-10 cm in the first, to around 1.5 cm in the second. It is clear from this, that early growth of *Rhizpohora* mangle seedlings rely chiefly on internal resources derived originally from the parent (Pannier and Pannier, 1975). As these become depleted in the growing seedling, however, height extension slows and the plant eventually dies under the closed canopy. During this time, the leaf node production rate remains relatively constant, around 3.7 $\pm$ 0.3 nodes/year (Duke and Pinzon, 1992).

Furthermore, the density of seedlings is patchy, and depends on tides and topography, but in addition, there appears to be another previously unexpected factor. This is evident from several observations of mangroves forests in Panama. First, propagules of established seedlings are invariably found buried by at least one third of their length into the substratum. This observation was unusual since the substratum in these mature forests is often not soft silt, but rather a tough matt of fibrous roots, apparently impenetrable to floating seedlings. Second, seedlings are often positioned away from established prop roots (Fig. 6), where they were expected to be established if entrapment amongst roots was important. In fact, those near to roots appears disadvantaged with severe leaf damage caused by herbivorous crabs. Thirdly, smaller crabs make convenient, propagule-size burrows (around 15 mm diameter, slightly larger than the diameter of *Rhizophora* hypocotyls) through the root matt (Fig. 6b). Therefore, in consideration of these observations and other, we suggest that establishment of *Rhizophora* propagules, chiefly takes place by drift-placement into these convenient crab holes.

Figure 4. (a) Litter fall samples of mature hypocotyls of *Rhizophora mangle* collected over one year (1989-1990) from both exposed and sheltered habitats in Bahía Las Minas. These show distinct seasonality with pronounced peaks in the second quarter of 1990. (b) They supply a seedling bank of one to three year old recruits established at similar densities under the closed canopy of *R. mangle* forests, notably for sheltered habitats in this case. The plots compare densities of living recruits for all groupings of particular leaf node counts (means 3.3 ± 0.2 nodes. seedling^{-1}, scored in July 1990, with others which died during the year (mean 6.2 ± 0.2 nodes.seedling^{-1}). Both are classified by the number of nodes on the main stem above the hypocotyl which can be taken as a measure of age since annual node production rates measured in similarly shades sites are constant (3.7 ± 0.3 node.year^{-1}). Notice also that, in July, the 1990 cohort of established seedlings has one node and the 1989 cohort has four to five nodes. These data identify the turnover time of he seedling bank to be around two to three years

Their rapid subsequent development of holding roots ensures that they become established quickly. As an alternate hypothesis, it is possible that falling propagules spear into the substratum may explain these apparently self-planted seedlings, but this is considered less likely based on the observation of seedlings being equally common under prolific seedling-bearing trees and sterile ones alike. Furthermore, `crab-hole planting' is favoured over root entrapment since those crabs which damage leaves, mentioned earlier; apparently prefer to stay on the roots. Such observations need to be assessed further, but the notion of seedlings becoming planted commonly in crab holes interesting implications in the evolution of both the forests, their propensity to vivipary, and the presence and behavior of the crabs. For example, while there does not appear to be any immediate benefit to the small crabs, they do benefit indirectly by helping maintain the seedling bank which inturn maintains the forests they depend on.

In any case, these observations show how these forests appear well-prepared for small-scale deforestation. Accordingly, when a break in the canopy occurs, well-established recruits in the seedling bank are expected to grow rapidly to refill the gap (Fig. 7). Seedlings growing in open canopy conditions are known to have double leaf node production rates, and annual height increases of around 20 to 30 cm (Fig. 5B). This, however, does not demonstrate, that individual plants can respond to the dramatic changes in light conditions when a previously closed canopy is damaged, and a light gap is created. But, clearly the putative advantage of the seedling bank depends on it. Therefore, the idea of seedlings in the bank being important in gaps, is currently being tested in a small study where light gaps were created over seedlings of measured growth rates under previously closed canopies. After six months, there is no significant difference in growth rates between control sites and created light gaps, but this is not surprising as will be shown later. In this case, seedling growth was followed retrospectively using the sequence of leaf scar nodes along the main stem (Duke and Pinzón, 1992). Examples of this will be presented latter in the discussion of natural recovery in deforested areas following the Bahia Las Minas oil spill, since the oil spill provided light gaps of known age over a wide range of mangrove habitats.

Irrespective of whether seedling recruits were survivors of the seedling bank, or not, however, their growth after the creation of the light gap is expected to follow the schematic model presented in Figure 8. This five recovery stages, `a' to `e', showing the faster growing, chiefly older cohorts, which take their position in the mature forest canopy while the younger cohorts reform the seedling bank. Intermediate-aged survivors die-off since they are denied light by older and larger plants. The time for this recovery process is not known, and obviously depends on rates of growth, and sites characteristics.

Figure 5. **(a)** Seedlings of *Rhizophora mangle* growing in the shade, under a closed canopy of the same species, show rapid extension, between 2-8 cm/node, for the first three or four nodes during the first year. However, their growth subsequently slows to a minimal level, around 0.5 cm/node, in the second and third year. This lower rate reflects the minimal spacing of leaf node scars along the main stem. **(b)** In contrast, seedlings growing in the open, showed both rapid early extension and subsequent increased growth in a seasonal response with annual peaks of internodal extension. These data reveal the difficulties in assessing performance of seedlings less than two years old

Some early evidence from the studies of tree growth in Panama, suggest that this may be quite rapid for *R. mangle*. This is based chiefly on the growth of trees around ten years old, based on aerial photographs. These were followed retrospectively using leaf nodes (Duke and Pinzón, 1992) which were fortunately visible along twelve meters in height. The growth history of these trees was constructed based on node height, notably extending at a rate of approximately 10 cm. node $^{-1}$. Thus, in the plot of tree height and node number (Fig. 9), this showed a curve which can be compared with the sigmoidal curve of the logistic equation (Odum, 1971). These trees, therefore, grew slowly at first with height approaching a putative climax at `K' for the logistic equation, around 13 meters. This idea, although requiring the refinement of a better mathematical model, is in agreement with the type of development expected for trees which grow and attain specific stand heights, depending on location. In mangroves, this is notable in transects across the topographic profile, but it is also influenced greatly by climate, salinity, tidal inundation frequency, and site exposure. Therefore, gap closure may be achieved after one or two decades when young trees attain the height of surrounding mature forests.

The Impact of Oil on Mangrove Forests and their Natural Recovery

In April 1986, an estimated eight million litres of oil was lost from a ruptured land tank at the Refinería Panama site in Bahía Las Minas on the Caribbean coast of Panama (Fig. 2; Jackson *et al*., 1989). The subsequent spill took place in two important phases. In the first, most of the oil was trapped in a central embayment for several days. At this time, it was fresh and concentrated, forming a 5 mm thick layer throughout the estuary (approximately 2 km^2). As expected, the impact in this place was severe and approximately half the surrounding forested areas of mangroves were killed within a month. Trees probably died from a combination of toxic and suffocating effects. In any case, few remained alive from the waters' edge to half-way up the intertidal range. The second phase resulted when rainfall increased estuarine outflow and a temporary wind shift together washed the oil over some retaining booms, and out to sea. When the wind returned to normal shortly afterwards, and blew on-shore again, this oil was the deposited on other mangroves, extending more widely across the bay from Punta Galeta to Punta Muerto, and beyond (Jackson *et al*., 1989) On this occasion the impact was patchy, and many sites faced the open sea were associated with major channels. With few exceptions, these sites were all characterized by bands of deforestation behind rows of one or two trees bordering the waters' edge (Figs 1a and 10a). Others formed characteristics crescent shapes for sites on exposed faces of small islands and headlands, or funnel shapes where they were associated with smaller drainage channels. In each case, shape was apparently related to topographic

Figure 6. (a) In Bahía Las Minas, seedlings of *Rhizophora mangle* in the seedling bank are often grazed by herbivorous small crabs, destroying most of their leaf surface. However, these crabs apparently prefer not to cross the substratum, and those seedlings growing away from prop roots of mature trees are generally left undamaged. **(b)** In the substratum of these same forests, there are small crab burrows, around 15 mm in diameter at the surface, scattered across the surface. They penetrate the tough fibrous root matt, and provide convenient holes in which hypocotyls of slightly lesser diameter are planted. This 'crab-hole planting' hypothesis possibly explains how seedlings typically have at least a third of their length, around 15 cm, beneath the tough substratum. It also has important implications for the evolution of both vivipary and the role of these small crabs

Figure 7. This sketch represents a transect of a mangrove forest through time, describing a simple model of the processes of canopy recovery following light gap creation in *Rhizophora mangle* forests. Notice, on the left of the profile, the seedling bank under the mature forest canopy before creation of the light gap. After gap creation, there is a phase where seedlings grow rapidly to refill the gap and reform the canopy, albeit at a lower level. Other recruits continue to join the seedlings bank and may contribute to canopy recovery, but it is more likely they will perish when they become more shaded by advanced neighbors. In the same way, as foliage density increase, the seedling bank will reform under this new canopy. The first phase of canopy closure may be quite rapid in some sites, occurring in less than five years, but full gap closure in the second phase is expected to take up to 20 years, depending on site

contours because oil tended to accumulate at upper levels of tidal variation at the time. This might have something to do also with the curious survival of trees lower in the topographic zone. And, since these trees were also awash with oil, it is believed that the higher deposition of oil on their trunks somehow missed critical breathing surfaces, presumably located lower on trunks and exposed roots. In any case, the effect was obviously also catastrophic for intertidal fauna, and this was marked by an overwhelming smell of rotting flesh in the bay area for several weeks following the spill (cubit, pers.com.).

Figure 8. This series of schematic plots depicts a model of gap recovery in forests of *Rhizophora mangle,* based on age and density of plants. Notice, in the mature forest, the two disparate groups representing the seedling bank on the left, and the mature trees on the right. After the creation of the light gap when larger trees are removed, the younger plants progress right from the seedling bank group (a to e) to eventually draw apart from that group, prior to refilling the gap

This negative impact was obvious soon after organisms came in direct contact with oil, although response time varied for particular ones. This ranged from intertidal animals with thick coatings of oil dying after two or three days, to mangrove trees with oiled roots taking approximately one month before losing their leaves. For *Rhizophora* species, total defoliation is indicative of their imminent death, and in Bahía Las Minas this resulted in extensive areas of deforestation which are clearly visible today, five years later (Fig. 1b). The delay in tree death appears to be normal since it was observed also in other oil spill sites (Cintrón *et al*., 1981). Other species, notably *Laguncularia*, were more fortunate apparently, since pre-spill individuals are often observed in the oil-deforested sites, previously dominated by *Rhizophora*. This identifies a major responses difference for different mangrove species, and the ability to recover from total defoliation may account for the greater impact presently observed in *Rhizophora* forests. In this context, it would be interesting to compare areas of defoliation with those of subsequent tree death. However, this is no longer possible for the Bahía Las Minas spill, but it would be informative to follow the relationship in other instances. Furthermore, this impact is expected to extend beyond biota coated with oil, since there is recent evidence of possible leachates from oil, adversely affecting sub-tidal sessile biota in the same spill (Guzman *et al*., 1991).

It is also obvious that oil has remained in these mangrove areas long after the spill. This is mostly trapped below the anaerobic substratum where it apparently entered during the initial impact, assisted by diurnal fluctuations of tides. It presumably penetrated crab burrows which later became blocked as they fell into disuse since the inhabitants were dead. In any case, there appears to be myriad of air-tight reservoirs, or pockets, of oil in the substratum which may be likened to a giant sponge since walking on its surface still causes oil to squeeze out. In addition, heavy rain will also disturb the substratum and flush out these pockets causing minor new oil slicks in surrounding channels. Clearly, the biological impact from this spill is expected to continue for at least two reasons. First, sites of deforestation must cope with regeneration. Second, all sites in the vicinity must cope with the presence of residual oil.

Sites of deforestation must contend with both missing trees and canopy, referring both to their primary production and physical structure. Furthermore, where trees are missing, the nature of the substratum has changed considerably, essentially since it is now more exposed. In this way, it is subject to a wider range of temperatures, desiccation, and erosion form rainfall and other water movement. These different conditions are not likely to support the same flora or fauna present earlier. Therefore, those species able to utilize gaps represent the first stages of natural habitat restoration. During this same, there is a chance that sites will be permanently altered with the inclusion of new species. This effect is compounded for sites of oil spill deforestation by both the extensive areas and the presence of oil. In this way, different species may become established, and others excluded because of the influence of oil. Consider one example, notably for those crabs which eat certain species of mangrove propagules (Smith *et al.,* 1989). In sites where these were removed, clearly, the usually eaten tree species would then have an opportunity to become established.

Figure 9. Four trees of *Rhizophora mangle* were sampled from an apparently single-aged stand approximately ten years old. The two plots present data of **(a)** mean heights and **(b)** mean internodal extension, derived from leaf scar nodes which were clearly visible along the entire 12 m length of the main stem of each tree. In addition, and in conjunction with each plot, the best-fitting curve for the logistic equation is included for comparison. In this way, the notion of these trees appeared to some maximal height; around 13 m approach (K)

Another post spill effect is more evident only three or four years after the spill. This involves the mobilization of rotting and broken tree fragments. It is less important in sheltered sites, but in exposed locations, especially where the frontal trees were killed, the substratum is notably scoured by the bull-dozing movement of wind and wave-driven windrows. These are made up chiefly of the fragmented remains of trees killed during the initial impact of the spill. Furthermore, the bull-dozing process removes most seedlings that had become established beforehand. It is suggested that colonization and re-establishment of these sites is significantly retarded, and may possibly be altered permanently.

Clearly, many organisms have re-colonized deforested sites, and oil trapped in the substratum appears to be generally tolerated. In many sites, most seedlings appears to be growing normally (Fig. 10b), possibly because their roots avoid the pockets of oil. Crabs, which are also present, may have similarly directed burrows. In this way, oil may be trapped indefinitely in the substratum while the forests continue to regenerate. Nevertheless, there are clear indications that surviving mature forests of *R. mangle* are still influenced by remaining oil. Therefore, while few additional trees appear to die, their remaining canopies are measurably thinner, and their estimated levels of canopy leaf biomass for the various habitats is 23-33% less than in matching sites with no oil (derived from unpublished local observations). Furthermore, leaf longevity is estimated to be reduced by 18%. All this indicates mature mangroves in Bahía Las Minas are still adversely affected by oil. This is possibly due to the loss of below-ground roots during the spill, and the amount lost may be proportional to the reduction of canopy leaves.

So far, the impact of oil has been described chiefly in terms of its effect on mature mangrove trees, notably *R. mangle* which died in the now deforested sites and which survive in surrounding area. In the usually well-defined deforested sites, however, it was wrongly assumed initially that all *Rhizophora* died in the bands of deforestation. The studies in Panama have shown for the first time that there are many survivors from the pre-spill seedling bank. And, it is expected they will play an important role in natural recovery of such areas, as proposed in the hypothesis of canopy recovery in natural light gaps (Fig. 7). Their survival following this spill may be related to the critical air breathing surfaces, suggesting that these have different tolerances and/or vertical ranges in trees and seedlings.

Nevertheless, the discovery of surviving seedlings in oil-deforested areas is based on retrospective records found in sequences of leaf scar nodes along the main stem (Duke and Pinzón 1992), chiefly because the present studies commenced three years after the spill. As suggested earlier, the growth of these seedlings are expected to change from under-canopy values of 3-4 nodes per years, to around 7-8 per year in open-canopy sites (Fig. 5). Accordingly, the seedlings in oil deforestation sites appear to have grown first under a closed canopy, indicated by more than six nodes of limited internodal extension, up to 2-3 cm/node, followed by more rapid height extension in distinct seasonal pulses around 9-10 cm/node. Furthermore, ages of these seedlings were estimated using these pulses, plus the number of main stem nodes, and this confirmed they were older than the oil spill.

Figure 10. **(a)** Deforestation resulting from the 1986 oil spill eastern parts of Bahía Las Minas (Fig. 2) is characterized by a row of two or three surviving trees along the waters edge. This photo, taken in May 1991, shows the gap left by missing trees. The tree line once extended across the picture from those on the left, at the waters' edge, to those higher up the topographic profile, on the right. Notice also the seedlings of *Rhizophora mangle* in the deforested area. **(b)** Five years after the spill, these seedlings are now growing as well as those in un-oiled light gaps, but earlier on, their growth was apparently suppressed by oil remaining in the substratum

Of further importance, peaks of internodal extension also appear to reflect a diminishing influence of residual oil on the growth of these seedlings following the spill, depending on site. Consider the examples of four seedlings from four different sites in Bahía Las Minas (Fig. 11). Three are from different areas of oil-deforestation, and the other is from a natural light gap. All are apparently older than their respective light gaps, and all show marked seasonal fluctuations of internodal increments. Notice the abrupt increase of peak values for the un-oiled seedling (Fig. 11a), whit its light gap appearing sometime prior to 1989. This was partly confirmed from aerial photographs. However, it is not known whether there is a significant delay, as presented, in the growth response under natural conditions. But, this is not expected to be longer than one year, since seedlings in oiled light gaps often show significant increases after one year from the spill, in 1986. This depends on the site however, notably regarding the presence of oil. In the first instance (Fig. 11b), the site is very exposed to waves and wind and there is virtually no protective barrier of lower intertidal mature survivors. In this case, growth increases abruptly as observed in the seedling from the un-oiled gap site, while those from noticeably more sheltered locations had greater delay in growth, and only progressive increases (Figs. 11c and 11d). This is suggestive of a negative influence of oil, which diminishes more rapidly in sites of greater exposure.

These individuals are considered to be very important in habitat recovery since they represent the first cohort of contenders for the new canopy. And, as light is so important for the growth of *Rhizophora* seedlings, all younger recruits are expected to be appreciably handicapped. This observation has great importance for the discussion on `assisted' planting later in this treatment. For the moment, however, it is important to consider seedling growth further, by comparing growth in oiled and natural (or un-oiled) sites of gap recovery. It is clear already those individual seedlings both survive oil spill and continue to grow afterwards, apparently recovering well where they have survived. But, how does this relate to large numbers of individuals, and is forest recovery likely to be significantly influenced further by the presence of the remaining oil. Unfortunately, it was not possible to make an appropriately balanced assessment, since no natural control forest gaps of equivalent size and age to oil-deforestation sites were available. Nevertheless, several studies highlight the apparent success of natural recovery in oil-deforested gaps in Bahía Las Minas.

In one case, growth over one year (1989-90) was monitored in 216 seedlings, for all age groups from the time of the spill, and throughout the range of oiled and un-oiled habitats. These

Figure 11. These plots sequences of internodal extension by node for four natural recruits of *Rhizophora mangle* in Bahía Las Minas. The first (a) growing in a natural light gap in a sheltered site, while the others (b-d) are growing in areas oil-deforestation where site conditions range from very exposed (b), exposed(c) to sheltered (d). These were scored on two occasions, noted in their respective legends, providing a measure of node production rate. Accordingly, nominal annual peaks have been identified. Notice that each apparently survived the creation of their respective light gaps, marked by vertical dashed lines. Also notice the abrupt increase in internodal extension, and node production rate, in the un-oiled site and the very exposed oiled site, while the more sheltered oiled sites have depressed peaks of internodal extension that progressively increase following deforestation

were grouped in this treatment as sheltered and exposed sites. The results for three parameters of growth, including node production, height increase and mean internodal length, are presented in Table 1. These identify a significantly greater node production rate in oiled sites, and a non-significantly difference between habitats (2-way ANOVA for site means of annual node production normalized as reciprocal transformation, grouped by habitat, P<0.509, and the presence of oil, P<0.001). The reason for this unexpected result is believed to be due the greater size of oil-deforested light gaps, compared with natural ones. As noted earlier, a greater amount of light would contribute to higher node production rates. By comparison there are no significant differences for height estimates (2-way ANOVA for site means of annual height increase normalized as log transformation, grouped by habitat, P<0.412, and the presence of oil, P<0.111). There is, however, a relationship between these parameters with node production and height (log transformation) being positively correlated (r=0.766, n=214, P<0.001). These data are presented in a plot (Fig. 12), which displays the range of the respective parameters and the line of best-fit for the linear regression coefficients. Notice, for the lower range of node production rates, extrapolated seedling heights increase by around one centimeter per year, or 0.5 cm/node. This is very close to the physical length of leaf scar node, and indicates their maximal density on the stem, and zero internodal distance (Duke and Pinzón 1992). Also notice that as node production and height increases, the range of annual height production also increases, indicating the independence of these parameters when node production rates are high, notably above eight nodes per year. In general, these data clearly indicate that growth of seedlings in oiled and natural gap sites are growing at comparable rates now, four years after the spill, and that oil did not have a negative effect on the growth of these seedlings.

Natural recruitment of *R. mangle* seedlings has been very high in some oil-deforested sites in Bahía Las Minas (Fig. 10), but this is clearly variable and mean densities range from <0.1 to 23.4 seedlings/m^2. These estimates were taken approximately four years after the spill, and they represent components of both annual stocking supply rate, and survivorship. Given that comparable densities are observed regularly in un-oiled sites, and the comparable growth rates noted above, then it is assumed that the major influencing factors are chiefly natural. In this bay, however, these factors may have been influenced also by a massive planting experiment conducted by the Refinería Panamá (Teas *et al.*, 1989). In view of this, the processes of natural recruitment and seedling growth will be further considered in conjunction with an appraisal of this planting project.

Table 1. One year growth, 1989-1990, scored for 216 natural recruits of *Rhizophora mangle* growing in natural light gaps and oil-deforested areas of mangrove forests in Bahia Las Minas and nearby. Sites were grouped in two habitat types including, exposed and sheltered. Parameters (1se) include leaf node production, height increase, and mean internodal length. Seedling age ranged from less than one, to five or six years, and node production rate was not related to size or putative age.

	Mean annual production (1se) of seedlings in deforested areas			
	Exposed sites		Sheltered sites	
	oiled	un-oiled	oiled	un-oiled
Node number	8.9 (0.5)	7.4(0.1)	8.4 (0.2)	7.7 (1.3)
Height increase (m)	0.438 (0.144)	0.297 (0.034)	0.364 (0.07)	0.538 (0.242)
Internode length (cm)	4.6 (1.2)	3.7 (0.1)	4.1 (0.7)	6.0 (2.5)

'Assisted' Recovery of Mangrove Forests in Panama

Some oiled areas may recover after 4-5 years, but sites of deforestation will undoubtedly take onwards of 25-30 years, depending on the time it takes for trees to reach maturity. So, the question that must be asked when faced with the aftermath of oil-deforestation, is whether we can assist recovery, either by site modification and further clean-up of oil, or by planting. In providing assistance we presume that the natural processes are unable to repair the damage. Accordingly, we assume that either the supply of seedlings is reduced, or their natural establishment might be inhibited by the presence of oil. But, there is always a risk that interference with this fragile habitat may worsen the situation. Therefore, when the decision is made to plant mangroves, for example, we should be obliged to follow their fate indefinitely, whilst we might still learn about the benefits of the particular assistance provided.

This is especially important in a system where the relationship between cause and effect, notably for identifying positive responses to our assistance, is likely to take many years. Furthermore, this same learning process would include developing better planting strategies which might include "enhancement" measures, in an attempt to insulate seedlings from oiled substratum whilst they become established. Clearly, all such considerations are spill-specific, but the studies in Panama offer some important insights which will be useful in formulating assisted recovery procedures in the future.

The oil spilled in Bahía Las Minas reportedly killed around 75 hectares of mangrove forests, representing possibly around 10% of forested intertidal areas. This is presently being quantified as part of a larger study of the longer term impact of this spill on mangrove forests. Shortly after the spill, the Refinería Panamá started an active testing program in anticipation of implementing a large-scale planting program. These tests established a procedural methodology, and using this, they reportedly planted at least 86,000 seedlings over the next year (Teas *et al*, 1989). It is of interest that, apparently twice this number may have been planted eventually. In any case, most seedlings were planted with some broad spectrum fertilizer and clean soil since this was shown to improve early growth and survival.

The intensity of this planting effort can be gauged by estimating the density of planted seedlings based on the values reported above, notably for at least 70% of the deforested area, and up to double the reported plantings. Altogether, this computes as a range of 0.1 to 0.3 seedlings/m^2, notably in the lower range of standing stock densities for natural recruits, reported earlier and summarized in Table 2. These were estimated from an array of three replicate quadrats for each of 12 oil-deforested sites in the Bahía Las Minas (Fig. 13). Sites were chosen for balanced set of planted and not planted locations in the two habitat types, namely exposed and sheltered. Seedlings in the quadrats were tagged and scored for several parameters including, height, girth, and number of nodes on the main stem. Also, the seedlings were carefully identified as being planted or not, based on several factors including, substratum disturbance, different soil and/or plastic bags. The estimates of density for planted recruits clearly correspond with the expected estimate derived above. It was also learned from this data that there where two major planting efforts made approximately one year apart. The second effort appeared much more extensive than the first, including exposed sites, with most sheltered sites planted twice. The data on densities taken in April 1990, clearly show that the contribution

Figure 12. These two plots compare node production rate and height increase during one year, 1889-1990, for 216 natural recruits of *Rhizophora mangle* growing in light gaps or deforested areas. Data are grouped according to habitat condition being exposed or sheltered, and whether sites were oiled in 1986. One plot **(a)** shows data plotted on normal untransformed scales, and the second **(b)** shows the same data replotted with a log transformation of height increase. The significant regression of best-fit is plotted for the latter case since it appears that this adequately describes the trends observed. The first plot shows the separation of oiled and un-oiled seedlings where node production rates and highest. The second plot displays the regular trend across the range of node production rate, and a minimum which corresponds with rate noted earlier in shaded seedlings, around 0.5 cm/nodes (fig. 6)

of the massive planting exercise was quite small compared with natural recruitment, both within the same sites where there were 5-11 times more natural recruits, and compared with sites of no planting where there were 11-39 times more natural recruits. These data were further analyzed to consider the contribution of planting to particular cohorts, and this assessment is summarized in Table 3. Notice, four cohort groups were followed, notably matching each of the two plantings, and those older of younger. According to these estimates, the contribution of those planted is still quite low, even for their respective cohorts.

From this data, it is clear that large-scale planting is a numbers game, and the high levels of natural recruitment alone, question the justification for such an effort. On this occasion, natural recruitment was clearly adequate for most sites in Bahía Las Minas, and notably also at the time of planting. But, this assessment also found further problems with this effort, by showing a significant negative impact on natural recruitment where planting took place. In Figure 14, the data already discussed are presented in four histograms with densities of each of thirteen node classes in sites grouped by habitat and whether they were planted or not. Notice the trend from greatest densities in sheltered, non-planted sites to exposed, planted ones, and furthermore, both effects were significant (2-way ANOVA for sites means of total seedling densities normalized with a square-root transformation, grouped by habitat, $P < 0.001$, and the presence of planted seedlings, $P < 0.026$).

The causes of a this negative effect on natural recruitment, possibly arise from several factors. Firstly, cutting of standing dead timber and roots would remove shelter for all seedlings, as well as providing destructive mobile material later on. Secondly, tramping of substratum would cause compaction and/or release of trapped oil, and both deter seedling growth. Thirdly, digging holes for either drainage of trapped oil or planting of new seedlings would allow greater erosion during periods of heavy rain or high tides. And fourthly, all the previous actions would interfere with natural recruitment, either by damaging survivors of the seedling bank and latter recruits or by inadvertently deterring establishment of new recruits. In latter case, for example, crab-hole planting, suggested earlier, would not occur if crabs or their burrows were disrupted, as would be the case where there was excessive sites access.

Nevertheless, despite this negative impact o general sites recovery, planted seedlings did apparently grow better than their natural recruit counter-parts. This was assessed by tallying all information on heights of both planted and natural recruits of the same node numbers in the same sites. As these covered a range of node numbers, the estimates were reduced to mean internodal distances, for heights above the hypocotyl, and the results are presented in Table 4. In all cases, there were significantly greater height increases for planted recruits in both habitats and cohorts. Clearly, the "enhancement" measures utilized in this planting effort did have a decidedly positive influence on the growth of planted recruits.

Table 2. Mean densities of R. mangle seedlings in number/m^2, for 12 oil-deforested sites in Bahia Las Minas, scored in April 1990. Sites were grouped equally in four categories based on whether they had been planted or not, and as either exposed or sheltered habitats

	Refinery planted sites		Sites no planting
	planted	**natural**	**natural**
Exposed mangrove	0.16 (0.05 – 0.25)	0.80 (0.05 – 1.17)	1.79 (0.31 – 2.64)
Sheltered mangrove	0.26 (0.12 – 0.34) {0.11}* {0.15 (0 – 0.22)}**	2.77 (1.25 – 4.44)	10.18 (1.97 – 23.4)

***= First planting of seedlings in mid 1986; **= second planting of seedlings in mid 1987**

Figure 13. In Bahía Las Minas, fourteen study sites were chosen to compare planted (heavy symbols) and not planted locations (lighter symbols) in areas of deforestation from the 1986 oil spill. Sites were further grouped according to two habitat conditions, exposed (squares) and sheltered (circles)

However, this positive benefit was out-weighed by the apparent disruption of the otherwise greater natural recruitment. It is further exacerbated by the gloomy prospects for most planted seedlings. This prediction is based on data showing the importance of light, where the winning competitors have the greatest height and canopy size. In consideration firstly of height only, these data are shown in four histograms of the densities of height classes in the two habitats and planted and non-planted sites (Fig. 15). By contrast with data presented similarly for nodes (Fig. 14), the greater densities are skewed right with seedlings of greatest height

Table 3. Mean densities of natural and plantes seedlings/m^2 (1 se) for particular stem node classes of *Rhizophora mangle* for 48 quadrats (12 m^2 each) in 16 oil-deforested sites in two major mangroves habitats in Bahia Las Minas (Fig. 13). These were scored in April 90 and correspond with surviving cohorts before, during and after those planted, around mid 1986 and mid 1987 (Teas et al., 1989). Site are further categorized according to planting activities, as planted once, twice or undisturbed. Virtually all recruits are natural, and where values include planted seedling, a second figure for natural recruits only is presented in squared brackets

		Mean density (1 se) per m^2 for four Node Classes Node Classes for seedling cohorts before, during and after planting			
Habitat	**Site condition**	**>33 'older'**	**19-33 'first planning'**	**10-18 'second planning'**	**<10 'younger'**
Exposed	Planted once	0.02 (0.01)	0.39 (0.20	0.48 (0.22) [0.31 (0.19)]	0.06 (0.03)
	Undisturbed	0.01 (0.01)	0.74 (0.31))	0.22 (0.12)	0.76 (0.37)
Sheltered	Planted once	0.03 (0.03)	3.00 (0.61)	1.01 (0.24) [0.92 (0.22)]	0.68 (0.24)
	Planted twice	0.13 (0.07)	1.22 (0.07) [1.07 (0.09)]	0.42 (0.10) [0.25 (0.11)]	0.40 (0.15)
	undisturbed	0.72 (0.27)	6.36 (3.27)	0.97 (0.84)	1.06 (0.87)

Table 4. Mean internodal distance (1 se) along the main stem, above the hypocotyls, for 130 planted and 208 natural recruits of *R. mangle* in Bahia Las Minas. These were compared from data collected in April 1990 for each of eight sites in exposed and sheltered habitats. Seedlings were chosen to be approximately the same age, as determined by equivalent node classes, either 19 - 33 nodes for those first planted around mid 1986, and 10 – 18 nodes for the second planting around mid 1987

	Mean Internodal Distance (cm) along the main stem above the hypocotyl		
Seedling type	**Exposed sites**	**Sheltered sites**	
	Second planting	**First planting**	**Second planting**
Natural	2.11 (0.16)	2.35 (0.26)	3.69 (0.32)
Planted	3.03 (0.33)	3.67 (0.31)	4.14 (0.31)

usually having lowest densities. Notice also that few of the planted recruits are present in the upper height or age classes. And, in reference to the proposed model of gap recovery (fig. 8), only a smaller number of older and larger individuals will ultimately contribute to the future mature canopy. Now, in consideration of canopy density or total leaf biomass, this is expected to increase up to some maximal value, notably observed in mature forests. This would represent the end of the initial phase of gap recovery during which the substratum was only partially shaded, and younger seedlings colonizing more open positions may still contribute to canopy closure. Subsequent development in the second phase would then involve direct competition between neighboring plants, as the requirements for greater canopy space for each individual increases with height and age. Furthermore, during this latter phase, the substratum is expected to be shaded, as in a mature forest, and the seedling bank would be reestablished. In this phase also, areal leaf biomass density is expected to be relatively constant and independent of either tree density or height.

To assess the present status of recruitment and gap recovery in oil-deforested sites, seedling density and height were compared with standing leaf biomass. The latter was estimated from the allometric relationship equating tree heights and girths to dry weight of leaves, recorded by Cintrón and Schaeffer-Novelli (1984). This was calculated per tree in the quadrats, and total densities per m^2 were then estimated, since the area and number of trees was known. These values were then presented for all sites in two plots (Fig. 16), comparing leaf biomass with seedling height and density.

Figure 14. These four plots of node classes and density of *Rhizophora mangle* seedlings, compare changes related to two grouping of data, notably for habitat condition as exposed or sheltered, and whether sites were planted or not (Fig. 13). Planted recruits are identified by the white portions of the histogram bars, in the lower plots. Notice the trend from highest densities of natural recruits in sheltered, not planted sites, to lowest densities in exposed, planted sites. Also note bimodal peaks with the younger group (node 2= 4-6 nodes), probably representing the new seedling bank proposed in the model in figures 7 and 8

These show leaf biomass having a significantly closer relationship with site density (r= 0.865, n= 41, P<0.001), than with seedling height (r= 0.449, n= 41, P<0.005), suggesting that height is less important in this process. Nevertheless, four years after the spill standing leaf biomass in the range of sites, increased as suggested earlier, approaching the levels observed in mature forest canopies.

These values were derived from litter fall and shoot data collected over one year in the same area, and the means annual values are relatively constant between habitats, depending chiefly on whether sites were oiled, 336-346 g/m^2, or not, 452-484 g/m^2. Notice that these mean estimates closely match maximal values computed for the more densely stocked quadrats (Fig. 16a), notably sheltered, not planted sites. These sites are therefore the most advanced, having presumably achieved canopy closure, albeit at a relatively low height. It is also evident that exposed sites are severely disadvantaged, and that the planting effort failed to significantly help this obviously vulnerable habitat.

In general, these data show differing effects and influences, and although this planting effort apparently provided no benefit toward the present recovery of mangroves in Bahía Las Minas, there are some positive lessons. First, the growth of planted seedlings was significantly improved with fertilizer and fresh soil. Second, the recovery of particular sites, notably in exposed locations, could be assisted by planting. In order to prevent windrow-scouring of these sites, however, it is suggested that simple wooden structures, such as post, be positioned amongst planted and/or natural recruits to protect them until they are big enough to withstand scouring by larger drift fragments.

Figure 15. These four plots of height classes and density of *Rhizophora mangle* seedlings, compare changes related to two grouping of data, notably for habitat condition as exposed or sheltered, and whether sites were planted or not (Fig. 13). Planted recruits are identified by the white portions of the histogram bars, in the lower plots. Notice the trend from highest densities of natural recruits in sheltered, not planted sites, to lowed densities in exposed, planted sites. Also note how height classes, unlike node classes (Fig. 14), are skewed left. This indicates that while there are many older recruits, these are not equally tall, and height growth is being suppressed, presumably by lack of light. Clearly, only those recruits in the greater height classes will have any chance of contributing to the mature canopy

Conclusions

As we are unable to protect mangrove forests from oil spills, then we must fully assess our options for subsequent action, by deciding whether assistance is likely to be beneficial. First, we need to consider the logistic practicality and biological impact of removing oil as carefully as possible. Clearly, natural and assisted recovery could be influenced by a continued presence of oil in the substratum. However, it might be better that this is tolerated whilst it breaks down naturally, since the alternative of attempting to remove it, could result in even greater and more lasting impact. Second, we should consider the benefits of planting seedlings to replace dead trees. Both these steps have been taken in the past, but their long term success has not been adequately evaluated. Or, at least, the information is not readily available.

Figure 16. These two plots compare estimates of standing leaf biomass (g/m^2) with density and height *Rhizophora mangle* seedlings in planted and not planted sites in exposed and sheltered habitats. Significant linear regressions are plotted showing the trends. These sites are mostly in the first phase of gap recovery (see text, and Fig. 7), since many of the estimates of standing leaf biomass fall well below mean annual estimates for nearby mature forest canopies, around 400 ± 50 g/m^2. Notice that seedling sites with the closest estimates are sheltered, not planted locations

For this reason, there are no improvements to our rudimentary knowledge of post-spill habitat restoration in mangroves, enabling us to better assist recovery of these forests in the future. In the case of planting, for example, we do not know if previously planted sites have returned to normal, than comparable sites that were not planted. Does planting improve on natural recruitment? While the answers to such questions are expected to be site dependant, we, don't know about the longer term performance in any sites where earlier efforts assisted with habitat recovery. Furthermore, it appears natural recruits were ignored in earlier efforts, assuming them to be unimportant. This is a mistake however, since sites access and so on, is likely to counter-act the good-intentions of planting, as found in Bahía Las Minas. Therefore, it is strongly recommended that planting be re-thought in terms of assisting natural recruitment, instead of replacing it. Consider the analogy of a human patient being treated by a doctor who applies a selection of remedies that basically supplement the patients own ability to recover. Likewise in mangroves, the natural recovery processes must not be ignored, and whatever steps improve the rate of return to "normal", pre-spill conditions, is in the best interests of all concerned.

In this chapter, we have presented a wider view of post-spill recovery of mangrove forests, by considering natural processes operating in the ecosystem. In this way, we have shown these forests to be well-prepared for small-scale deforestation, since it is apparently their major process of turnover, regeneration and succession. They essentially anticipate deforestation with an undercanopy seedling bank established recruits, apparently able to grow rapidly when greater light conditions are presented by the creation of a gap in the canopy.

Clearly, there is still much to learn, but it is hoped that future efforts to restore mangrove forests might include consideration of natural processes, some of which are discussed in this treatment. Accordingly, and based on our observations and others (e.g. Cintron and Schaeffer-Novelli 1983), a tentative protocol for post-spill efforts might include the following steps:

1. Protection. Protect mangrove forests from spilled oil.

2. Clean-up fresh oil. Carefully remove oil reaching mangrove trees, where practical. This would include wiping oil coated on the vulnerable trunk and root surfaces, without using solvents, or harsh emulsifiers. Furthermore, during these efforts, extreme care should be taken not to damage surviving seedlings in the seedling bank, or tramp on the substratum.

3. Minimize site damage. The cutting and removal of trees, dead or alive, should be discouraged, since seedling recruits rely on these remaining structures for shelter and support.

4. Quantify extent of oiling. The extent of the impact needs immediate quantification for future reference. This entails mapping the coastal areas affected, and identifying the areal extent of mangrove forests, of oiled places, and of later deforestation. For This task, it would be essential to have suitable aerial photographs flown immediately. For areas of deforestation, both tree and animal species most affected need to be characterized and identified.

5. Assess natural recovery potential. Natural recovery needs to be evaluated, once the extent of obvious damage is known, notably deforestation. The extent of un-oiled habitat, where this exists, could be considered the future source of propagules, for either natural recruitment or planting. The decision to plant would depend primarily on the proximity of respective of mangrove species, and the opportunities for free dispersal of propagules to sites of deforestation. Planting should only be necessary if it can be shown that natural processes are failing, or they could be beneficially accelerated. In exposed sites, there is the added problem of erosion possibly causing permanent changes to site topography. This problem is apparently assisted by the destruction of recruits by the scouring action of windrow drift. In these cases, it might be more beneficial to position degradable wooden structures in the substrata, to protect young seedlings.

6. Establish evaluation sites. Sites of future scientific evaluation need to be established immediately. This is necessary for the establishment of basic data on forest structure and species composition of deforested areas. These will disappear after only a few years. Other scientific sites could be set up with quadrats and marked individual seedlings. In this way, future recruitment and growth of existing seedlings could be accurately followed. This requires regular sites visits over a long period. All these latter points require re-evaluation according to the current status of available knowledge.

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Research Information Needs on U. S. Mangroves: Recommendations to the United States National Oceanic and Atmospheric Administration's Coastal Ocean Program From an Estuarine Habitat Program-Funded Workshop

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Background

In l988 the U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA) initiated a Coastal Ocean Program (COP) with management initiatives designed to refocus its activities to support three program elements: (l) prediction of coastal ocean degradation and pollution; (2) conservation and management of living marine resources; and (3) protection of life and property in the coastal region of the United States. The overall COP has a national rather than regional focus. The programs that have evolved under the aegis of the COP are listed below, are described in more detail by U.S. Department of Commerce (l990):

- Estuarine Habitat Program — designed to evaluate the functional role of estuarine and coastal habitats in supporting living marine resources and to determine the extent of and rates of change of these habitats.

- Nutrient Enhanced Productivity Program — designed to address nutrient overenrichment in coastal waters of the U.S.

- Coastal Fisheries Ecosystem Program — designed to determine how natural environmental variability influences the productivity of coastal and estuarine living marine resources.

- Toxic Chemical Contaminants Program — designed to evaluate the cumulative degradation of coastal organisms, sediment, and water by mixtures of toxic chemicals.

- Physical Impacts Program — designed to address the impacts of episodic and persistent alteration of coastal systems on marine resources.

The Cop Estuarine Habitat Program

The Estuarine Habitat Program (EHP) of the COP was established because estuaries and their associated coastal systems are extremely valuable components of the marine environment and are being impacted by man-induced stresses with resulting losses of living marine resources. Two thirds of the Nation's commercial and recreational marine fisheries harvest is estuarine dependent. In fact, estuaries provide food, shelter, migratory pathways, and spawning grounds for over 70 % of the commercial fisheries landed in the United States. These were worth $5.5 billion to the Gross National Product in l986. In addition, recreational fishing generates annual expenditures of over $l3.5 billion, while contributing significantly to the quality of life for l7 million anglers (Mager and Thayer l986, NMFS Operational Guidance l990).

As human populations increase in the coastal region estuaries are placed under increasing pressure. They are fringed with cities and attendant industries, they serve as transportation corridors, recreational sites, and dumping grounds for society's waste products. Excess nutrients may alter estuarine food webs or lead to conditions that reduce oxygen levels in the water column. Toxic compounds, including halogenated and petroleum-hydrocarbons, occur in fishes and sediments in concentrations warranting concern. Various pathologies in fishes and crustaceans have been linked with waters receiving agricultural drainage or effluent from heavily industrialized areas. Less dramatic but equally insidious are changes in the clarity and volume of water reaching estuarine habitats (Kenworthy *et al*., l988; l989 and references cited therein). Silt and particulates from dredging, upstream erosion, or eutrophication reduce the intensity of light reaching estuarine vegetation. The upstream with drawal or addition of large quantities of water in association with domestic, industrial, and/or agricultural uses also may disrupt estuarine habitats and the organisms they support.

The United States House Committee on Merchant Marine and Fisheries recently issued a report entitled "Coastal Waters in Jeopardy: Reversing the Decline and Protecting America's Coastal Resources". The report states:

The evidence of the decline in the environmental quality of our estuaries and coastal waters is accumulating steadily. The toll of nearly four centuries of human activity becomes more and clearer as our coastal productivity declines, as habitats disappear, and as our monitoring systems reveal other problems... The continuing damage to coastal resources from pollution, development, and natural forces raises serious doubts about the ability of our estuaries, bays, and near coastal waters to survive these stresses. If we fail to act and if current trends continue unabated, what is now a serious, wide spread collection of problems may coalesce into a national crisis by early in the next century?

It is the vegetated wetlands in estuaries (seagrasses, salt marshes and mangroves) that provide the refuge, food resources and nursery areas for a majority of commercially important, estuarine species (e.g., Peters *et al*., l979, Ferguson *et al*. l980, Kenworthy *et al*., l988, Short *et al*., l989). However, more than half of the original acreage of coastal wetlands of the United States has been lost, and the rate of loss appears to be increasing (Tiner, l984, Kean *et al*., l988). Thus, California has lost 87% of its original 3.5 million acres of coastal wetlands. Dramatic declines have also been observed in Florida and in the submerged seagrass beds of Chesapeake Bay. In the southeastern United States, where estuarine-dependence of fisheries is greatest, the loss of coastal wetlands is most pronounced. Louisiana alone is losing 50-60 square miles of wetlands annually. Loss of coastal wetlands results in decreased yields of those species dependent on these habitats. There has been a decline in fish and shellfish harvests of 42% in the southeastern U.S. since l982; a 66-96% decline in shad, striped bass and river herring in the Chesapeake Bay; a 65% decline in salmon in California; and a 60-80% decline in striped bass in San Francisco Bay, all concomitant with losses of habitat and diversions of freshwater to coastal areas. Thus, the President of the United States has declared a "no net loss" policy for the Nation's wetlands.

NOAA has resource management responsibilities for the nation's living marine resources throughout their range. Accordingly, NOAA is charged with ensuring the continued productivity of the habitats that support these commercially important species.

The EHP, initiated a l989, focuses special attention on seagrass and saltmarsh-dominated wetlands, and linkages among these and other habitats, because of their importance to the production of living marine resources. Federal and state habitat managers need more quantitative information on the functional mechanisms by which wetlands support living marine resources. Managers need to know the location, extent, and rate of loss or modification of existing wetlands. Finally, managers need to know how to restore and/or create these habitats more effectively. Information on which to base management decisions must be easily available in the form of "...accurate maps depicting where

wetlands exist, [and]...information banks containing the results of research on the functioning of wetlands, and on restoration and creation efforts (Kean *et al*., l988)." Accordingly, the three basic and interrelated objectives of the EHP are:

1. To determine how coastal and estuarine habitats function to support living marine resources. This includes research on factors causing habitat degradation and loss, as well as on methods for habitat restoration.

2. To determine the location and extent of critical habitats and the rate at which these habitats are being changed or lost. This includes satellite, aerial photographic and surface level surveys to map habitat location and extent, and to determine change through time.

3. To synthesize the new and existing information in the form of mechanistic models of habitat function of use to managers in protecting, conserving, and restoring critical habitats.

Details on the specifics of the EHP research program elements are available from the U.S. Department of Commerce, NOAA Coastal Ocean Program Office, Washington, D.C. 20230.

While the initial effort of the EHP has been on seagrass and salt marsh habitats and their restoration, the EHP has organized workshops to bring scientists and managers together to provide recommendations on future directions of the research program. One such workshop was convened in St. Petersburg, Florida, in l989, to develop an outline on research and information needs on mangrove habitats in the U.S. The senior author of this paper (GWT) serves as the co-chairman of the Technical Advisory Panel of the Estuarine Habitat Program, and the co-authors of the paper (RRT, SCS, and PFS) served as academic and U.S. Federal workshop coordinators. Others who contributed to the workshop results and their affiliations are listed below:

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The following represents the recommendations group of scientists and managers to the NOAA Coastal Ocean Program's Estuarine Habitat Program should the EHP fund an effort directed at mangroves in coastal areas of the United States.

Recommendations to the NOAA Coastal Ocean Program's Estuarine Habitat Program for Research Directions on Mangroves

Introduction

Mangroves are a dominant wetland type in the southeastern U.S. They also are found in lesser amounts in other areas of the country and its trust territories. Collectively, four species (red, black, white, and buttonwood mangroves) comprise the "mangrove" forests.

These species singularly or in combinations occupy wide ranges in the coastal zone from regularly flooded tidal regimes to higher elevations that may receive tidal waters only several times per year or during storm events. In spite of their extent, the functional roles of mangroves in supporting primary and secondary productivity in coastal waters, while believed to exist, are poorly understood. Some roles are apparent (e.g., habitat afforded by red mangrove prop roots), but other attributes such as energy flow, linkages to fishery resources, water quality maintenance functions, etc., have been inadequately studied or remain undefined.

It is critical to understand what roles mangroves play in the environment and what products and services (e.g., fishery production, nutrient cycling, storm and wave attenuation) that the different mangrove habitats provide. This need arises because mangroves are under the same pressures as the more widely distributed salt marshes and seagrasses, i.e., direct loss or alteration of mangrove habitat by human development and indirect alteration from varied landward and seaward activities. In the last century many of the estuaries in the southeastern U.S. already have lost more than half of the mangroves that once existed. Mangroves are also a fragile habitat that can be lost to natural events. Examples include the destruction of mangroves in Puerto Rico and the Virgin Islands by Hurricane *Hugo* in 1989 and periodic freeze damage in Florida.

Losses of mangroves continue and efforts at conservation and replacement have met with variable success. Indeed, mangrove restoration projects are widespread; even though functional values of these projects in relation to natural forests are unknown and little follow-up has been accomplished to determine relative success. Current projections from global change research envision global warming and sea level rise that will contribute to great changes in mangrove forest acreage in the Gulf and southeastern U.S. in the next century.

Management and Research Issues

Mangroves occur along the coastlines of all Gulf coast states,Puerto Rico, and the U.S. Virgin Islands; small areas of introduced species are also present in southern California and in Hawaii. The largest regional area, encompassing some 250,000 hectares, occurs in south Florida. Whereas much of the total U.S. mangrove forest area is protected under the jurisdictions of parks, sanctuaries and refuges, this coastal resource is being progressively diminished by a variety of natural and anthropogenic actions. These include such phenomena as: **(1)** removal for coastal development, **(2)** deprivation of freshwater from upland watersheds, **(3)** severe freezes such as occurred in December of 1989, **(4)** clearing for charcoal production, **(5)** oil spills and water pollution, **(6)** competitive exclusion by exotic tree species, **(7)** illegal cutting or removal, **(8)** coastal erosion, and (9) mosquito control activities.

As a result of the progressive loss in vegetated area and in the corresponding functional diversity, the life support base for many nearshore fisheries is being increasing placed at risk. This occurs through the loss of physical habitat and the variety of food webs which are based on **1)** the enrichment and dispersal of mangrove leaf debris and dissolved organic matter and **2)** associated algal and phytoplankton production. This affects both nearshore pelagic and demersal fisheries, as well as a number of high-value benthic-feeding crustacean and mollusk species. Also at risk are the benefits that healthy mangrove vegetation provides through physical shoreline protection and the maintenance of nearshore water quality.

Whereas no direct measures (other than advance planning) can be taken to prevent habitat losses due to increasing climatic extremes and the projected rise in sea level, there are measures that can be taken on the basis of a much improved data and information base. This is based on the recognized fact that protective regulatory policies are best implemented when there is a factual basis. Accordingly, this report identifies a variety of actions and habitat alterations affecting the integrity of the mangrove ecosystem, and offers a priority listing of research initiatives to streng then the information base. This listing also includes an outline for the development of performance standards for mangrove restoration/creation projects, and a set of evaluation criteria for incorporation in the appropriate research projects.

Research Priorities

I. Food Webs

The prevailing paradigm regarding food webs of mangrove-dominated estuaries is that they are based on the processing of mangrove detritus, in the past focusing almost exclusively on whole leaves and large particulate organic matter (POM). Recent research indicates that the chemically-complex dissolved organic matter (DOM) may have equal ecological significance as POM, particularly at the microbial and meiofaunal levels. POM may serve as a source of rapidly-released soluble organics and ensuing flocculants utilized by microorganisms and small benthic feeders.

Large POM decomposition proceeds at a much slower rate following bacterial nitrogen fixation and fungal alteration of leaf and wood carbon compounds. In salt marsh estuaries, it

has been recently demonstrated that relative trophic importance of marsh grasses to filter feeders and higher trophic levels varied both along the length of the estuary and with the presence/abundance of other carbon sources such as algae or seagrasses. An analogous situation may exist in mangrove estuaries.

Objective 1: To determine the contribution of mangroves to estuarine secondary productivity relative to contributions from phytoplankton, benthic micro- and macroalgae, and seagrasses.

Demonstrating the linkage between mangrove primary production and secondary productivity is of high priority. Food web research needs to evaluate: **1)** the significance of DOM in sustaining an alternate food web based on heterotrophic organisms and provision of flocculants to benthic feeders, including chemical signature techniques to identify critical phylogenetic groups, environmentally induced shifts in those groups, and experimental feeding/growth studies using lower trophic level invertebrates; **2)** the distribution of higher trophic level organisms in various mangrove habitats in relation to gut content analyses; and **3)** the use of food web tracers such as stable isotopes.

II. Productivity/Structure

Little effort has been devoted to understanding the relationships between structural and functional attributes of mangrove communities and how these change during stand development. Canopy size, leaf biomass, stand density and biomass, assimilation products and production rates all vary over time and likely affect the quality and quantity of exportable materials. The relative roles of sediment characteristics such as salinity, sulfides, water logging, nutrients and bioturbation as factors influencing mangrove productivity are also poorly understood.

Objective 2: To assess the relationships between mangrove community structure, environmental factors and productivity.

Characterization of the dynamic nature of mangrove productivity is essential in determining the influence of mangroves on the productivity of adjacent coastal habitats. Research is necessary to address those factors controlling the internal structure and function of maturing mangrove stands. In addition, it is recommended that the Coastal Ocean Program's Habitat Mapping component develop protocols that will enable characterization of forest structure, successional status and type.

Mangroves are a subset of the suite of coastal primary producers, but they may directly influence primary and secondary productivity in adjacent waters. The proportional contribution of mangroves to the total primary production of any given estuary is poorly known, as is the latitudinal variation in proportional production in a range of mangrove estuaries. In addition, materials exported from mangroves may stimulate or reduce both primary productivity in adjacent habitats and faunal utilization.

Objective 3: To determine the relative contributions of mangroves, phytoplankton, benthic micro- and macroalgae, and seagrasses to estuarine primary productivity and how mangrove materials affect the productivity of adjacent waters.

Priority research will address: **1)** quantification of the rates of primary production of the plant community components within and among estuaries; **2)** mechanisms and overall effects of exported mangrove materials, such as nutrient enrichment, stimulation of regeneration, stimulation/ inhibition of aquatic primary productivity by lignins and tannins, increased faunal utilization of mangrove habitats, and how these are influenced by hydrological regimes; and 3) development and testing of a predictive model of the factors that control primary production in mangrove estuaries.

Objective 4: Determine ecological processes associated with recovery and succession of mangrove ecosystems. The restoration and creation of mangrove habitats depends on fundamental information concerning processes that control the recruitment and establishment of mangrove trees in coastal environments. There is very little understanding of the relative role of gap dynamics and edaphic factors as agents in growth and dynamics of mangroves. What are natural recovery rates of mangrove ecosystems following natural and human induced alterations? How can ecosystem regeneration be enhanced by site improvements such as seeding, removal of woody debris, and changes in elevation? What are the relative impacts of perturbations such as hurricanes, freeze, introduction of exotic species, and toxic materials on the succession of mangroves? The goal of this research objective is to establish construction guidelines for site improvements and initial conditions that will lead to specific successional patterns in restoration of damaged mangrove ecosystems. Mangroves are particularly vulnerable to damage from hurricanes including defoliation and uprooting. Recovery from hurricane damage in mangroves has been slower than upland forests. Changes in productivity and recovery patterns in different forest types must be documented and studied. Mangroves may be perturbation-dependent systems, yet this does not mean that natural regeneration occurs at rapid rates. What and how can these factors be manipulated to enhance recovery rate of mangroves damaged by hurricanes?

There are preliminary models of mangrove zonation and succession that may have application to the restoration of mangrove habitats. In addition, mapping efforts may contribute to long term understanding of successional patterns of mangrove vegetation.

Objective 5: To determine the significance of hydrology on successional patterns in mangrove habitats. Hydrologic trends should include both long-period climatic oscillations and large scale regional analyses.

Mangroves occupy environments subject to changes in water level which are dependent on balance of tides, upland runoff, river discharge and precipitation. Throughout the development of the stand, structural and functional characteristics are influenced or determined by hydrology. The close coupling of mangroves to other hydrologic units in the landscape suggests that alterations in regional hydrology may induce changes in mangrove vegetation and functional patterns. Mangrove areas in arid environments fluctuate in size as a response to soil salinity. Cyclic patterns in rainfall (periods of prolonged drought) have been cited as causal agents of massive tree mortalities.

III. Habitat Utilization

Past research on the importance of mangrove habitats for fishes and invertebrates has focused primarily on fringing red mangroves. Whereas the subtidal habitat of mangrove-lined tidal creeks and bays is relatively easy to sample, the densely vegetated intertidal habitats of red, black and white mangroves has prevented all but a few quantitative evaluations of fish and invertebrate usage patterns. This is particularly true of the poorly-researched white mangrove, which appears to have a lower salinity tolerance, a higher tolerance of anoxic sediments, high growth rates, large leaf litter production (fate unknown), and thus a well-defined niche in the mangrove community mosaic. Each habitat type may export DOM that generates chemical cues regulating the presence/absence and abundance of estuarine organisms and thus the predictable spatial and temporal patterns of marine life.

Determining the types and numbers of organisms that exploit these habitats, the functional aspects of habitat usage, and how mangrove carbon is transferred to higher trophic levels is critical. These data will permit analysis and modeling of the linkages between variations in mangrove productivity (natural and human-induced) and variations in faunal abundance, particularly of fishery organisms.

Objective 6: To quantify the direct utilization and ecological functions of man-grove habitats for estuarine fishes and invertebrates over a range of forest types and tidal/hydrological regimes.

Priority research will address: **1)** developing quantitative sampling methodology for various forest types and conducting intercalibration of methods; **2)** comparing spatial and temporal variation in habitat use by fishes and invertebrates, particularly in relation to critical water levels that permit access; **3)** comparing food/feeding ecology and refuge potential in each habitat; and **4)** contrasting these patterns and functions among mangrove, emergent marsh, seagrass and non-vegetated habitats.

IV. Nutrient cycling

Objective 7: Determine the function of mangroves in maintaining water quality of estuarine ecosystems.

Mangroves may influence nutrient dynamics and associated coastal ocean productivity by either removing or contributing primary nutrients to coastal ecosystems. The mass balance approach has been used to determine whether wetlands are either a source or sink of nutrients to the coastal zone. However, there are not published studies of nutrient budgets for mangrove ecosystems. The application of exchange techniques to determine the flux of nutrients in mangrove ecosystems should be investigated. The roles of burial and denitrification as processes associated with the fate of increased levels of nitrogen in the coastal zone are of particular importance.

The role of storms as mechanisms that redistribute nutrients and materials should be assessed. The pulsed nature of exchange should be evaluated as to influence on nutrient and organic matter dynamics of coastal ecosystems.

Objective 8: To determine processes associated with immobilization of nutrients within mangroves ecosystems such as microbial decomposition/enrichment processes and recycling.

The nutritionally important aspect of particulate litter decomposition is nitrogen enrichment, which is postulated to result from bacterial nitrogen fixation coupled with fungal alteration of leaf carbon compounds. Together with retranslocation of nutrients in the forest canopy, these processes provide primary nutrients for the productivity of mangrove ecosystems. These processes may be important relative to exchange in maintaining the fertility of mangrove ecosystems.

V. Restoration / Succession of Damaged Ecosystems

Objective 9: To determine the effectiveness of mangrove restoration/creation/mitigation projects in terms of mangrove community productivity and of faunal utilization patterns.

The effectiveness of restored management habitats in functional equivalency to undisturbed mangrove habitats is poorly understood.

The time frame for reaching natural growth and production rates has not been followed in these constructed mangroves, nor have the time courses for development of biogeochemical cycles and natural fish and invertebrate communities. There exist ample sites with documented restoration dates in which to conduct these multidisciplinary studies. Data gathered from these research sites can be used by management agencies in their review of habitat alteration proposals.

Objective 10: To determine effects of natural and human induced perturbations on microbial decomposition/enrichment processes.

Perturbations can alter microbial communities and processes; for example a shift from aerobic to anaerobic surface waters will eliminate fungal communities and promote bacterial anaerobiosis.

Therefore it is important to understand how different microbial communities function during decomposition/enrichment and to evaluate various perturbations, such as natural environmental changes, with the additive effects of toxic compounds and their breakdown products.

Objective 11: Assess the significance sealevel variations as factors contributing to successional patterns and loss of mangrove habitats.

Tidal amplitude and the slope of terrain determine the intertidal area available for mangrove establishment. Tidal flooding frequency and duration influence floristic, structural and functional patterns. Changes in tides include diurnal and seasonal water levels, semi-annual and 18.6 year variations, and long-term eustatic rise in mean sea level. The influence of these tidal variations on the structure and function of mangroves need to be determined in different geographical locations.

Objective 12: To assess impacts of anthropogenic contaminants. Important, expensive and being done by others, but needs to be covered.

VI. Synthesis/Modeling

Objective 13: To develop ecological models of mangrove ecosystems to evaluate the role of mangroves in coastal ecosystems Ecological models can be used in conjunction with field and laboratory approaches to obtain a better understanding of mangrove ecosystems. Models can be used to systematically conceptualize ideas about mangroves and thus are a way of hypothesis formulation and testing. Spatial models can address such questions as the fate and effect of exported material and how migratory organisms use mangroves. Also, ecological models of succession and associated ecological processes may assist in design of restoration efforts of damaged mangrove ecosystems.

Objective 14: To produce a synthesis of existing information on ecological processes of mangroves relative to the key management issues associated with these ecosystems.

Scientists and managers need to synthesize existing knowledge of ecological processes of mangroves that address key management issues of mangrove habitats. A document will be prepared to aid in the evaluation of impacts of proposed alterations to mangrove and estuarine habitats.

Prioritization of Research Objectives

Because the functional linkages between mangrove communities and other communities are poorly understood, we place the highest priority on topics which examine the functional role of mangrove communities in the coastal landscape. The role of mangroves in supporting coastal productivity, Objectives 1, 3, 5, 6, 7, 13, and 14, are particularly important.

Conclusions

This set of objectives addresses management information needs on this habitat type in the southeastern United States, and should provide a template for research proposals elsewhere as well. The Estuarine Habitat Program of NOAA's Coastal Ocean Program intends to use the results of this workshop to guide funding of mangrove research in the future, particularly in terms of their linkages with other estuarine and coastal habitats.

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Ecología y Manejo de los Manglares en la Laguna de Términos, Campeche, México

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Resumen

El presente capitulo concentra la información científica generada para los manglares de la Laguna de Términos, que son los mas representativos del Golfo y Caribe de México, presentando: **1)** aspectos de estructura y función que han sido generados desde hace 18 años por diversos investigadores; **2)** se señala su vínculo productivo con los ecosistemas vecinos (marinos y terrestres); **3)** las nuevas líneas de investigación sobre el valor económico de sus servicios ambientales; **4)** los distintos usos a que es sometido el mangle como árbol (en sus cuatro especies reportadas para México) aún con su estatus dentro de la NOM-059-ECOL-1994 de "Especies con requerimiento de protección especial", y que como ecosistema se localiza dentro de un Área Natural Protegida (Área de Protección de Flora y Fauna "Laguna de Términos"). Se incorpora la propuesta de tres grandes zonas de manejo de acuerdo a sus características principales de hidrología, edafológicas, estructura, función, valor económico integral (comercial y biodiversidad), y nivel de riesgo de impacto con el propósito de marcar algunas pautas de manejo que contribuyan a la protección, conservación, restauración y monitoreo ambiental de este ecosistema costero crítico.

Abstract

The present chapter concentrates the scientific information generated for the mangroves of the Terminos Lagoon, that they are the most representative of the Gulf and Caribbean of Mexico, presented: **1)** structure and function aspects that they have been generated from 18 years by various researches; **2)** is indicated their productive link with the adjacent ecosystems (marine and land); **3)** the new trends of research on the economic value of their environmental services; **4)** the different uses to the fact that is submitted the mangrove as tree (in their four reported species for Mexico) yet whith their status within the Mexican Official Norm NOM-059-ECOL-1994 of "Species with special protection requirement", and thet as ecosystem is located within a Protected Natural Area (Area of Faunal and Flower Protection "Terminos Lagoon"). It is incorporated the proposal of large three management zones according to their principal hydrology, edafologic, structure, function, integral

economic value (commercial and biodiversity), and level of impact risk characteristics, in order to appoint some managing standards that contribute to the protection, conservation, restoration and environmental monitoring of this critical coastal ecosystem.

Introducción

El conocimiento ecológico de una región es el elemento fundamental para la aplicación viable de técnicas y políticas públicas de manejo de los hábitats y recursos naturales críticos que busquen incidir en el horizonte del desarrollo sustentable de dicha región geográfica. Para este capítulo, se reconoce que en la zona costera del sur del Golfo de México, la interdependencia ecológica entre: la cuenca hidrológica del Usumacinta - los humedales costeros de Laguna de Términos y sus sistemas fluviolagunares asociados- Sonda de Campeche es necesaria de entender de forma integral para desarrollar estrategias en el manejo de los recursos naturales costeros.

El grado de vinculación a nivel de hábitats, causan gradientes físicos, químicos y biológicos evidentes que han sido observados, primero de forma separada y actualmente de forma holística, frente a las diferentes problemáticas ambientales de los efectos de las actividades antrópicas que inciden en este importante escenario ambiental, tales como: la pesca artesanal, la pesca industrial, la navegación interna y externa a la Laguna de Términos, la exploración, extracción y conducción de hidrocarburos, la agricultura y ganadería en tierras bajas incluyendo humedales, los asentamientos humanos (regulares e irregulares), la tala ilegal del manglar, desarrollo turístico, carreteras costeras y la protección de recursos naturales y hábitats críticos.

Es relevante señalar que el manglar presente en la región de la Laguna de Términos (127,000 ha) conforma al hábitat más representativo, el más estudiado del Golfo de México y Caribe Mexicano, y el de mayor riesgo de persistencia ante usuarios de alto impacto (PEMEX, taladores y productores de carbón, avance de la mancha urbana). Es por ello que en el presente libro se consideró pertinente desarrollar un capítulo específico de ecología y manejo de los manglares de la Laguna de Términos.

El presente capítulo se estructura en cuatro partes: **1**) En la primera, se da un síntesis, de la principal información ecológica generada para uno de estos hábitats críticos de la Laguna de Términos como lo es *el manglar*, objeto de este estudio. Se proporciona información sobre el conocimiento disponible del recurso a nivel de estructura, función y servicios ambientales, se describe el estatus de área natural protegida de la región de la Laguna de Términos que es la localidad de dicho ecosistema de manglar. **2**) La segunda, consiste en integrar los grupos más distintivos de estos hábitats, para posteriormente identificar su vulnerabilidad ante sus principales fuentes de alteración antropogénica y natural. **3**) En la tercera se presentan algunas posibilidades de cambio en el hábitat ante estas alteraciones y su impacto en la biota que se localiza en ellos (residentes, visitantes cíclicos, visitantes ocasionales) y; **4**) La cuarta fase se conforma con la propuesta de estrategias de manejo integral de este hábitat crítico.

Ecología

Inicialmente, se trabajó en conocer su entorno ambiental de los manglares, su estructura, distribución, abundancia y funcionamiento básico (Tablas 1 a 3), (Day *et al*.. 1982, Yáñez-Arancibia y Day, 1982, Ley Lou, 1985 y, Day *et al*., 1987, Day et al., 1996 entre otros). Posteriormente otros trabajos se enfocaron en identificar y dimensionar las entradas naturales de energía y la producción natural que resulta de los subsidios energéticos, el balance de masa de los nutrientes y la función de los manglares en el ciclo integral de los nutrientes en la zona costera (Day *et al*., 1988, Rivera-Monroy *et al*., 1995, Twilley y Day Jr., 1998 y Yáñez-Arancibia y Lara-Domínguez, 1999 en este libro). A principios de la década de los 90´s se inician estudios de valoración económica de los servicios ambientales del manglar para la región de la Laguna de Términos (Tablas 4 a 7). Posteriormente se han hecho estudios para conocer los servicios ambientales de este recurso ya que al ser considerado un recurso de acceso abierto en la frontera tierra-mar, sin registros, sin evaluación ni programa forestal y sin registro de la obtención de leña y carbón, el hábitat está siendo impactado sin conocerse cuantitativamente la dimensión del mismo (Yáñez-Arancibia *et al*., 1993 y Yáñez-Arancibia *et al*., 1995). Finalmente en cuanto a su normatividad, el recurso es protegido al clasificársele de acuerdo a la Norma Oficial Mexicana (NOM-059, 1994) como especies con “requerimiento de protección especial”.

Tabla 1. Parámetros estructurales pata bosques de manglar en tres localidades de la Laguna de Términos (modificado de Day *et al*., 1981 y 1988: Jardel *et al*., 1987 y Bárcenas *et al*., 1992)

sitio	especie	altura prom. del dosel (m)	densidad (ind/ha)	frecuencia (%)	área basal (m^2/ha)	diámetro medio (cm)	indice de complejidad	valor de importancia
Pom-Atasta		25					50.7	
	R. mangle		230	34.3	27.8	39.25		35.3
	L. racemosa		180	25.7	20.9	38.49		27.2
	A. germinans		110	22.9	0.8	30.59		17.1
	C. erecta		50	8.6	16.7	65.00		13.4
	P. aquatica		40	8.6	0.1	6.20		5.1
	Totales		610	100	66.5			100
Estero Pargo		6					31.5	
	R. mangle		4,591	61.1	12.9	5.1		57.0
	L. racemosa		5,574	34.3	9.5	6.5		38.0
	A. germinans		345	4.6	0.9	5.3		5.0
	Totales		7,510	100	23.3	-		100
Boca Chica		20					68.9	
	R. mangle		510	15.2	1.7	5.3		54.8
	L. racemosa		960	28.6	11.5	10.5		32.6
	A. germinans		1,890	56.2	21.0	8.6		12.6
	Totales		3,360	100	34.0			100
Boca Atasta	*R. mangle*			6				
	L. racemosa			19				
	A. germinans			66				
	C. erecta			9				
Laguna de los Negros	*R. mangle*			7				
	L. racemosa			92				
	A. germinans			1				
Estero de Bahamita	*R. mangle*			13				
	L. racemosa			14				
	A. germinans			64				
Isla Aguada	*R. mangle*			4				
	L. racemosa			1				
	A. germinans			95				

En relación a la superficie ocupada por manglar, ésta es de 127,000 ha (Terán y Santisbón en Yáñez-Arancibia *et al*., 1993). En cuanto a situación jurídica de a la región de la Laguna de Términos cabe señalar que desde 1994, ésta fue declarada área natural protegida de carácter federal con la categoría de Área de Protección de Flora y Fauna, con desarrollo de un plan de manejo que identifica a los manglares como hábitat crítico, situación que hace más obligados los estudios de evaluación y monitoreo del manglar, así como la necesidad de generar estrategias de manejo.

La necesidad de administrar y hacer uso racional con programación de inmediato, mediato y largo plazo de la zona costera y sus recursos naturales, determina que para la región de la Laguna de Términos, se planifique el uso de los mismos. Es por ello que el valor de que los manglares se hayan estudiado y monitoreado los factores ecológicos en estrecha relación con el entorno ambiental e influencia antrópica de la región, se magnifica y acelera la viabilidad de su manejo.

Un primer paso fue identificar los nueve diferentes subsistemas o hábitats críticos (Yáñez-Arancibia y Day, 1982 y Day *et al*., 1988). De entre ellos, los manglares tanto de tipo ribereño dominado por *Avicenia germinans* o mangle negro (localizados en parte del Sistema Fluvio-deltáico-lagunar-estuarino que comprenden principalmente las zonas de Pom-Atasta, Puerto Rico-Los Negros, Palizada-Del Este, Chumpán-Balchacah, Candelaria-Panlau) y por otro lado el como los de tipo de borde presentes en el litoral interno de las Isla del Carmen y la zona frontal del borde continental de la Laguna de Términos, que es caracterizado por *Rhizophora mangle* o mangle rojo.

Este hábitat crítico, como el resto de los hábitat que constituyen la región de la Laguna de Términos se encuentran bajo la influencia de las condiciones climáticas y eventos meteorológicos que caracterizan al sur del Golfo de México como la significativa precipitación con promedio de 1200-1600 mm y el fuerte aporte de agua dulce y material terrígeno (junio-octubre), los vientos del norte, que ya han sido

Tabla 2. Tipos de manglar de la Laguan de Términos, Campeche (modificado de Jardel *et al*., 1987)

Tipo	Localidades respectivas	Características	Clasificación de Lugo y Snedaker (1974)
I	Boca chica, Laguna y Estero de Lodazal, Laguna del Los Negros, Laguna de Pom-Atasta	Orillas de esteros, ríos y lagunas interiores con aporte de agua dulce y nutrientes; sobre sedimentos aluviales. Árboles altos (10-32 m) bien desarrollados y con fustes rectos. *A. germinans* dominante y en segundo término *R. mangle* y *L. racemosa*	manglar ribereño
II	Estero Pargo, Estero Bahamita, Isla Aguada, Boca de Sabancuy	Presente en barras arenosas. Costas y riberas de lagunas y esteros con marcada influencia marina. Sedimentos de origen marino. Árboles de 5-8 m de altura. *R. mangle* dominante en bordes y el interior *A. germinans*	manglar de borde
III	Bajos frente al Estero Bahamita, Boca del Estero de Sabancuy, Boca de Atasta, Boca de Pargos	Islotes de *R. mangle* formados por la colonización de bancos poco profundos, muchas veces consolidados por *Thalassia testudinum*. Inundados permanentemente. Árboles menores a 5 m de altura	manglar inundado
IV	Sur de Laguna de Términos entre Balchaca y Chacahito	Depresiones alejadas de ríos, con aporte de agua dulce por lluvias y escorrentía. Drenaje deficiente, suelos de textura pesada. *A. germinans* dominante y aparece formando rodales monoespecíficos. Densidad baja y árboles menores a 10 m de altura	manglar de cuenca
V	Centro de Isla del Carmen (transición con dunas costeras), canal de Ciudad del Carmen	Manglares arbustivos menores a 3 m de altura, formados por *A. germinans*, *R. Mangle*. Suelos arenosos bien drenados, exposición a vientos fuertes, escaso aporte de agua dulce, dan lugar a condiciones de aridez	manglar achaparrado
VI	Arrollo Canales, Río Palizada, Lagunas de San Francisco y El Vapor	Transición de manglar con pantanos de agua dulce. *R. magle* abundante forma un bosque de galería mezclándose con especies arboreas de selva baja inundable. Abundantes bromelias, orquídeas y lianas. Árboles de 5 a 10 m y hasta 25 m de altura	maglar ribereño

Tabla 3. Estimación de la producción primaria neta de las especies de manglar en Boca Chica y Estero Pargo (g/m^2/año). Datos de: Day *et al*., 1982 *; Jardel *et al*., 1987 **; Vera Herrera *et al*., 1991 [1]: Jimenez, 1994 [2]

Componente / Localidad	Boca Chica	Estero Pargo	Laguna de Los Negros	Bahamita	Isla Aguada
Crecimiento de madera	*	*	**	**	**
Avicenia germinans	802.3	73.1	328.5	226.30	365.0
Laguncularia racemosa	304.0	345.5	328.5	237.25	-
Rhizophora mangle	99.5	353.3	255.5	175.20	240.90
No identificado	0	0	219.0	164.25	321.20
Crecimiento Total de Madera	**1,205.8**	**771.9**	**1,131.5**	**803.00**	**927.10**
Hojarasca	*	*			
Hojas	880.8	594.2			
Flores y frutos	252.7	191.9			
Madera	118.4	48.0			
Hojarasca Total	**1,251.9**	**834.1**			
Biomasa leñsa (ton peso seco/ha)			217.48 [2]	141.27 [2]	182.53 [2]
Producción Primaria Neta Anual	2,457.7	1,606.0			
Producción de hojarasca anual estimada para toda la región de Laguna de Términos = 716,000 ton [1]					

discutidos a detalle por diversos autores (Yáñez-Arancibia y Day, 1982). Asimismo es preciso señalar que este subsistema constituye el mínimo nivel de información ecológica para un enfoque holístico en el manejo del ecosistema y sus recursos.

Para la Laguna de Términos es bien conocido que los hábitat crítico como el manglar y los pastos marinos significan la productividad y persistencia de biodiversidad ecológicamente significativa y de importancia pesquera.

Tabla 4. Parámetros físicos y económicos considerados par aestimar los costos totales y los ingresos totales de la actividad extractiva de madera de manglar en la región de la Laguan de Términos, Campeche (Yáñez-Arancibia *et al*., 1995) (**precios de 1994; 1 dólar = 3.5 pesos**)

Parámetros Físicos y Económicos	Cantidad	Unidad de Medida
Taladores de manglar para leña y carbón	205	individuos
Taladores de manglar para construcción	47	individuos
Taladores por lancha	4	individuos/lancha
Tasa de corte con hacha	7	árboles/individuo/día
Tasa de corte con motosierra	18	árboles/individuo/día
Días de tala de manglar por mes	4	días/mes
Costo de oportunidad de mano de obra en la zona	5,460	$ / año
Tasa de depreciación de la lancha	10	% / año
Tasa de depreciación del motor de la lancha	20	% / año
Tasa de depreciación del equipo de corte	20	% / año
Tasa de interés a plazo fijo	15	% / año
Costo de inversión de la lancha	17,000	$
Costo de inversión del motor de la lancha	10,200	$
Costo de inversión de la motosierra	3,500	$
Costo de mantenimiento del equipo	2,700	$ / año
Costo de lubricantes y combustibles por km (lancha)	1.7	$ / año
Distancia promedio recorrida por lancha /día de corte	15	km/día
Precio promedio de madera de mangle	136	$ / ton

Tabla 5. Valor de algunos usos directos de los manglares de la región de la Laguna de Términos, Campeche identificados por Yáñez-Arancibia *et al*., 1995 (precios 1994)

Usos	Producto total (ton/año)	Precio ($/año)	Ingreso total Anual ($/año)	Costo total Anual ($/año)	Ingreso neto ($/año)
Madera para carbón	14,760	136	2'007,360.00	530,300.00	1'477,060.00
Madera para construcción	2,256	204	460,224.00	142,140	318,084.00
Total	17,016		2'467,584.00	672,440.00	1'195,144.00

En cuanto a la superficie ocupada por manglares es de 127,000 ha, que asociada a la vegetación acuática emergente como el tular, popal, y carrizal, conforma parte importante de los humedales de Tabasco-Campeche que son una unidad ecológica que no debe ser fragmentada ni aplicar políticas de usos diametralmente opuestas si se quiere proteger a su biota que se distribuye ampliamente en dichos humedales.

La distribución del manglar de borde que rodea a la Laguna de Términos evidencia la dominancia de *R. mangle* dentro de la zona intermareal como parte de la interfase tierra-mar con predominancia de los procesos marinos, asociados a vegetación acuática sumergida de pastos marinos (*Thalassia testudinum*, *Halodule wrightii* y *Syringodium filiforme*) que se distribuyen principalmente en el litoral de la Isla del Carmen (externo como interno) y en las porciones y alrededor del litoral de las zonas este y sureste de la Laguna de Términos, con la presencia de sedimentos arenosos mezclados. En contraste en las zonas meso-oligohalinas como los sistemas fluvio-lagunares conforman la estructura ribereña donde para el caso de Términos predomina *A. germinans* (mangle negro) asociados a pastos emergentes como tulares-popales y carrizales (*Thypha* sp) y vegetación acuática sumergida de agua dulce (*Valisneria* sp, *Cabomba* sp entre otras). Con sedimentos lodosos finos.

Tabla 6. Valor del uso indirecto del manglar en la Laguna de Términos, Campeche, a a través de pesquerías de especies con diferente grado de dependencia ecológica con el ecosistema de manglar aplicando el modelo de Ruitenbeek (1992) (modificado de Yáñez-Arancibia *et al*., 1995). Precios 1er semestre de 1994

Pesquerías dependientes del manglar	Grado de dependencia β	Valor ($/ha/año)
Camarón	0.21	9,635.00
Ostión	0.28	185.00
Jaiba	0.11	71.00
Pargo	0.14	57.00
TOTAL		9,948.00

Tabla 7. Valores económicos de los bienes y servicios ecológicos primarios del ecosistema de manglar en la Laguna de Términos, Campeche anexando su método de estimación (tomado de Yáñez-Arancibia *et al*., 1995)

Servicio ecológico	Tipo de uso	Valor ($/ha/año)	Método de estimación
Madera para carbón	Directo	11.5	Ingreso neto
Madera para construcción	Directo	2.5	Ingreso neto
Pesquerías dependinetes	Indirecto	9,948.00	Función-producción-modificada
Hábitat crítico de especies en peligro de extinción	No-uso (conservación)	6.4	Valuación contingente
Servicio de filtrado natural de aguas residuales	indirecto	7,524.00	Costo alternativo

En cuanto a su impacto por parte del hombre, el problema de tala ilegal es significativo en la región de la Laguna de Términos, e incluso de 1991 a 1995 tuvo un incremento significativo y por ello es importante generar algunas propuestas de manejo del recurso.

En el caso de la Laguna de Términos, el estudio de los manglares ha pasado por las etapas de conocimiento: florístico, fisiológico, ecológico (Day *et al*. (1982), Yáñez-Arancibia y Day (1982), Day *et al*. (1987), y Day *et al*. (1988). - primero a nivel de estructura (Tablas 2 a 4) y posteriormente a nivel de función como hábitat crítico con localización estratégica en las fronteras funcionales con otros ecosistemas como lo son: el ecosistema marino el terrestre y el atmosférico (Figura 1), y posteriormente estudios del valor económico de sus funciones ambientales (Tablas 4 a 7), y desarrollo de los primeros modelos para aplicarse a su manejo (Seijo *et al*., 1994).

Grupos Distintivos y Vulnerabilidad

Aunque la diferencia entre manglares de borde y ribereños, en los parámetros de estructura, es pequeña, los valores son ligeramente más altos en los manglares ribereños de Boca Chica. Sólo la densidad de árboles es más alta para los manglares de borde (Estero Pargo) (Day *et al*. 1996). En relación a las medidas anuales del diámetro de los troncos permiten distinguir con base al análisis de siete años (Day *et al*., 1996), que *Rhizophora mangle* tienen el menor crecimiento en Estero Pargo, mientras que la tasa de crecimiento en *Laguncularia racemosa* se incrementan después de superar la capa de vegetación primaria indicando una preferencia por la luz solar directa.

Los valores más altos de crecimiento y producción total para las tres especies principales ocurren durante lluvias y los inferiores durante nortes con valores ligeramente más altos para Boca Chica.

Se estima la producción de hojarasca en los manglares de borde en 8.3 ton/ha/año. La producción de hojas en Laguna de Términos es de aproximadamente 716,000 ton/año.

En cuanto a sus características de salinidad en agua y suelo, en los manglares ribereños, la salinidad en agua varía de 0 a 5 ‰ y en suelo de 20 a 50 %. Mientras que en los manglares de borde varían de 20 a 40 ‰ , Mientras que en los

Figura 1. Áreas naturales protegidas (ecosistemas) en el Estado de Campeche, sur del Golfo de México

manglares de borde varían de 20 a 40 ‰ y para salinidades de suelo varían de 5 a 95 ‰. Las altas salinidades afecta la permeabilidad de la membrana o los procesos osmóticos de las plantas, por lo que es considerada como un factor de control en cuanto a la distribución de las cuatro especies de mangle (Vera-Herrera *et al*., 1991). Los registros de salinidad en el sustrato, de acuerdo a las evaluación de siete años (Day *et al*., 1996), permiten señalar que no se presentan cambios estacionales pero si fuertes diferencias espaciales de este valor.

Todo ello se ha analizado ya que la salinidad es considerada un factor importante para controlar la distribución de especies de manglar. En el caso de Términos no se han observado cambios estacionales significativos pero si fuertes diferencias espaciales.

Resultados preliminares de fitoplancton muestran que el agua drenada de manglares a bajas adiciones significativamente incrementa la producción. Y esto lo hace importante, particularmente en la época de secas (Rivera-Monroy *et al.,* 1995.

Aunque se conoce que los bosques de manglar tienen diferentes estructuras no es claro que haya diferenciación en las funciones ambientales asociadas a cada comunidad de manglar. Contestar esta pregunta es importante para el desarrollo de planes de manejo, así como para proponer estrategias diferentes para usar y conservar mangles de borde, ribereños y de cuenca.

Entendiendo que el desarrollo del manglar es controlado por la hidrología, fisiografía y el clima, el crecimiento y desarrollo del mangle es mejor donde los subsidios de precipitación, descarga de ríos y marea son grandes. La cubierta de manglar es más extensa en:

- Costa de bajo relieve con intrusiones profundas de marea;
- Regímenes macromareales que crean topografía adecuada y saltos de transporte, materiales y propágulos;
- Las zonas costeras con gran influjo fluvial que proveen nutrientes y crean ambientes de baja salinidad;
- Humedad o climas húmedos que mantienen substratos con bajas salinidades, generalmente donde la precipitación es más de 2,000 mm/año y sin una pronunciada estación de secas;
- Ambientes abrigados donde los manglares de raíces someras, sus semillas y los árboles están protegidos desde las raíces superiores por olas y corrientes;
- Áreas de sedimentos ricos que promueven la construcción de suelo y la ocupación por manglar. Los terrígenos son fuentes adicionales significativos.

Zonificación. Los principales patrones de zonificación antes señalados más la topografía y microtopografía existente en este humedal costero y la particular utilización por la biota del manglar, se distingue la siguiente Zonificación para los manglares en la Laguna de Términos (Fig.1):

1. Manglares de cuenca del complejo lagunar Pom-Atasta-Puerto Rico-Los Negros (Zona 1).

2. Manglares ribereños de los sistemas fluvio-lagunares localizados al sur de la Laguna de Términos y Estero de Sabancuy (Zona 2).

3. Manglares de borde, ubicados en el litoral interno de la Isla del Carmen y en su borde continental (Zona 3).

Esta zonación presenta diferente grado de vulnerabilidad tanto a las actividades antrópicas como a los fenómenos meteorológicos como frentes fríos y tormentas en época de nortes y tormentas y huracanes en épocas de lluvias.

La zona que presenta menor grado de vulnerabilidad al impacto de tormentas tropicales y huracanes es la *Zona 1* por su localización en una zona protegida en un complejo lagunar paralelo a la línea de costa, desarrollado en una planicie deltaica en entre el Río San Pedro y San Pablo y el Río Palizada, recibe los escurrimientos del Río San Pedro y San Pablo a través de un tapon artificial que se abrió en 1994 en época de lluvias fuertes. El bosque de manglar es un bosque muy maduro de alta estabilidad ecológica con el mayor Índice de Complejidad (Bárcenas *et al*., 1992), presenta los valores más altos de área basal y altura y los menores de densidad. Este bosque de manglar se ha estimado tener una edad promedio de 100 años (Twilley y Yáñez-Arancibia com. pers. y Bárcenas *et al*., 1992) (Cuadro 2). Por la ubicación del complejo lagunar y la distancia de comunicación con la boca estuarina de la Laguna de Términos, la influencia de la marea es la mínima de la región, lo que tienen que ver con el poco transporte de materiales. También se registra baja salinidad en el suelo que permite un mayor desarrollo estructural. También debe señalarse que esta porción de la región de Laguna de Término es la que registra el mayor nivel de precipitación (1,600-2,000 mm/año), aporte de nutrientes a través de escurrimientos del Río San Pedro y San Pablo y un poco del Río Palizada en temporadas de fuertes lluvias.

Por lo que respecta a su impacto humano, históricamente las poblaciones cercanas como Isla del Carmen, Atasta, Puerto Rico, Nuevo Progreso y Palizada han utilizado la zona para extracción de leña, caza y pesca en su ribera, posteriormente es a partir de principios de la década de los 70 que ocurren las actividades de Petróleos Mexicanos de exploración, comunicación conducción, y explotación, que han provocado desde tala del mangle hasta alteración de flujos por desarrollo de caminos y establecimiento de derechos de vía a lo largo de sus sistemas de distribución y conducción de gas y petróleo, alteración del hábitat de las Lagunas de Pom-Atasta, e impacto a la fauna por ruido y desplazamiento al establece sus instalaciones como la Estación de recompresión de Atasta y pozos actualmente abandonados como el de Xicalango y el futuro establecimiento de una Planta de Producción de Nitrógeno. Actualmente también en esta zona se realiza la principal actividad de tala para producción de carbón, situación que se agudizó a partir de 1990-1991 por el incremento en el consumo de pollos al carbón (Yáñez-Arancibia *et al*., 1994).

Zona 2. Estos manglares de manera natural se presentan más vulnerables a impactos de erosión marina, elevación del nivel medio del mar, oleaje de tormenta e impacto por huracán, así como impacto por avenidas o desborde de los ríos en situación de fuertes lluvias. La banda de manglar se ha ido adelgazando por estos efecto naturales, principalmente en la zona central de Chumpan-Balchacah (Fig. 1). El principal impacto antrópico aquí ha sido la tala de manglar, principalmente en la desembocadura del sistema fluvio-lagunar de Palizada-Del Este y el establecimiento de asentamientos (unifamiliares pero frecuentes) que hacen uso del manglar para construcción, leña y recientemente venta para producción de carbón en Isla del Carmen. Por lo que corresponde a la subzona de Sabancuy, su primer impacto fue antrópico al recibir el incremento del medio marino y la consecuente salinización de suelo por la apertura de una boca artificial en el Estero de Sabancuy. Posteriormente el principal impacto natural lo constituyó el huracán *Roxane* (1995) que parte de inducir salinización de suelo, indujo un impacto humano al destruir la carretera costera y obligar a reconstruir la carretera en zona más adentro. De manera crónica la elevación del nivel medio del mar tendrá también sus consecuencias ambientales sobre la distribución y recomposición estructural del manglar en esta Zona 2, que es la que presenta mayor riesgo de ser impactada por una actividad potencial como los es la camaronicultura en caso de no planificarse ambientalmente dicha actividad.

Zona 3. De manera natural ha recibido el efecto de la erosión marina, aunque en menor grado que la Zona 2, efecto del oleaje de tormenta. Pero el impacto humano ha sido mayor ya que ha ido siendo desplazado en sentido oeste-este por la mancha urbana y desarrollo industrial de PEMEX, cuyo efecto se puede apreciar en el 75 % de la longitud de la Isla del Carmen.

Cambio de Hábitat y su Impacto en la Biota

Zona 1. Dadas las características y riesgos ya señalados esta Zona 1 se considera que esta Zona presenta el riesgo de tener una significativa alteración en su función de hábitat crítico, particularmente en la porción norte del complejo lagunar de Puerto Rico-Los Negros-Pom-Atasta debido a varios procesos o programas asociados con el llamado desarrollo de la Península de Atasta; el primero es que ante las expectativas de desarrollo esa zona puede presentar impacto de: asentamientos humanos u obras de infraestructura industrial (plan de nitrógeno, planta despulpadora, producción de carbón, proyectos de acuacultura, y la consecuente facilidad de acceso para cacería (en terrenos antes no accesibles), todos ellos localizados en la zona periférica o zona de influencia a dicha Zona 1. Y aunque se desarrollan actividades alternativas no se deja de demandar carbón en la Isla del Carmen, situación que mantiene el nivel de tala aunque esté prohibida.

Con respecto al impacto a la fauna silvestre, Correa Sandoval y Luthin (1988), Ogden *et al*. (1988) y Correa Sandoval (1992), establecen la importancia de conservación de este hábitat crítico para las aves migratorias y en especial para la cigüeña jabiru (*Jabiru mycteria*), ya que esta especie utiliza las copas de los mangles de mayor altura para la localización de sus nidos. Para las aves migratorias acuáticas es importante el mantenimiento del la calidad de los cuerpos de agua del complejo lagunar y de su producción primaria y secundaria en donde la productividad del manglar tiene una importancia indirecta. De todo el sistema de humedal de la región de Términos, esta zona es la de menor accesibilidad y en consecuencia la biota tiene un buen corredor biológico que une manglar con las porciones de sabana hacia el Río Palizada.

Zona 2*.* La delgada franja de manglar es una zona de nivel intermedio de transformación en donde los efectos de las actividades de agricultura ý ganadería en zonas inundables se han presentado con mayor frecuencia. Son importantes lugares de descanso para las aves locales y migratorias como garzas, cormoranes,

pájaro bobo, gallineta, entre otras. De acuerdo a las tendencias a finales del siglo XX estos sistemas pueden verse impactados directamente por programas de desarrollo como camaronicultura.

Zona 3. Definitivamente esta zona es la de mayor presión humana y se estima que sólo los bordes de los canales o esteros comunicantes con el litoral interno de la isla del Carmen y los sistemas de islotes son los que resistirán dicho impacto a largo plazo sino se llevan a cabo programas de protección. Hasta el final de la década de los ochentas era factible encontrar ejemplares del venado cola blanca en esta zona, actualmente ya no. Sólo se han registrado aves locales y migratorias, murciélagos, reptiles como serpientes y cocodrilos y roedores silvestres que están siendo desplazados por ratas y ratones producto del avance d la mancha urbana.

Estrategias de manejo del recurso

Las estrategias de manejo del manglar en Laguna de Términos deben de atender dos vertientes: Una es con respecto al las presiones de impacto ambiental como ecosistema ante el cambio climático mundial y en particular la elevación del nivel medio del mar, mayor impacto de huracanes y disminución de precipitación pluvial. La segunda vertiente es la relacionada con la deforestación y alteración sus sistema hidrológico por parte de las actividades antrópicas y sus requerimientos de protección y conservación por la situación de arrea natural protegida de la región de Laguna de Términos agregada a la situación normativa de protección de las cuatro especies de mangle. Ambas vertientes de atención hacen que las estrategias de manejo del ecosistema de manglar sean obligadas y urgentes.

Acciones generales en toda la región

Monitoreo ambiental del ecosistema de manglar, evaluación periódica de sus principales características de: densidad, distribución, crecimiento, producción de biomasa, altura de los árboles, características del suelo (composición y salinidad), estado de salud del manglar, evaluación estacional de las condiciones climáticas prevalecientes.

Monitoreo Hidrológico: Análisis del sistema hidrológico prevaleciente en las tres zonas identificadas en este capitulo, valoración de la permanencia o modificación de los flujos de agua dulce principales (ante obras humanas o ante eventos meteorológicos)

Monitoreo de su valor de Hábitat: Para las tres zonas principales identificar y cuantificar el valor como hábitat de acuerdo a los grupos florísticos y faunísticos que se identifiquen en cada Zona (que se tendrán de acuerdo a los estudios de inventarios considerados en el plan de manejo del área protegida para los hábitat críticos.

Incorporación de las acciones de conservación y restauración del ecosistema de manglar de la laguna de Términos a las políticas publicas de crecimiento económico que se apliquen en la región, situación que idealmente debe de darse a través del plan de manejo (de corto, mediano y largo plazo) del área protegida.

Las características geomorfológicas asociadas con las obras humanas presentes en el Área Natural Protegida de Laguna de Términos, han influido de manera diferente a toda la superficie ocupada por manglar, es por ello que en el presente artículo se han caracterizado las tres Zonas ya discutidas, y estas diferencias hacen que también las estrategias de manejo del manglar puedan dividirse en generales y particulares de cada Zona.

La tala tiene que detenerse, desarrollar acciones de manejo de dicho hábitat crítico, que de acuerdo a lo antes descrito en este capítulo, se considera que pueden ser diferentes en las tres distintas zonas delimitadas en este capítulo. Dentro del Plan de Manejo del Área Protegida y su Componente de Investigación Científica se propone para el caso de los hábitat críticos como el manglar, la conformación de grupos de trabajo en relación a: **1)** el manglar (para valorar su fisiología, características de estructura, función y alteraciones ante procesos naturales y otros acentuados por el cambio climático), **2)** el recurso agua del cual depende el manglar (análisis de la cuenca hidrológica, volumen y su variación anual, calidad del agua, alteración del régimen hidrológico ante obras humanas); **3)** Flora y Fauna asociada al manglar; d) Análisis de influencia de actividades antrópicas presentes en la Laguna de Términos (deforestación, erosión, sedimentación, eutroficación; **4)** Desarrollo de normatividad a nivel de reglamento del área protegida y leyes estatales que fortalezcan y sumen a la normatividad federal para proteger el manglar.

Zona 1. Es la zona de mayor amplitud, donde se encuentra el bosque de mangle con mayor grado de madurez, en donde la mayor proporción de biomasa se queda dentro y donde se proporciona el mayor número de hábitats para la biota local y migratoria, así como por su localización y amplitud es la zona que presentan

mayor proporción de vínculos con los ecosistemas terrestre y estuarino. Por el lado de los servicios ambientales al hombre se tiene que: es la zona de mayor superficie para el proceso de fijación de CO_2; proporciona amortiguación a los eventos de inundación a las poblaciones asociadas al sistema lagunar Los Negros-Puerto Rico-Atasta-Pom; disminuye en este mismo sistema lagunar los procesos de azolve por terrigenos y se conforma como una eficiente trampa de contaminantes (pesticidas, fertilizantes) y contribuye con la mitigación a la calidad del agua en dicho sistema lagunar; proporciona áreas de caza para autoconsumo a los pobladores de la Península de Atasta y de la Isla del Carmen; proporciona material de leña y construcción en mayor proporción (por su abundancia, tamaño y por su localización) que las otras dos zonas.

En esta Zona PEMEX ha desarrollado parte del tendido de tubería de conducción de gas e hidrocarburos e incluso tiene zonas de exploración identificadas, y en su zona noroeste de influencia inmediata se construirá una planta de producción de nitrógeno que llevará implícito el tendido de tubería a la planta recompresora y a la zona marina de la Península de Atasta.

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El Manejo de los Manglares en el Pacífico de Centroamérica: Usos Tradicionales y Potenciales

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Resumen

En Centroamérica la zona costera se ha considerado tradicionalmente un sitio marginado y de escaso interés social y económico, los manglares no han escapado a esta visión marginal y el interés para estos sistemas ha sido poco. Los manglares, como muchos otros ecosistemas costeros, son altamente dependientes de procesos que ocurren fuera de las fronteras del ecosistema. De acuerdo a la experiencia generada en Centroamérica, en el manejo de pantanos pueden diferenciarse tres niveles de complejidad: el manejo regional, el manejo de área y el manejo de sitio. La cuenca del río Térraba, en la costa sur del Pacífico de Costa Rica es uno de los más grandes del país (4,766 km^2). La complejidad de la información requerida para el manejo de estas regiones involucra un considerable esfuerzo al planificar y reunir información. El manejo de un área de manglar involucra el planificación y utilización de un manglar específico y sus subsistemas asociados (canales, albinas, playones, pantanos). En estos convergen diferentes intereses y múltiples usos son posibles. Un área de manglar deberá ser zonificada de acuerdo a los usos potenciales que posea. Al zonificar, se deberá incluir en todos los casos, un área núcleo de protección absoluta. Esta mantendrá muchos de los servicios y funciones que en forma natural provee un ecosistema de manglar. Dentro de un manglar se podrán encontrar otras zonas cuyo uso potencial dependerá de las condiciones ecológicas y socioeconómicas dominantes. En términos generales éstas pueden resumirse de la siguiente manera: Zonas de uso forestal, Zonas de interés cultural, Zonas de estanques o salinas, Zonas de pesca y colecta de moluscos, Zonas de interés turístico y educación ambiental, Zonas de conservación de vida silvestre, Zonas para cultivos en suspensión y Zonas para la apicultura. El manejo de un sitio se refiere a las prácticas de manejo que se dan dentro de una zona específica de un manglar.

Abstract

In Center America the coastal zone has been considered traditionally a marginalized site and of scarce social and economic interest the mangroves have not escaped to this marginal scope and the interest for these systems has been little. The mangroves, as many other coastal ecosystems, are highly dependent of processes that occur outside of the ecosystem frontiers. According to the experience generated in Center America, the mangrove management can be differentiated three

complexity levels: the regional management, the management of area and the site management. The basin of the río Térraba, in the south coast of the Pacific of Costa Rica is one of the largest of the country (4,766 km^2). The complexity of the information required for the management of these regions involves a considerable effort upon planning and gathering such information. The management of an mangrove area involves the planning and utilization of a specific mangrove and their associated subsystems (channels, albinas, playones, swamps). In these areas converge different interest and multiples uses are possible. An area of swamp must be zoned according to the potential uses that possess. Upon zoning, must be included in all the cases, an core ara of absolute protection. This mantain many of the services and functions that in natural form provides to mangrove ecosystem. Within the mangrove can be found other zones whose potential use depends of the ecological and socioeconomic dominant conditions. In general that zones can be summarized in the following way: Zones of forest use, Zones of cultural interest, Zones of ponds or saline, Zones for fishing and mollusks collection, Zones of tourist interest and environmental education, Zones of wild life conservation, Zones for culture in suspension, and Zones for the apiculture. The managing of a site is referred to the management practices that are given within a specific zone of a mangrove.

Introducción

El istmo centroamericano posee una de las mayores longitudes de costa con relación a su área territorial. Por cada kilómetro de costa existen únicamente 80 km^2 de continente. Cualquier punto de su territorio se encuentra a menos de 200 km de distancia de una de las costas y cerca del 70% de su población vive a menos de 100 km de la costa.

A pesar de la relativa importancia de la zona costera en Centro América, ésta ha sido considerada tradicionalmente un sitio marginado y de escaso interés social y económico. Los manglares, como parte importante de la zona costera, no han escapado a esta visión marginal y el interés por estos sistemas ha sido poco. Este desinterés se evidencia en la escasa atención que los manglares del Pacífico de Centro América han despertado. Hasta hace pocos a os, el conocimiento científico sobre estas áreas estaba limitado a nociones de tipo taxonómico y biogeográfico.

En el campo de las políticas de manejo el panorama no es muy diferente. Los procedimientos que regulan la utilización de los manglares en el istmo son extremadamente laxos e indefinidos. Es así como diferentes instituciones reclaman exclusividad jurisdiccional sobre los manglares. Esta indefinición ha producido conflictos de intereses entre municipalidades, organismos forestales, cuerpos militares, instituciones de investigación y agencias de conservación.

La carencia de una cohesión administrativa se ve agravada por la falta de información sobre aspectos ecológicos, sociológicos, económicos y legales. La información requerida en el manejo de un área de manglar es de naturaleza claramente interdisciplinaria. De acuerdo a la experiencia generada en Centro América, en el manejo de manglares se pueden diferenciar tres niveles de complejidad: el manejo regional, el manejo de área y el manejo de sitio.

Manejo Regional

Los manglares, como muchos otros ecosistemas costeros, son altamente dependientes de procesos que ocurren fuera de las fronteras del ecosistema. Modificaciones en las descargas de los ríos que irrigan estos bosques, alteraciones en la calidad de estas descargas, o cambios en el régimen energético del estuario asociado, pueden afectar al ecosistema de manglar.

El manejo regional se entiende como la visión global que comprende a varias áreas de manglar, la zona costera adyacente y las cuencas hidrográficas que irrigan esas áreas de manglar. En esta perspectiva de manejo, el ecosistema de manglar forma parte de una red de ecosistemas encontrados en la región de análisis. Un golfo, una bahía o un gran complejo deltáico, generalmente incluyen varias unidades de manglar que conforman la región de análisis.

Las potenciales alteraciones que pueden impactar el ecosistema de manglar están fuertemente determinadas por los procesos que alteran las rutas de entrada de energía y materia al ecosistema. Las alteraciones producidas dentro de las cuencas hidrográficas asociadas a los manglares de la región, pueden alterar los suministros de nutrientes y agua dulce. Los manglares pueden también ser afectados cuando sedimentos y contaminantes son arrastrados a lo largo de la zona costera por corrientes de deriva litoral. Cambios en el nivel del mar pueden, a nivel regional afectar la distribución de los manglares. De esta forma ríos, mareas y corrientes litorales se convierten en los vectores principales de influencias exógenas a los manglares de la región. El olvidar la interdependencia de los ecosistemas puede resultar en problemas serios al implementar planes de manejo.

Existen casos evidentes de mal manejo regional en gran parte de los manglares del istmo centroamericano. Los pesticidas aplicados en las cuencas hidrográficas entran al sistema del manglar a través de la descarga de los ríos asociados. Las actividades agrícolas realizadas en las cuencas hidrográficas de la costa Pacífica de Centro América son por lo general muy intensas, la alta densidad poblacional de estas zonas y el abuso en la utilización de plaguicidas presupone un fuerte impacto de la contaminación sobre los sistemas estuarinos. Domínguez y Paz (1988) reportan significativos niveles de bioacumulación de organofosforados en diversos organismos estuarinos en los manglares de Jaltepeque, El Salvador. En este área se encontraron organofosforados (metil-ethil-paration) a concentraciones de 3.49 ppm en peces como *Pomadasys* sp. En moluscos comercialmente explotados (*Anadara* sp) se reportaron concentraciones de 4.30 ppm.

La cuenca del río Térraba, en la costa sur del Pacifico de Costa Rica es una de las más grandes del país. (4,766 km^2). Alrededor del 63% de la cuenca esta erosionada y cerca del 23% está considerada como seriamente erosionada debido a prácticas agrícolas, ganadería y deforestación. (Chong, 1988). El volumen de sedimentos en suspensión descargados por esta cuenca fluctúa entre 548,000 y 4,120.000 toneladas por a o. Debido a esta gran carga de sedimentos, los bancos de moluscos asociados a la boca del río Térraba y las poblaciones de peces se han visto afectados por el efecto de la carga de sedimentos (Chong, 1988a). Similares efectos negativos de un mal manejo de la cuenca hidrográfica asociada se da en otras regiones de la costa centroamericana. Tanto por su extensión como por el área de las cuencas hidrográficas asociadas, las regiones de la costa Pacífica de Centro América presentadas en la Tabla 1, requieren de un adecuado manejo regional.

La complejidad de la información requerida para el manejo de estas regiones involucra un considerable esfuerzo al planificar y recopilar la información. Una de las herramientas más útiles para el análisis de manglares a este nivel, son los sensores remotos. Las imágenes de satélite permiten inventariar y clasificar tipos de bosque, patrones de drenaje, patrones en el uso de la tierra, redes de carreteras y otros elementos. Esta información es utilizada para clasificar ecosistemas y definir las rutas de conexión entre los diferentes ecosistemas de la región (Benessalah, 1988). Este tipo de análisis ha sido empleado por el Instituto Geográfico de Panamá (Anguizola *et al,* 1990) para realizar un inventario de los manglares, a nivel nacional. El inventario fue basado en imágenes (1:250,000) del Landsat Multispectral Scanner (MSS) con una resolución de 50x50 mts. Para inventariar manglares y albinas asociadas se interpretaron compuestos de falso color de las bandas 1, 2 y 4 del MSS. Comprobaciones adicionales fueron hechas utilizando fotografía aérea, blanco y negro pancromático a escalas de 1:20,000 a 1:60,000.

Tabla 1. Regiones de manglar que por su extensión e importancia requieren de un urgente manejo a escala regional en la costa Pacífica de Centro América

Región de manglar		Área de manglar aproximada (km^2)	Ríos asociados
El Salvador	Bahía de Jaquilisco	180	Grande de San Miguel
Honduras	Golfo de Fonseca	470	Choluteca, Nacaome, Negro, Guascorán
Nicaragua	Estero Real	190	Tacomapa, Villanueva, Palo Blanco, Grande, Sauce, Olomega
	Crinto-Poneloya	100	La Barra, La Garita
Costa Rica	Golfo de Nicoya	150	Tempisque, Tárcoles, Barranca, Jésus Maria, Arajuez, Guacimal
	Sierpe-Térraba	170	Sierpe Térraba
Panamá	Golfo de Chiriquí	446	Pedregal, Chico, Chorcha, Tabasan
	Golfo de Montijo	235	San Pablo, San Pedro de Jesús, Angulo
	Golfo de San Miguel	464	Sabana, Balsas, Congo, Cucumate, Chucunaque, Tuira y Sambu

Figura 1. Ejemplo de la estratificación realizada en el Golfo de Fonseca, Honduras. R= *Rhizophora*, A= *Avicennia*, R/A= rodales mixtos, r= regeneración, 1m= rodal maduro, 4m= rodal bajo estrés, 2j= rodal joven, RA= *Rhizophora* de cobertura densa, AA= *Avicennia* de cobertura densa, RB= *Rhizophora* de cobertura media

Debido a limitaciones técnicas y económicas el uso de fotografía aérea es preferido en Centro América. Un inventario de los manglares de la costa Pacífica de Honduras fue realizado por la Corporación Hondureña de Desarrollo Forestal (COHDEFOR, 1987) basado en fotografía aérea, pancromática blanco y negro a escala 1:20,000. El inventario determinó un total de 46,710 ha de manglar, 14,240 ha de playones, 8,291 ha de estanques de camarón y 1292 ha de salineras en la región del Golfo de Fonseca. Además de realizar una zonificación de los diferentes tipos de cobertura se realizó un inventario forestal por estratos, con cálculos de volumen en los bosques de la región. En esta misma área se han realizado otro tipo de zonificaciones como el mapeo de áreas de pesca artesanal y hábitats de aves migratorias (AHE, 1985).

En Costa Rica, se han hecho comparaciones históricas sobre el cambio en la capacidad de uso de los manglares del Golfo de Nicoya, durante los últimos 20 años. Para ello se utilizaron fotos aéreas pancromáticas de varias escalas (Jiménez, 1990). La totalidad de manglares (15,173.6 ha) mas 976.7 ha de estanques (camaroneras y salineras) y 583.17 ha de albinas fueron inventariadas. El volumen total de madera en los bosques de manglar de la región del Golfo de Nicoya fue calculado en 557,050 m^3. Las pérdidas se han limitado a un 6.7% de la cobertura boscosa encontrada hace 20 a os (1,095.9 ha). La mayor parte de esta pérdida ha sido debido a la construcción de 632 ha de estanques y cerca de 350 ha se han perdido debido a usos tales como agricultura y urbanización. Un análisis adicional dentro de esta región fue realizado por Kapetsky *et al*. (1987) con el objeto de determinar el potencial de acuacultura asociada a la región del Golfo de Nicoya. En este estudio se utilizó programas de información geográfica (Earth Resources Aplications Software, ELAS) alimentados por datos de sensores remotos (Landsat Thematic Mapper) con comprobación de campo. Los datos sobre cobertura de manglares, tipos de suelos, redes de comunicación y electricidad, fueron utilizados para determinar las áreas aptas para diferentes tipos de prácticas acuaculturales en la región.

Un inventario forestal realizado en la costa Pacífica de Nicaragua (Departamentos de León y Chinandega) fue basado en información proveniente de fotografías pancromáticas blanco y negro. El análisis de las 10,600 ha de

manglares de esta región incluye el cálculo de áreas, coberturas por estratos, volúmenes forestales y además el análisis de aspectos socio-económicos de las comunidades asociadas. (Gutiérrez, *et al.*, 1990).

La mayor parte de la información obtenida a nivel regional esta orientada al inventario de la cobertura total y por estratos de los bosques de manglar, y sólo en algunos casos los análisis han incorporado otros aspectos como condiciones socioeconómicas o redes de comunicación. La visión integral en el análisis regional ha sido descuidada y la conexión de los manglares de cada región con otros ecosistemas y procesos ha sido olvidada. El desarrollo de lineamientos técnicos y legales para el manejo a nivel regional es sensiblemente deficiente en el istmo centroamericano. Debido a su trascendencia acciones a este nivel son prioritarias.

Manejo de Área

El manejo de un área de manglar involucra la planificación y utilización de un manglar específico y sus subsistemas asociados (canales, albinas, playones, pantanos). En estas áreas convergen diferentes intereses y múltiples usos son posibles (Tabla 2). Las actividades de índole productiva, de protección absoluta o aquellas que implican la conversión de sitios son, en muchos casos, incompatibles entre sí. Aún, entre las actividades productivas, se pueden dar casos de incompatibilidad. Por ejemplo, la corta de árboles para la extracción de carbón y corteza no es recomendable en zonas donde las poblaciones de moluscos de interés comercial son abundantes.

La presión de uso que muchas áreas de manglar soportan en Centro América es impresionante. Un ejemplo patente de esta situación es el manglar de la Barra de Santiago, El Salvador. La población de Barra de Santiago es actualmente de más de 2,800 personas. Este manglar está constituido de 2,000 ha, gran parte de ellas afectadas por un huracán. Cerca de 20 le adores se dedican a la extracción comercial de 400 m^3 de leña/año/leñador. Además, la población restante utiliza mayoritariamente el manglar como fuente de leña consumiendo anualmente alrededor de 12 m^3 de leña por familia. La fauna de la zona se ve también afectada. Los componentes faunísticos más explotados para fines de consumo y comercialización (Tabla 3) muestran claros síntomas de sobrexplotación. Según versiones locales, las poblaciones de punches (*Ucides occidentalis*) y conchas (*Anadara tuberculosa*), han declinado en talla y número en los últimos años. Las poblacioes de tihuacales (*Cardisoma crasum*) se encuentran en serio peligro de desaparecer del área (Aquino, 1982). Sin embargo, es posible encontrar en la Barra de Santiago aproximadamente 15 recolectores de punches, que regularmente extraen cada uno alrededor de 3 docenas de cangrejos por día. La extracción de concha (*Anadara* sp) está generalmente a cargo de mujeres que recolectan alrededor de 60 conchas por día. Alrededor de 250 personas se dedican regularmente a la extracción de camarones y pesca con atarraya, redes y cuerdas dentro del estero de Barra de Santiago. Además existe, un número indeterminado de pescadores ocasionales que provienen de otras zonas. Las principales especies pescadas incluyen lisas, meros, pargos, róbalos, jureles, oleatadas, sardinas, caites y bagres. Ocasionalmente se capturan garrobos (*Ctenosaura* sp) e iguanas (*Iguana* sp).

La fuerte presión que los manglares reciben en la costa Pacífica de Centro América es en gran medida resultado de las condiciones socioeconómicas imperantes. En los poblados asociados a los manglares de El Salvador la mayor parte de los pobladores viven en condiciones de pobreza muy aguda. Gran parte de las poblaciones carecen de servicios de salud adecuados y suficientes. El acceso a los centros educativos es difícil. En los poblados aledaños al Estero Jaltepeque, El Salvador, el 62% de las viviendas carecen de agua potable, servicio sanitario o energía eléctrica. Las viviendas en la mayor parte de los casos poseen un solo cuarto y en el 100% de los casos están construídas de palma o bahareque (Renderos *et al*., 1975). Los índices de alfabetismo y asistencia escolar son muy bajos y en la mayor parte de los poblados inferior al 36.3% (Yanes *et al*., 1990). En las zonas costeras de El Salvador se calcula que cerca de 24,000 familias dependen en algún grado de los manglares (Yanes *et al*., 1990). Estas familias, viven en la periferia de las áreas de manglar. Además de consumir leña y fauna se dedican a otras actividades tales como la agricultura, la producción de sal, y la crianza de animales domésticos (Yanes *et al*., 1990).

En el área de Sierpe-Térraba, Costa Rica, se encuentran cerca de 580 personas que directamente dependen de los recursos del manglar. En la mayor parte de los casos (89%) ellos viven permanentemente dentro o en la periferia del manglar. Las viviendas cercanas a los ríos y canales son construidas de madera y sobre pilotes. En las playas y sitios arenosos las viviendas son construidas de palma, y techo de lámina metálica. Sólo un 5% de ellas poseen piso y el 89 % de ellas poseen servicios sanitarios, aunque el 69% son letrinas. En esta área el 52% de las viviendas poseen un pozo de agua.

Tabla 2. Ejemplo de análisis descriptivo de dos áreas de manglar para determinar sus usos potenciales

Parámetro	Evaluación del parámetro	
	Isla del Encanto	**Borde del estero Tripa de Pollo**
Volumen de madera	422.1 m^3	369.4 m^3
Cant./ corteza aprovechable/ha	32 árboles= 100 quintales	12 árboles= 37.6 quintales
Extensión de área boscosa	100 ha	86 ha
Estado de regeneración natural	Reg. Inicial: 5.66 plantas de 01/ha 11.821 plantas de 04/ha Reg. Avanzada: 160 plantas de 01/ha 464 plantas de 04/ha	Reg. Inicial: 907 plantas de 01/ha 3.766 plantas de 04/ha Reg. Avanzada: 266 plantas de 01/ha 609 plantas de 04/ha
Intensidad de inundación de mareas	mareas mínimas de 12 cm de altura	mareas mínimas de 8 cm de altura
Canales con flujo de agua moderado	no existen	no existen
Planicies sin vegetación	existen	existen
Textura del suelo	franco limoso	franco limoso
Proximidad de la fuente agua	3 m	2 m
Fauna con valor alimenticio	no existe	no existe
Permanencia de las especies	residentes	residentes
Especies melíferas/ha	0	0
Tiempo de floración	abril-mayo-junio	abril-mayo-junio
Periodos de lluvia y sequía	lluvia: mayo-noviembre sequía: diciembre-abril	lluvia: mayo-noviembre sequía: diciembre-abril
Precipitación media anual	3,676 mm	3,876 mm
Número de meses secos	4	4
Belleza escénica	paisaje común, típico del área	paisaje de interés especial o sensitivo
Riqueza de ambientes	sólo especies de manglar	de manglar, helechos, y spp asoc.
Fauna asociada de valor recreativo	21 sp IAR: 23 ejemplares en 45’	24 sp IAR: 24 ejemplares en 45’
Accesibilidad del área	carretera transitable	carretera transitable
Facilidad de Transp. en el manglar	canales navegables	can naveg. y posibilidad de senderos
Proximidad de centros urbanos	30’ navegando con motor de 10 hp	25’ navegando con motor de 10 hp
Existencia de vegetación inalterada	veg. intervenida por el hombre	veg. intervenida por el hombre
Objetivos nacionales de conservación	entre otros: “mantener un estado inalterado a ciertas áreas…”	entre otros: “mantener un estado inalterado a ciertas áreas…”
Hábitats representativos de spp de interés científico, social o económico	no existen	no existen
Diversidad y representatividad de sp	21 sp no únicas en ambientes de maglar	24 sp no únicas en ambientes de maglar

El índice de analfabetismo es del 12% y la mayor parte de los niños de edad escolar asisten a las escuelas primarias. Son pocos los pobladores que poseen algún título de propiedad o concesión legal y sólo el 26% de los pobladores declaran tener derechos sobre sus terrenos. El 40% de los grupos familiares de la zona dependen de la captura de moluscos y agricultura de subsistencia, el 30% depende de la pesca y cerca del 17% dependen de la extracción de carbón y corteza. La extracción de oro y el turismo son otras actividades que se realizan en la zona. La renta *per capita* en la zona no supera los $570 anuales lo que representa un tercio del ingreso per capita promedio del país (Martín, 1988).

Tabla 3. Productos faunísticos extraídos del manglar de Barra de Santiago, El Salvador

Moluscos	Crustaceos
Curiles *Anadara similis*	Tihuacales *Cardisoma crasum*
Conchas *Anadara tuberculosa*	Punches *Ucides occidentalis*
Casco de Burro *Anadara grandis*	Jaibas *Callinectes toxotes*
	Jaibillos *Callinectesarcuatus* Camarones *Penaeusstylirostris* *Penaeusvannamei* *Penaeusoccidentalis* Camaroncillo *Trachypenaeus* sp

Tabla 4. Número de personas por actividad productiva asociadas a diferentes áreas de manglar en la costa Pacifica de Nicaragua

Número de Personas por Actividad			
Comunidad	**pescadores**	**leñadores**	**Concheros y puncheros**
Salina Grande	36	18	46
El Realejo	55	27	18
Rep. Fed. Alemania	4	64	32
Corinto	75	20	5
Las Peñitas	60	30	10
Poneloya	36	9	55
Los Brasiles	-	-	100
Producción y tiempo invertido en cada actividad			
Actividad	**Producción/día (kg)**	**Horas/día**	**Ingreso mensual $**
Pesca Costera	45	11	436
Pesca Estero	18.2	7	174
Leña	300 rajas	9	54
Concha	10 docenas *	7	54
Punche	5 docenas	7	36

$= dólares en diciembre 1990; *= peso promedio de una pingua comercial (40 gr) de los cuales el 18% representa el peso húmedo de la carne

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En Panamá los asentamientos humanos asociados a áreas de manglar son peque os. El

70% de ellos están constituidos por menos de diez viviendas. Los asentamientos se dan generalmente en una franja costera adyacente al manglar, o a las orillas de los canales. Mas del 40% de las viviendas analizadas poseen piso de tierra y el 70% de las viviendas carecen de energía eléctrica. En el área del manglar del Golfo de Montijo el 49% de las casas carecen de agua potable o letrinas, el 87% de ellas no tienen luz eléctrica (D'Croz *et al*., 1990).

En Nicaragua 30% de los pobladores que viven en la periferia de las áreas de manglar dependen exclusivamente de los manglares. Las actividades de producción en estas áreas (Tabla 4) son en algunos casos combinados con actividades como el cuido de casas de veraneo y la agricultura de subsistencia (Gutiérrez *et al.,* 1990).

Debido a la gran cantidad de usos potenciales dentro de un área de manglar y el posible conflicto entre algunos de ellos es necesario realizar una adecuada zonificación del área como paso inicial para su manejo. La mayor parte de los manglares de la costa Pacífica de Centroamérica han sido considerados tradicionalmente Reservas Forestales, bajo la administración de los cuerpos administrativos del estado a cargo de los bosques estatales. Sin embargo, algunas áreas de manglar son administradas por otras instituciones estatales encargadas de otro tipo de áreas como los Parques Nacionales o los Refugios de Vida Silvestre y están, por lo tanto, ubicadas en categorías de protección más estricta.

Un área de manglar deberá ser zonificada de acuerdo a los usos potenciales que posea. Al zonificar, se deberá incluir en todos los casos, un área núcleo de protección absoluta. Esta mantendrá muchos de los servicios y funciones que en forma natural provee un ecosistema de manglar. La extensión del área núcleo será función de la extensión total del manglar y de la presión de uso que éste posea. Esta zona, deberá incluir una sección representativa de las diferentes bandas de vegetación encontradas en el área (Vegetación Nuclear, Vegetación marginal, entre otras).

Dentro de un manglar se podrán encontrar otras zonas cuyo uso potencial dependerá de las condiciones ecológicas y socioeconómicas dominantes. En términos generales éstas pueden ser resumidas de la siguiente manera:

Zonas de Uso Forestal

Deberán incluir como mínimo sitios con volúmenes relativamente altos de madera y corteza. Además de cualidades de alta regeneración y la existencia de especies de interés comercial. La ausencia de gradientes pronunciados de salinidad intersticial en los sitios es necesaria.

Zonas de Interés Cultural

Incluyen sitios con edificaciones o remanentes de interés cultural o arqueológico. Muchas áreas de manglar en Centro América fueron intensamente utilizadas por comunidades indígenas. Basamentos y concheros son encontrados en los márgenes de canales y ríos o en sitios elevados dentro del manglar.

Zonas de Estanques o Salinas

Deberán buscarse zonas de albinas o helechales (*Acrosthichum* sp), las cuales deberán estar cerca de un canal para asegurar el suministro de agua con un alto nivel de calidad. El suelo deberá poseer una textura impermeable que asegure escasa o nula infiltración. Además los suelos deberán tener un bajo potencial de acidificación. El clima del área determinará si es posible practicar la producción de sal, a través de la evaporación solar. La existencia de caminos y acceso a la energía eléctrica son necesarios para el desarrollo de actividades de acuacultura.

Zonas de Pesca y Colecta de Moluscos

Estas zonas deberán tener una baja carga de sedimentos y ser sitios mesohalinos, con un bajo o nulo impacto de la explotación forestal. Sólo en áreas con presencia de *Rhizophora* o *Pelliciera* se logran encontrar poblaciones importantes de *Anadara* sp. Sitios con aguas de bajo contenido salino no son adecuados para la pesca comercial de peces. Al mismo tiempo una adecuada calidad del agua es necesaria, sobre todo en sitios donde se extraen moluscos filtradores.

Zonas de Interés Turístico y Educación Ambiental

La existencia de sitios con alta belleza escénica, gradientes pronunciados de vegetación que permitan observar una alta variedad de especies y la proximidad a áreas urbanas que provean servicios básicos para el turismo y la educación ambiental son requisitos básicos de este tipo de zonas.

Zonas de Conservación de Vida Silvestre

Estas zonas son importantes para la protección de sitios de anidamiento o forrajeo de aves, residentes o migratorias. Los sitios transicionales donde se mezcla la vegetación de manglar con otro tipo de vegetación, asi como las planicies fangosas son áreas donde se concentran gran cantidad de avifauna. Ambientes salobres representan hábitats importantes para poblaciones de reptiles.

Zonas para Cultivos en Suspensión

Estos sitios deberán estar protegidos de la influencia de vientos fuertes y poseer profundidades menores a los cinco metros. Los parámetros bioquímicos del agua (*v.g*. salinidad, calidad) deben ser controlados antes de iniciar actividades de cultivo en suspensión. Disponibilidad de alimento y ausencia de contaminación son aspectos importantes de evaluar en estos sitios.

Zonas para la Apicultura

En áreas con extensiones considerables de *Avicennia* o *Laguncularia* las actividades apiculturales pueden ser importantes. La existencia de una estación seca bien definida en el área es un factor importante. Rutas de acceso al sitio del apiario, suelos secos y bien drenados próximos al manglar son necesarios.

Poca información existe sobre la zonificación de un área de manglar en Centro América. En Costa Rica se dise ó una metodología de zonificación con el fin de alcanzar un manejo integral de un área de manglar (Sánchez, 1986). Esta metodología considera aspectos como extracción forestal, protección de vida silvestre, acuacultura, pesca, recolección de moluscos y turismo. La metodología indica los pasos necesarios para determinar los usos potenciales de un área de manglar y los análisis requeridos para determinar la factibilidad de explotar esos recursos. Mediante la utilización de matrices cualitativas se determina la compatibilidad de los diversos usos potenciales y la capacidad de uso de un área de manglar (Tabla 5).

Además de incluir aspectos biofísicos, el análisis de las actividades a realizarse deberá involucrar la valoración de aspectos socio-económicos antes de decidir el uso de cada sitio. Algunas actividades que implican la conversión de áreas de manglar o ambientes asociados (*e.g*. albinas, playones, helechales, etc.) representan además de un impacto ecológico, un impacto socioeconómico considerable dentro del área. El caso típico de este problema es la construcción de estanques para el cultivo del camarón. Esta actividad puede representar la destrucción de considerables extensiones de manglar dentro de un área. Un ejemplo ya clásico de este impacto fue la operación de una granja de camarones en el Golfo de Nicoya, Costa Rica (Webber y Webber, 1978). Para esta granja se utilizaron varios cientos de hectáreas de bosques de *Rhizophora* sp para la construcción de estanques. El impacto de la acidez generada por el disturbio de los suelos del manglar, afectó negativamente la operación de acuacultura y la llevó a la quiebra en pocos años.

El impacto ecológico, en este caso fue evidente, pero el impacto socioeconómico en el área no fue analizado. El área afectada fue desprovista de cientos de hectáreas de manglar que anteriormente proveían de leña, carbón, moluscos y pesca a los poblados adyacentes y fue sustituida por planicies deforestadas de poco valor ecológico.

Dichosamente, debido a estas y similares experiencias en otras partes del mundo, las empresas camaroneras han buscado ubicar sus estanques en áreas adyacentes al manglar, donde el impacto ecológico es menor. De las 20,000 has ocupadas por la industria camaronera en el Golfo de Fonseca, Honduras, más del 95% de ellas fueron construidas en albinas desprovistas de vegetación. Estos ambientes son de baja productividad e importancia ecológica. El impacto socio-económico, en este caso, ha sido relativamente menor. De las 20,000 has citadas, sólo 721.5 has (3.6%) eran bosques de manglar y 133 has (0.66%) eran playones dedicados a la pesca artesanal (Wainwhright, 1989).

Mientras el impacto ecológico de las camaroneras tiende a disminuir, su potencial impacto socioeconómico debe ser evaluado. Un potencial impacto socioeconómico de la industria camaronera es el desplazamiento de peque os operarios o cultivadores artesanales. Estos grupos tienen escasa capacidad de inversión y generalmente no poseen títulos de propiedad o concesiones debidamente legalizadas. Las grandes empresas camaroneras, por el contrario, son llevadas a cabo por grupos política y económicamente muy influyentes. Este tipo de empresa es intensiva en capital y no en mano de obra; al alcanzarse la fase de operación de los estanques las actividades de cultivo no representan una fuente de trabajo importante para la zona. McCoy (1979; citado por Bailey, 1988) calcula que en Panamá 20 ha de estanques pueden ser operados por una persona y un gerente. Solo durante las épocas de cosecha se aumenta la demanda por mano de obra. De esta forma se reducen las alternativas locales de producción y se aumenta la dependencia de los trabajadores con trabajos estacionales y labores no especializadas de baja remuneración (Bailey, 1988).

La importancia de los productos forestales ha influido fuertemente el enfoque de los planes de manejo en áreas de manglar. En la mayor parte de las áreas donde se ha dado algún tipo de inventario o zonificación, el análisis ha sido puramente forestal. Lamentablemente sin el enfoque de uso múltiple en este tipo de estudios. La principal información obtenida se refiere a la cobertura de manglares y a veces la composición de géneros dentro del área de manglar.

Tabla 5. Matriz de compatibilidad entre diferentes usos potenciales en un área de manglar

usos	usos	Aprovechamiento forestal	Acuacultura		Pesca y caceria	Prod. Estacional de miel	Producción de sal		Educación recreación y turismo	Conservación *in situ*
			Sist. flotantes	estanques			Sal cocina	estanques		
Aprovechamiento forestal		-	1	0	2	1	2	0	1	0
Acuacultura	Sist. flotantes	1	-	0	2	2	1	0	1	1
	estanques	0	0	-	1	0	1	1	0	0
Pesca y caceria		1	2	1	-	2	1	1	1	0
Prod. Estacional de miel		1	2	1	1	-	1	0	2	2
Producción de sal	Sal cocina	2	1	1	1	1	-	1	1	0
	estanques	0	1	2	1	0	1	-	0	0
Educación recreación y turismo		1	1	0	1	2	1	0	-	2
Conservación *in situ*		0	1	0	0	2	0	0	2	-

0= usos totalmente incompatibles; 1= usos ocasionalmente compatibles; 2= usos totalmente compatibles

Un intento somero de realizar un plan de manejo integral de un área de manglar ha sido desarrollado en Costa Rica para el manglar Térraba-Sierpe (Chong, 1988b). En este documento se ofrecen directrices detalladas para el manejo forestal de esta área de manglar incluyendo además directrices para actividades como la extracción de moluscos, la acuacultura, apicultura, turismo, pesca y manejo de vida silvestre. De acuerdo a la zonificación realizada mas de 2,600 ha de este manglar son aptas para el manejo de poblaciones de moluscos (*Anadara* sp). Sin embargo, la falta de recursos financieros y técnicos impide la implementación de estos planes.

En la mayor parte de los inventarios y planes de manejo de áreas de manglar, la interpretación de fotografía área pancromática, blanco y negro ha sido la herramienta principal. Con esta técnica se han podido clasificar áreas de manglar de acuerdo a su composición genérica (*Rhizophora* y *Avicennia*) utilizando el tamaño de copa, el tono y la altura del dosel (Jiménez, 1990). Un conocimiento regular de la ecología y distribución espacial de las especies en el área es muy útil durante el proceso de fotointerpretación.

El manejo de áreas de manglar en Centro América es apenas incipiente. En Costa Rica el manejo de los manglares del Térraba-Sierpe se ha venido dando a través de concesiones otorgadas a grupos organizados. Un grupo trabaja en la extracción de moluscos (*Anadara tuberculosa*) y la pesca mientras otro grupo trabaja en la explotación de subproductos forestales: le a, carbón, corteza y postes. Las concesiones se otorgan por períodos de varios a os y el control de las actividades es realizado a través de inspecciones periódicas. La implementación de planes de manejo es, sin embargo, nula. Los beneficiarios extraen el producto sin seguir directrices técnicas y basados más en su capacidad de extracción y la demanda del mercado. En otras zonas del istmo la explotación del manglar está regulada mediante permisos otorgados a individuos. Estos permisos indican el volumen de leña o madera que puede ser extraído. Sin embargo, el control sobre la cantidad real extraída es muy deficiente en la mayor parte de los países.

Los planes de manejo están ausentes aún en la mayoría de aquellas áreas con fuertes presiones de uso. La generación de lineamientos técnicos que involucren criterios socioeconómicos y la promulgación de legislación que regule las concesiones y permisos de extracción son acciones urgentemente necesitadas en los manglares de Centro América.

El desarrollo de programas de educación ambiental y educación técnica dirigidos a las comunidades adyacentes al área de manglar es una forma efectiva de mejorar el manejo de un área.

Manejo de Sitio

El manejo de un sitio se refiere a las prácticas de manejo que se dan dentro de una zona específica de un manglar. Pueden ser prácticas de aprovechamiento forestal, recolección de moluscos o medidas de protección de un sitio particular dentro de un manglar. La información requerida es mas detallada y específica.

Como en el caso del manejo de área, la experiencia en manejo de sitios en Centro América ha sido fundamentalmente forestal. El Salvador fue uno de los primeros países en realizar prácticas en manejo de sitio. En 1969 se hicieron cortas experimentales en varias parcelas dentro de los manglares de Bahía La Unión, en la Bahía de Jiquilisco y en el Estero Jaltepeque. El manejo de las parcelas consistió en talas razas en las cuales se dejaron 40 árboles por hectárea como “semilleros”. Los rendimientos por hectárea en estas cortas varió entre 80 y 220 m^3/ha. La regeneración de las áreas intervenidas fue muy satisfactoria con densidades de hasta 12,000 plántulas/ha. Con base en esta información se diseñó un Plan de Manejo Forestal con cortas rotativas y un ciclo de corta de 20 años. Este plan, sin embargo, no llegó a implementarse (Dirección Recursos Naturales, 1972).

En Nicaragua se realizó un inventario forestal (IRENA, 1986) dentro de un sitio de aproximadamente 100 ha denominado estero Canta Gallo. Se determinó para este sitio un volumen total aprovechable de 4,719 m^3. Se construyó, además, una tabla de volumen para *Rhizophora* sp siguiendo la fórmula:

$$V_{tcc=} \mathbf{10}^{-4.91796} \times DAP^{2.70} \times Alt.^{1.08757}$$

Donde: V_{tcc}= volumen total con corteza en m^3, DAP es diámetro a la altura del pecho en cm y Alt. es la altura total del árbol en m. Este inventario, fue el paso previo para un plan de manejo que sin embargo, no se llevó a cabo.

En Costa Rica se elaboró, un plan de manejo forestal para un sitio de 296.4 ha (Playa Garza) dentro de la Reserva de Manglar Térraba-Sierpe (Chong, 1988a). El Plan estaba orientado básicamente a la producción de madera para carbón. Basado en fotointerpretación de fotografía aérea blanco y negro pancromática (escala 1:20,000) se cartografió y se realizó un inventario forestal del sitio de estudio. La sección con bosque aprovechable se dividió en 85 franjas entre 1.5 y 2.6 ha cada una. Cerca de 15.5 ha fueron designadas como área de protección en los márgenes de los canales. Se calculó un rendimiento total para el sitio de 29,644 m^3 con

18,467 m^3 de *Rhizophora* sp y 11,166 m^3 de *Pelliciera rhizophorae*. El rendimiento periódico promedio, según una rotación de 25 años, fue calculado en aproximadamente 1,185.0 m^3/año. En este caso, la implementación de este plan de manejo tampoco se llevó a cabo.

El manejo de sitio en los manglares de Centro América, no ha logrado alcanzar altos niveles técnicos. Las actividades de producción son llevadas a cabo con técnicas rudimentarias y poco eficientes. La mayor parte de los sitios que están siendo utilizados no poseen un inventario o una planificación adecuada. Aún para aquellos que cuentan con inventarios y planes de manejo no se ha logrado la implementación de los planes elaborados.

La participación de grupos locales organizados es un elemento importante en el manejo de un sitio. A través de este grupo se logra una mejor difusión de los criterios técnicos necesarios para el manejo así como una mejor planificación y control de las actividades productivas. Al mismo tiempo los beneficios del manejo se distribuyen directamente entre los pobladores locales de las zonas adyacentes.

Descripción de las Principales Actividades Productivas en la Región

Las actividades de aprovechamiento forestal en los diferentes sitios son las más comunes y pueden ser orientadas a varios tipos de productos. En muchas áreas de manglar de Costa Rica y Panamá el aprovechamiento del recurso forestal está dirigido a la producción de carbón. El carbón de manglar es de muy alta calidad, con un poder calorífico de 7.46 mil kcal/kg. Como punto de comparación el bunker (Gfuel OilH) tiene un poder calorífico promedio de 10.2 mil kcal/kg. La producción anual de carbón en los diferentes sitios es considerable. En los manglares de Chame y Azuero, en Panamá, se producen un total de 118,200 sacos/año (7,448 m^3) de carbón (D'Croz *et al.*, 1990). En los manglares de Térraba-Sierpe, Costa Rica se producen alrededor de 19,500 sacos/año de carbón (1.227 m^3)

La demanda por carbón de manglar es generalmente insatisfecha. Esto se debe principalmente a la carencia de tecnologías adecuadas de producción y adecuados planes de manejo que resulten en una producción sostenible y continua.

La producción de carbón, en la mayoría de los sitios, se realiza en hornos artesanales de tierra Estos hornos se alimentan con trozas de madera generalmente de 5-20 cm de diámetro y hasta 1,0 metro de longitud, las cuales son cortadas con hacha o sierra eléctrica. La extracción de la madera se hace manualmente, sin utilización de cables, *winches* u otros aparatos. La madera es llevada a tierra firme en botes o cayucos.

Los hornos generalmente usados en la costa Pacífica de Costa Rica son excavaciones de un largo variable (5-12 m), un ancho de 1.7 y una altura de 0.75 m. La fase de quemado dura de 8 a 9 días. Los rendimientos de estos hornos son relativamente bajos, debido a deficiencias en el manejo de la producción. Por ejemplo, la madera que alimenta los hornos es recién cortada y con corteza, lo que provoca que una parte importante de la combustión se emplee en secar la madera húmeda. En los hornos empleados en el delta Térraba- Sierpe, Costa Rica los rendimientos son de aproximadamente 11.9% en peso promedio (Chong, 1988a).

Alternativas más rentables de producción están siendo exploradas en manglares de Costa Rica. De acuerdo a resultados preliminares la construcción de hornos tipos casamance (Fig. 2) representan una alternativa muy simple y económica. Las pruebas realizadas por nuestro Laboratorio en los manglares del Sierpe-Térraba reflejan un mayor rendimiento de estos hornos (25% en peso promedio), utilizando madera descortezada y rajada. Este sistema aprovecha el flujo de aire caliente, generado en la combustión, para ir secando la madera apilada. De esta forma se invierte menor combustión en el secado de la madera. Otra alternativa de mayor inversión es la construcción de hornos tipo colmena. El modelo más recomendado es el de 3 m de diámetro, el cual, requiere alrededor de tres mil ladrillos para su construcción (Fig. 3). Este tipo de horno posee una capacidad de 12 m^3 y produce entre 850-1000 kg de carbón por ciclo. El ciclo de quema es de aproximadamente 8 días.

El horno de ladrillo puede ser desarmado y transportado a otro sitio y posee una vida útil de aproximadamente 10 años. Una ventaja adicional de este tipo de horno, es que se le puede adaptar un condensador a la chimenea (Fig. 3) y a partir del humo generado en la combustión, obtener residuos piroleñosos (acetona, ácido acético, alquitranes, etc). Alrededor de 50 galones de piroleñosos se pueden obtener en un ciclo de quema de un horno de 12 m^3 (ICAITI, 1984). Con este tipo de hornos el costo de la inversión puede ser cubierto en 3 meses.

Sitios óptimos para la producción de carbón deberán estar localizados cerca de donde se ubiquen los hornos; los cuales a su vez deberán tener un camino de acceso permanente para sacar el producto. Los sitios de corta deberán estar dominados por rodales de *Rhizophora* sp

Figura 2. Horno tipo casamance recomendado para mejorar el rendimiento de las carboneras tradicionalmente con baja inversión

Figura 3. Horno tipo colmena con el detalle del condensador utilizado en la extracción de piroleñosos

con volúmenes superiores a los 150 m^3/ha y diámetros promedios de rodal (*sensu* Cintrón, 1984) cercanos a los 20 cm. Los sitios con suelos consolidados favorecen la extracción del producto.

Los subproductos forestales de más demanda en los manglares de Centro América son la le a, madera, postes y otros usos similares. En el Pacífico de Honduras se extrajeron durante el periodo 1983-1989 un total de 34,200 m^3 de leña y 5,340 m^3 de madera (Wainwhright, 1989). Según esta fuente el 85% de los hogares del Golfo de Fonseca utilizan la leña como fuente energética. Además, las panaderías, ladrilleras, salineras y fábricas de cerámica utilizan la leña como fuente de energía. En El Salvador, la leña para fines domésticos es de gran importancia. El 97.5% de los volúmenes de leña comercializados son consumidos para este fin (Matus, 1990). En Nicaragua se reportan valores de extracción de 9,000 m^3/año para leña, 4,000-7,000 m^3/año para postes y 5,000 m^3/año para madera (Jiménez, 1988). En Panamá la venta de leña de realiza en forma de astillas. El mercado nacional demanda alrededor de 2 millones de astillas por año (equivalente a 1,000 m^3 de madera/año.). Se extraen además 266,000 varas utilizadas en el cultivo de hortalizas lo que representa un volumen de cerca de 16,100 m^3 y se extraen alrededor de 8.780 vigas para construcción que equivalen a cerca de 1.895 m^3 de madera. (D'Croz *et al*., 1990).

Otro de los usos ampliamente difundidos del manglar es la extracción de corteza. La corteza de *Rhizophora* sp contiene altas concentraciones (17-28%) de taninos del tipo condensado (catecoles). Al no ser descompuesto por fermentos este tipo de tanino es muy adecuado para la tinción de cueros.

La explotación de la corteza de *Rhizophora* sp es ampliamente practicada en la costa Pacífica de Centro América. En Honduras se extraen anualmente alrededor de 125,000 kilos/año (Wainwhright, 1989). En Panamá se extraen anualmente alrededor de 437,000 kilos de corteza, explotados principalemete en el área de Chiriquí (D'Croz *et al*., 1990).

Las existencias de este recurso son considerables en la mayor parte de los manglares de la región. En el Golfo de Nicoya, Costa Rica se estima que existen alrededor de 4,100 ha aprovechables para la extracción de corteza. Los volúmenes estimados de corteza en esa región son de 1.840-4.490 kilos/ha (promedio= 2.828 kg/ha; Jiménez, 1990).

Los métodos de extracción de corteza son rudimentarios. La extracción se hace a partir de árboles de diámetros mayores a los 30 cm. El volumen total de corteza (en m^3) en árboles de *Rhizophora* está dado por la relación:

$$\ln(y) = -853377 + 1.89727 \ln(x)$$

donde x es el diámetro del árbol en cm. En árboles mayores de 30 cm de diámetro el volumen de corteza utilizable es más del 85% del volumen total de la corteza (Chong, 1988). La conveniencia de utilizar árboles de más de 30 cm de diámetro representa un fuerte impacto dentro del bosque, pues son los árboles más grandes los que son utilizados. Al mismo tiempo, esto conlleva problemas de manejo del sitio pues los ciclos de rotación utilizados para la producción de corteza serán más largos que los utilizados para la producción de carbón. Idealmente se deberían utilizar parcelas que pudieran producir carbón y corteza simultáneamente.

La demanda de corteza de mangle, ha venido disminuyendo notoriamente en los últimos años, en la mayoría de los países del istmo. En la industria del cuero se ha venido sustituyendo el uso de la corteza del mangle por el de los extractos de taninos importados. Estos extractos, a pesar de su elevado valor son más rápidos y eficientes en la tinción del cuero. La principal causa del aumento en la importación de taninos es el deficiente procesamiento de la corteza de mangle. En el proceso de tinción con corteza de mangle no se utiliza el extracto de tanino sino la corteza en bruto; la cual es groseramente molida y colocada en una pila con agua para que el tanino se disuelva. La tecnología para la extracción de taninos de la corteza de mangle es relativamente sencilla y su aplicación una potencial alternativa para los mangleros del litoral. Curiosamente, la producción de extractos de taninos de la corteza de mangle se realizó hace algunas décadas en Honduras, en el área de San Lorenzo. Aquí se hacían maceraciones de la corteza, extracciones y condensaciones del extracto. Existía en esta zona una capacidad de producción de 60 toneladas métricas de extracto/mes a partir de 450 toneladas de corteza (Prats, 1958). Desafortunadamente, la técnica no ha sido difundida a otras áreas y de no renovarse la tecnología esta actividad se verá desplazada por la importación de taninos en forma de extracto.

La extracción de recursos faunísticos asociados a áreas de manglar es una importante actividad económica. En el Golfo de Nicoya, se extraen anualmente alrededor de 8 millones de pianguas (*Anadara tuberculosa*) de una poblacion estimada en 37.7×10^6 individuos (Jiménez, 1990). En el delta del Térrraba-Sierpe, Costa Rica, se extraen cerca de 5 millones de pianguas/año. La extracción de este producto en los manglares de El Salvador fluctúa, según las estadísticas oficiales, entre 180,000 y 6'200,000 pianguas por año (peso promedio= 40 gr).

El consumo de crustáceos provenientes de los manglares es también importante. En El Salvador se capturan anualmente entre 12,800-77,700 kg de jaiba (*Callinectes toxotes*). En el caso del punche (*Ucides occidentalis*) se capturan entre 16,800 y 119,600 kg por año, del Cangrejo azul (*Cardisoma crassum*) 200-300 kg y del Camaroncillo *Trachypenaeus* sp entre 76,400-97,800 kg por año.

El cultivo de camarones asociado a áreas de manglar es una actividad de creciente importancia. En el Golfo de Fonseca, Honduras existen cerca de 68 áreas de arrendamiento que ocupan una exensión de más de 2,0000 ha (Wainwright, 1989). En el Golfo de Nicoya se estima que cerca de 2,232 ha de áreas adyacentes a los manglares son aptos para la aquacultura de camarones (Kapetsky *et al*., 1986) y en El Salvador se calcula que más de 13,000 ha adyacentes a los manglares pueden usarse para ese fin. (Yanes *et al*., 1990).

El papel de los manglares en las pesquerías costeras, no debe ser olvidado. A través de su influencia en las cadenas alimenticias, los manglares mantienen grandes poblaciones de importancia comercial. Según las estimaciones de Pauly e Ingles (1986), cada hectárea de manglar es responsable de la producción anual de 150 kg de peneidos en la costa Pacífica de Nicaragua, 99 kg en la de Costa Rica, 185 kg en Guatemala y 88.6 kg en El Salvador.

La producción de sal se ha realizado tradicionalmente asociada a áreas de manglar, en climas secos estacionales. Las áreas intervenidas para este fin son considerables. Alrededor de 656 ha son utilizadas en el Golfo de Nicoya para la producción de sal. La extensión de los estanques utilizados para este fin fluctúa entre 1-80 ha (Kapetsky, 1987). Estas zonas son utilizadas para satisfacer el consumo de sal en Costa Rica, el cual fluctúa entre dieciséis y diecinueve millones de kilos por a o (Fundación Neotropica 1988). En El Salvador se reportan alrededor de 2,500 ha de salineras (Yanes, 1990). En Honduras 1,292 has son utilizadas por unas 130 empresas que producen cada una entre 40 y 480 toneladas por temporada (Wainwhright, 1990; Flores y Reiche, 1990).

La producción de sal se lleva a cabo con base en dos métodos: la evaporación solar y la cocción. En la evaporación solar se construyen estanques de variable extensión (promedio= 2 ha) que son posteriormente inundados con agua de mar, ya sea por bombeo o más corrientemente aprovechando la inundación de las mareas. La concentración de sales se aumenta a través de la evaporación solar en estanques de evaporación. Al alcanzar las sales una concentración del 20% la salmuera es pasada a las pilas de evaporación final. En estas pilas de concreto, ladrillo o plástico la sal precipitada es recogida. El empleo de plástico negro tanto en los estanques de concentración como en los de evaporación final abarata y acelera el proceso, mejorando además la calidad del producto.

La sal producida a través de la evaporación solar es de grano muy grueso, por lo que debe ser molida y si es destinada a consumo humano iodizada posteriormente.

En el sistema de cocción los pasos iniciales del proceso son similares. La diferencia radica en la parte final del proceso donde la salmuera es pasada a una pila de metal colocada sobre un horno de leña que acelera el proceso de evaporación final. Con este sistema de producción se consumen alrededor de 3,5 m^3 de leña para producir una tonelada de sal (Flores y Reiche, 1990). En las salineras que utilizan cocción se contrata como promedio 7 personas por empresa y el márgen de ganacia representa el 19% de la venta. Los costos de producción se dividen: el 27.2% en mano de obra, el 58,8 % por el costo de la le a y el 14,1 % para gastos de administración.

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La Reserva Forestal de Térraba-Sierpe, Costa Rica: Un ejemplo de Uso Adecuado del Manglar

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Introducción

La Reserva Forestal de Térraba-Sierpe está ubicada sobre la costa Pacífica de Costa Rica (Fig. 1). Con una superficie de 16,700 ha, es el bosque de manglar más grande del país. Esta reserva forestal cubre casi un 40% de la totalidad del bosque de manglar del país (Chong, 1988).

Durante muchos años, se han extraído productos del manglar de Térraba-Sierpe sin que se produzca un impacto negativo sobre el ecosistema. Sin embargo, en los últimos siete años, a medida que ha ido aumentando el número de familias que explotan los manglares para subsistir, la presión ha crecido notablemente. Esto es una consecuencia directa de la caída de la industria del banano a mediados de los 80's, del cierre de la compañía bananera en la región del pacifico sur de Costa Rica y del subsecuente desempleo. Hoy en día, los habitantes recurren a los manglares por ser su fuente de ingreso y de alimento más inmediata.

En Costa Rica, los manglares están protegidos por la ley. En 1977, todos los bosques de manglar fueron declarados reservas forestales (Decreto Ejecutivo No. 7210-A) bajo la jurisdicción de la Dirección General de Pesca y Vida Silvestre. Dos años más tarde, en 1979, por el Decreto Ejecutivo número 10005-A se puso a todos los bosques de manglar bajo la jurisdicción de la Dirección General Forestal (DGF) que, en la actualidad, controla el uso de todas las reservas forestales del país. Para poder extraer legalmente cualquier producto forestal de una de estas reservas, es necesario tener un plan de manejo aprobado por la DGF.

En los últimos años se han preparado dos planes de manejo para los manglares de Térraba- Sierpe; el de Chaves y Fonseca (1986) y el de Chong (1988). Sin embargo, por falta de fondos y de un claro apoyo local, éstos no se han podido llevar ejecutar a cabalidad.

En 1989, como respuesta a esta situación, la Unión Mundial para la Naturaleza (UICN), a través de su Programa de Humedales, empezó a trabajar con las comunidades locales en el manejo de parte de esta Reserva Forestal. Dicho trabajo, el cual aún está en proceso, se describe en este estudio de caso.

Figura 1. Reserva forestal Térraba-Sierpe, Costa Rica

Antecedentes

Los beneficios que proporciona la Reserva Forestal de Manglar de Térraba-Sierpe son muchos. Los recursos más importantes que actualmente se extraen de ella son: madera para la producción de carbón, leña y materiales de construcción, corteza para taninos y moluscos *(Anadara* spp). Sin embargo, la pesca que se realiza en el interior de los manglares es únicamente para la subsistencia, ya que tanto la pesca comercial, como la artesanal con redes, están prohibidas dentro de los canales de los manglares.

Está bien establecida en la literatura científica la relación directa existente entre los bosques de manglar y humedales costeros, y las pesquerías comerciales, deportivas y artesanales (c.f. Turner, 1977; Martosubroto y Naamin, 1977; D'Croz y Kiecinski, 1980). Algunos de los bancos comerciales de camarón más importantes de Costa Rica están en la Bahía de Coronado, inmediatamente afuera de la Reserva Forestal de Manglar de Térraba-Sierpe. Si se manejara en forma correcta, la pesca artesanal podría ser una fuente importante de ingreso y de alimento.

El potencial de la pesca de camarón asociada con Térraba-Sierpe se calcula en varios millones de dólares al año. Esto se suma al valor que representan los otros tipos de pesca. Anualmente se extraen de esta Reserva Forestal de Manglar cerca de 5 millones de moluscos de las especies *Anadara tuberculosa* y *Anadara similis.* Hay preocupación, sin embargo, de que estos moluscos estén siendo sobrexplotados, pues es frecuente encontrar individuos con tallas menores a las legales. (El Decreto Ejecutivo No. 13375 del 16 de febrero de 1982 indica que la talla mínima de captura de estas especies es de 47 mm).

La Reserva Forestal de Manglar de Térraba-Sierpe también proporciona servicios indirectos. Durante las inundaciones de 1988, causadas por el huracán Juana, los troncos y otros escombros arrastrados por la corriente no causaron daños más graves a las casas y propiedades gracias a las barreras naturales de manglares de las orillas.

En lo que se refiere al valor potencial de los productos forestales, Chong (1988) calculó que, en esta reserva, 1 hectárea de manglar puede equivaler a US $619 anuales.

La Población y los Recursos del Manglar

Existe una gran cantidad de pequeñas comunidades dentro de, y contiguo a, la Reserva Forestal de Manglar de Térraba-Sierpe. Las más importantes son: Coronado (215 habitantes), Tres Ríos (205), San Marcos (200), Tortuga Arriba (113) y San Buenaventura (110) (González, 1990). En las bocas de los Ríos Térraba y Sierpe también hay varios caseríos de 50 a 100 habitantes cada uno, y casi todos compuestos por familiares entre sí. En total, hay unas 1,700 personas que habitan la Reserva Forestal de Manglar de Térraba-Sierpe. Todos ellos dependen, en una u otra forma, de los recursos naturales que proporciona dicha Reserva.

Coronado es la más grande de las comunidades adyacentes a la Reserva Forestal. Está situada sobre la orilla norte del Río Térraba. La economía de esta comunidad se basa en la extracción de madera y de corteza del manglar. En 1988 se formó una cooperativa, “Coopemangle”, que es una organización de base, formada por mangleros que viven de la extracción de madera y corteza de los manglares. Coopemangle es el único grupo en Costa Rica con autorización legal para extraer productos forestales de los manglares.

Análisis del Enfoque

A pesar de que los manglares están protegidos por medio de la Reserva Forestal, los habitantes locales utilizan cada vez más sus recursos. Un reciente estudio realizado por Marín (1991) indica que la tendencia futura es a que se incremente la presión que se ejerce sobre estos recursos. Por lo tanto, a menos que se establezcan sistemas de manejo sostenibles, es probable que el manglar se degrade y que, a mediano plazo, los beneficios que éste proporciona se pierdan. Con el fin de enfrentar esta situación y de establecer formas de uso sostenido, se vio la necesidad de determinar las razones específicas por las que actualmente no hay una utilización adecuada del potencial económico de los recursos naturales renovables de Térraba-Sierpe. Este análisis de las causas de la presión ejercida sobre los recursos fue el primer paso dado por la UICN para abordar el problema. Este análisis determinó cinco problemas principales que presenta el uso actual de los recursos naturales de la Reserva Forestal de Manglar de Térraba-Sierpe.

Falta de Técnicas Eficientes de extracción y Procesamiento de Carbón y Taninos

El sistema tradicional que se usa en Térraba-Sierpe y en la mayoría de las regiones de manglar de Costa Rica para la producción decarb6n es muy ineficiente. Este sistema, conocido como “horno de fosa”, consiste en colocar sobre el suelo una pila de madera en forma rectangular (2 x 12 m). Los troncos son colocados horizontalmente de manera transversal al eje más largo de la pila, sobre unos durmientes o .plumas." Los troncos son apilados de la forma más compacta posible, rellenando los espacios entre los troncos con pequeñas ramas y raíces.

Los troncos se cubren con hojas de helecho (*Acrostichum* spp.), llamado localmente "negraforra". Sobre el helecho, se pone una capa de tierra de unos 10 a 15 cm de espesor. Ambos extremos de la pila permanecen abiertos, por lo que no hay un control adecuado de la entrada de aire. Por esta razón, el carbón que se obtiene usualmente está demasiado quemado y una cantidad importante se convierte en cenizas. Esto significa que los mangleros deben extraer más madera de la que se necesitaría de ser el sistema más eficiente.

Otro asunto a considerar se refiere al contenido de humedad de la madera. Entre mayor sea éste, mayor será la cantidad de calor que se necesita para convertirla en carbón. En estos momentos, la madera de manglar que usa *Coopemangle* no recibe ningún tratamiento de secado al aire. Al contrario, los troncos por lo general están totalmente saturados con agua al momento de apilarlos en los hornos de fosa, esto hace que una cantidad considerable de la energía que se podría utilizar para la producción del carbón, se gaste en los hornos durante el secado. Por lo tanto, la producción de carbón es menor y el impacto sobre el bosque es mayor, ya que se necesita extraer más madera para compensar el déficit de producción. El resultado es una pérdida de recursos humanos y forestales. Heikkilä (1990) ofrece un análisis de la producción de carbón por *Coopemangle.*

Actualmente, la corteza de manglar se vende directamente a las tenerías como materia prima. Al igual que en otros países de la región, los taninos se extraen en las tenerías usando un método muy rudimentario y con un rendimiento muy bajo. Se necesita mucho más tiempo para preservar el cuero usando corteza de manglar sin procesar que usando extractos de tanino. Por lo tanto, la demanda de corteza de manglar ha disminuido considerablemente. Hoy en día, casi el. 75% de los troncos de manglar que se usan para la producción de carbón no están descortezados.

Es evidente, que hay una considerable pérdida en la post-cosecha de los recursos del manglar. En otras palabras, mientras que se le dedican grandes esfuerzos a la cosecha del recurso, no se maximiza el valor que de éste se deriva.

La Comercialización de los Productos de Manglar no está en Manos de los Mangleros

En la actualidad, Coopemangle no tiene posibilidades de vender sus productos (especialmente el carbón) directamente a los mercados, pues no cuenta con los medios de transporte adecuados. Por lo tanto, los mangleros tienen que vender el carbón a intermediarios. En Coronado, el precio de venta del carbón es de 150 colones (US $1.10) por saco. A 20 km de ahí, en Ciudad Cortés y Palmar, el precio de venta es de 235 colones (US $1.75). En San José, la capital de Costa Rica, el precio al por mayor es de 520 colones (US $3.85). Con un sistema de mercadeo apropiado, el carbón de manglar de buena calidad podría alcanzar precios mucho más altos.

Debido a las limitaciones de transporte, Coopemangle tiene que venderle sus productos a precios muy bajos a aquellos compradores que si pueden transportar el carbón a los mercados. Por esta razón, el impacto sobre el bosque es mayor pues los mangleros deben extraer más cantidad de madera para obtener los mismos ingresos.

Escaso Conocimiento del Recurso y de su Potencial

La tradición determina, en gran medida, el uso que se les ha venido dando a las diferentes especies de manglar. A causa de esto,-algunas oportunidades de obtener mayores ganancias económicas no se aprovechan en su totalidad. Por ejemplo, mucha gente, incluidos los miembros de Coopemangle, han considerado a *Pelliciera rhizophorae* como una especie de manglar no deseable y que se debe eliminar. Chong (1988) calificó las áreas dominadas por *Pelliciera* como bosque no comercial. Sin embargo, está comprobado que la madera de *Pelliciera* es de muy buena calidad para muebles y construcción en general y que, en ciertas condiciones, podría ser de mayor valor comercial que la de *Rhizophora* que se ha considerado como la especie principal.

El Ecoturismo es otra actividad productiva cuyo potencial se comenzó a explorar en la Reserva hace apenas poco tiempo. Ya existen varios hoteles en la zona cuya promoción incluye el bosque de manglar. Coopemangle se

ha interesado por esta actividad, y ha comenzado a ofrecer giras guiadas por los canales y diferentes parajes de la Reserva, muchos de los cuales sólo un verdadero manglero conoce.

Existencia de Extracción Ilegal de Manglar

Coopemangle ha adquirido permisos para operar dentro de la Reserva Forestal de Manglar de Térraba-Sierpe. Sin embargo, hay una cantidad de mangleros ilegales que no cuentan con dichos permisos y que viven en los poblados situados en las desembocaduras de los Ríos Grande de Térraba y Sierpe, conocidas como "Las Bocas". El problema que causan estos extractores ilegales de manglar es doble. En primer lugar, dado que su actividad es ilegal, estas personas extraen la madera clandestinamente y su preocupación principal es que no los descubran. Por lo tanto, el impacto sobre el bosque es mayor en términos tanto de daños como de desaprovechamiento. En segundo lugar, estos trabajadores ilegales venden sus productos a precios inferiores a los del mercado. En la actualidad, esto representa una pesada carga para Coopemangle, por un lado, y por el otro, para los ilegales mismos, pues no están recibiendo una paga justa por su trabajo.

Esta situación es un círculo vicioso, para poder operar legalmente, los extractores ilegales deben obtener un permiso de la Dirección General Forestal (DGF). Para esto necesitan tener un plan de manejo y los ilegales no cuentan ni con los recursos económicos ni con la capacidad técnica para diseñarlo.

Escasez de Recursos Humanos y Recursos en General en la Dirección General Forestal para Llevar a Cabo sus Programas

Al igual que muchas instituciones que se ocupan del manejo de los recursos naturales en los países en vías de desarrollo, la DGF tiene una gran limitación de recursos financieros. En la actualidad, hay solamente una persona asignada a toda la Reserva Forestal de Manglar Térraba-Sierpe y lo mismo ocurre en otras reservas forestales de manglar. En resumen, las dificultades a las que se enfrenta la DGF son las siguientes:

a). Inexperiencia en lo que concierne al manejo, protección y uso integrado de los recursos de manglar;

b) Falta de fondos, vehículos, embarcaciones e instrumentos para emprender actividades a gran escala de manejo de manglares.

Juntos, los cinco factores puestos en relieve en los párrafos anteriores causan un impacto sobre los manglares en tres formas principales:

1) Se desperdicia una cantidad considerable de recursos. A pesar de las condiciones forestales favorables de la zona, se calcula que es una fracción pequeña del total extraído la que en realidad se aprovecha. Como consecuencia de esta falta de aprovechamiento, para que sea posible satisfacer las necesidades de los manglares, el impacto se extiende sobre una zona más amplia del bosque por unidad de tiempo.

2) Puesto que la madera que se cosecha no se utiliza en forma óptima, la ganancia está muy por debajo de su potencial. Esto, a su vez, induce a los mangleros a explotar zonas más amplias que las que en realidad requieren.

3) Estas prácticas han llevado a una degradación del bosque en ciertas zonas.

Hasta ahora, las prácticas de manejo poco sofisticadas no han causado un impacto negativo sobre la mayor parte del manglar de Térraba-Sierpe, porque la densidad poblacional es baja. Sin embargo, si como se espera (Marín, 1991), la densidad poblacional aumenta en un futuro cercano, crecerá la presión sobre los recursos de manglar. Deben, por lo tanto, tomarse medidas que promuevan un uso adecuado de los recursos naturales de la Reserva Forestal de Manglar de Térraba-Sierpe.

El Enfoque. La Respuesta

En respuesta a los problemas que enfrentan los manglares de Térraba-Sierpe y basándose en el análisis de éstos descrito anteriormente, la UICN, en asoció con el Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), dio comienzo a un proyecto para promover el uso adecuado de los recursos naturales de la Reserva Forestal de Manglar de Térraba-Sierpe para desarrollar una serie de alternativas de manejo de los manglares neotropicales. Se persiguen cuatro objetivos principales:

1) Darle fuerza a Coopemangle para que se desarrolle como una organización comunal capaz de manejar los recursos de manglar de manera sostenible.

2) Realizar *in situ* proyectos piloto que demuestren la viabilidad económica del uso sostenible de los recursos de manglar.

3) Proporcionar información a la comunidad y a los niveles técnicos y de decisión, sobre el potencial que tienen los recursos de manglar para contribuir al desarrollo rural.

4) Fortalecer la capacidad institucional de la Dirección General Forestal como institución gubernamental encargada de las Reservas Forestales de Manglar.

Las principales actividades que se están llevando a cabo para promover el cumplimiento de estos objetivos son las siguientes:

Mejoramiento en la Extracción y Procesamiento de la Madera para la Producción de Carbón

Después de analizar los métodos actuales de producción del carbón y las formas de extracción, en este momento se persigue el cumplimiento de cuatro etapas:

1) Poner a prueba diferentes métodos de extracción de madera del bosque, poniendo énfasis en un manejo más eficiente que provoque menos trastornos.

2) Construir dos barcazas que permitan transportar la madera a los hornos en una forma más rentable.

3) Construir instalaciones sencillas capaces de almacenar suficientes troncos para el secado al aire de la madera que precede a la producción del carbón. La cantidad de madera que se almacene será suficiente como para que sea posible una producción sostenida.

4) Construir tres hornos de ladrillo para producir un carbón de mayor calidad y aumentar la eficiencia del proceso. Los miembros de Coopemangle están recibiendo entrenamiento en la construcción y manejo de los hornos de ladrillo.

Al mismo tiempo, en Nicaragua se están estudiando los resultados del trabajo efectuado en mejoramiento de la eficiencia en la extracción del tanino a partir de corteza de *Rhizophora* spp. Una vez que se disponga de esta información, los resultados de dicho trabajo se aplicarán a Térraba-Sierpe.

Mejora en la Comerclalizaclón de los Productos de Manglar

Se está llevando a cabo un estudio de mercado sobre el carbón y los taninos de manglar y sobre la madera de *Pelliciera rhizophorae.* Asimismo, se logró adquirir un camión para permitirle a *Coopemangle* lograr el acceso con sus productos a los mercados. Con este camión, Coopemangle podrá llevar el carbón directamente a los mercados y, al mismo tiempo, traer a Coronado otros productos que se venderían a precios menores que lo acostumbrado.

Proyecto Piloto con *Pelliciera rhizophorae*

Gracias a experimentos iniciales, hoy día se sabe que *Pelliciera rhizophorae* seria muy buena madera para construcción de muebles y viviendas. Por lo tanto, se está llevando a cabo un análisis más detallado de las propiedades mecánicas de *P. rhizophorae* y de la factibilidad económica del uso sostenible. Además, se proyecta la adquisición de un aserradero portátil para procesar la madera de construcción y se iniciará un plan para mejorar las casas de los miembros de Coopemangle usando *Pelliciera rhizophorae* y otros recursos locales.

Inclusión de los Mangleros Ilegales a Coopemangle

Coopemangle accedió a aceptar a cualquier manglero ilegal como miembro. De esta manera, se espera extender a otras comunidades los beneficios que se deriven de este proyecto y, asimismo, eliminar el impacto negativo causado por la extracción no reglamentada de madera. A largo plazo, podrían establecerse otras cooperativas de manglar dentro de la reserva forestal, sobre todo en áreas lejos de Coronado. Las actividades que están ahora en proceso servirían entonces de modelo.

Fortalecimiento Instltuclonal de la DGF

Se proyectan dos áreas de acción:

1) El personal de la DGF recibirá entrenamiento en manejo, protección y uso integrado de los recursos de manglares. Esto se logrará por medio de seminarios, talleres y cursos de capacitación en el campo. A mediano plazo, estas actividades de capacitación se extenderán al personal de la DGF en otras reservas forestales de manglar.

2) Además, se le proporciona regularmente a la DGF asistencia técnica y documentación sobre el manejo de manglares.

Estudios Biológicos y Socioeconómicos

Haciendo énfasis en estas iniciativas de manejo, se ha emprendido una serie de estudios biológicos. Por medio de éstos, se levantará un mapa de las áreas donde se llevan a cabo actividades de extracción. Lo anterior es con el fin de evaluar la cantidad que se extrae de cada uno de los productos (carbón, leña, corteza, madera para la construcción, camarones,

mariscos y peces), cuantificar los índices de crecimiento de las especies de manglar en diferentes zonas de la reserva forestal, comparar calidad y cantidad de regeneración bajo diferentes esquemas de manejo en especial tala rasa y extracción selectiva, determinar áreas criticas para la conservación estricta, y establecer zonas para la preservación.

Al mismo tiempo, se está llevando a cabo una serie de estudios socioeconómicos detallados de los diferentes grupos sociales que usan los recursos de manglar. Este estudio hará énfasis en cuantificar la frecuencia con que se utilizan estos recursos, así como en .evaluar la importancia de los mismos en las economías familiares y locales. Posteriormente, los estudios socioeconómicos se enfocarán a evaluar el impacto que la implementación de los proyectos piloto, y el eventual plan de manejo que se diseñará, puedan tener en las comunidades asociadas a la Reserva Forestal de Térraba-Sierpe. Este seguimiento cumplirá con dos objetivos básicos: tomar las acciones correctivas que puedan ser necesarias y obtener experiencias que puedan ser utilizadas en otros manglares en la Región Neotropical.

Educación Ambiental y Concientización

El delegado de la DGF en Térraba-Sierpe inició un programa de educación ambiental muy exitoso e innovador con los niños de la escuela primaria de Coronado. Este programa, llamado - Educación en el Agua," busca que los niños palpen por sí mismos los diferentes componentes del ecosistema del manglar, la interdependencia del manglar con sus áreas adyacentes, la importancia del manglar en la zona costera y las acciones que ellos mismo pueden promover para conservar estos ecosistemas. Muchos de los niños participantes del programa son hijos de manglares.

El programa está siendo apoyado por el proyecto CATIE/UICN con el objeto de fortalecerlo, y difundir sus experiencias a otras comunidades de la reserva forestal de manglar.

Los Logros

Aunque ya se han analizado los problemas de la reserva de manglar de Térraba-Sierpe y ya se han determinado métodos para enfrentarlos, las actividades apenas están en pañales. Por lo tanto, es muy temprano para pretender grandes éxitos. Sin embargo, el enfoque descrito anteriormente cuenta con un apoyo local muy fuerte y un número importante de manglares ilegales ya se han incorporado a Coopemangle. *Coopemangle,* asimismo, ya está probando el primer horno de ladrillo bajo la supervisión de la Universidad Nacional (UNA). Además, se estableció un fondo rotativo para proporcionar un respaldo económico básico para el mejoramiento de la extracción de madera (mejores sierras y la compra de embarcaciones con motor fuera de borda). Este fondo rotativo permite la compra de dichos materiales con la ventaja de que Coopemangle puede reintegrar el dinero una vez aumenten las ganancias gracias al mejoramiento del proceso de extracción, procesamiento y comercialización. En apoyo a los esfuerzos de divulgación y concientización, en 1990 se celebró la “Fiesta del Mangle" para que la comunidad adquiriera un mayor conocimiento del valor del sistema de manglar. En estos momentos se prepara la Segunda Fiesta del Mangle, donde, entre otras actividades, los niños del programa "Educación en el Agua", invitarán a otros niños y adultos de comunidades aledañas, a participar en la siembra de propágulos de mangle.

Enseñanzas

A pesar de que este trabajo apenas está comenzando a desarrollarse, ya es fuente de una gran cantidad de enseñanzas.

1) Aunque la degradación de los recursos de manglar en Térraba-Sierpe todavía no es critica en comparación a otras áreas en Centroamérica y alrededor del mundo, el crecimiento de la población está conduciendo a un aumento en la presión sobre estos recursos. Por lo tanto, es urgente promover un uso adecuado de los recursos y establecer una estructura clara de manejo con la cual se pueda seguir adelante, para poder prepararse para el crecimiento de esta presión. Sería un error dejar que la presion alcance niveles insostenibles.

2) La existencia de leyes que crean reservas forestales de manglar constituye una base legal sólida. Asimismo, el hecho de que el Departamento Forestal emita permisos para que grupos organizados. como Coopemangle, utilice los recursos del manglar, descentraliza el control cotidiano sobre el uso de la reserva.

3) La prohibición de extraer productos del manglar sin un plan de manejo es un paso importante. A pesar de que los planes ya existentes tienen sus puntos débiles, este

proyecto de uso adecuado está diseñado para fortalecer y ejecutar dichos planes.

4) Coopemangle es un grupo comunitario bien estructurado, interesado específicamente en el manejo de los recursos de manglar. Además, la ley de cooperativas de Costa Rica reconoce legalmente a Coopemangle. Todo esto hace de dicha cooperativa una institución local transparente con la que el Gobierno central puede trabajar y a la que le puede delegar responsabilidades.

5) Un análisis de la situación socioeconómica y las actividades actuales de manejo ha permitido determinar las formas en las que los manglares pueden manejarse de manera más efectiva. Esto maximiza las oportunidades de éxito.

6) El programa de educación ambiental asociado es crucial para crear conciencia de la importancia del sistema de manglar y de la necesidad de controlar el uso de los recursos.

Las Limitaciones

Aunque todo parezca indicar que este proyecto augura un comienzo exitoso del trabajo de manejo de recursos de manglar con comunidades locales, es importante resaltar que el mantenimiento a largo plazo del bosque de manglar de Térraba-Sierpe dependerá de la conservación de la integridad ecológica e hidrológica de la cuenca. Por lo tanto, es importante que las autoridades costarricenses cuiden de la cuenca y que las decisiones de manejo de la misma incluyan un plan global a largo plazo para manejar los recursos del manglar.

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Considerations for the Use of Wetland Wastewater Treatment by Mangroves in the State of Campeche

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Abstract

Two major environmental problems currently affecting the coastal zone of Campeche are loss of mangrove wetlands and surface water pollution. The application of treated wastewater to mangroves can be a means of dealing with both of these problems. The benefits of wetland wastewater treatment include improved surface water quality, increased accretion rates to balance sea level rise, improved plant productivity and habitat quality, and decreased costs for conventional engineering treatment systems. Wetland treatment systems can be designed and operated to restore deteriorating wetlands and maintain existing wetlands. Hydrologically altered wetlands are appropriate for receiving municipal and some types of industrial effluent. Wetland wastewater treatment has been shown to be effective in treating municipal effluent. Both artificial and natural wetlands have been used for treatment. Sea level is rising between 1 and 2 mm/yr and this rate is projected to increase over the next several decades. Effluent discharge to wetlands should be incorporated into comprehensive management plans designed to increase sediment and nutrient input into mangrove wetlands, improve water quality, and result in more economical waste treatment.

Resumen

Actualmente dos problemas ambientales importantes afectan la zona costera de Campeche: la pérdida de pantanos de manglar y la contaminación de las aguas superficiales. El uso de los manglares como plantas de tratamiento de agua de desecho puede ser un medio para enfrentar ambos problemas. Los beneficios de los humedales como plantas de etratamiento determina mejorar la calidad del agua superficial, aumentar la tasa de acrecentamiento del terreno para equilibrar la elavación del nivel del mar, mejora la calidad del hábitat y la productividad de las plantas y disminuye costos en comparación con sistemas convencionales de tratamiento de aguas. Los sistemas de tratamiento de pantanos pueden diseñarse y operar para restaurar pantanos deteriorados y mantener humedales existentes. Los pantanos alterados hidrológicamente son receptores apropiados para recibir descargas municipales y algunos desechos de tipo industrial. Los manglares como plantas de tratamiento ha mostrado ser efectivos en el tratamiento de descargas municipales, tanto pantanos artificiales como naturales se han usado para este propósito. El nivel de mar sube entre 1 y 2 mm/año y este

valor se estima aumentará en las próximas décadas. Las descargas a pantanos deberían incorporarse en los planes de gestión diseñados para aumentar el flujo de sedimentos y el aporte de nutrientes a los pantanos de manglar, mejorando la calidad del agua, y resultando en un tratamiento de desechos muy económico.

Introduction

Wetlands have been used to treat wastewater for centuries, but only in the past several decades has this process been scientifically analyzed in a comprehensive way (Richardson and Davis, 1987). From an ecological perspective, interest in wetlands to purify effluent is based on a belief that the free energies of the natural system are both capable of and efficient at driving the cycle of production, use, degradation, and reuse (Odum, 1978). The basic principle underlying wetland waste treatment is that the rate of application must balance the rate of decay or immobilization. The primary mechanisms by which this balance is achieved are physical settling and filtration, chemical precipitation and adsorption, and biological metabolic processes resulting in eventual burial, storage in vegetation, and denitrification (Patrick, 1990; Kadlec and Alvord, 1989; Conner *et al*., 1989).

Both natural and constructed wetlands are used to treat wastewater. Constructed wetlands -those built to treat wastewater on non-wetland sites- can be designed to treat all forms of effluent from primary effluent through tertiary treatment and are designed as either surface or subsurface systems. The latter are used extensively in Europe (Watson *et al*., 1989) while both systems are used in the United States. In the US, natural wetlands are legally limited to providing only tertiary treatment of secondary waste. By the end of the 1980's, more than 500 natural wetland systems were used to treat wastewater discharge in the United States (Reed, 1991; EPA, 1987).

To a large extent, conventional treatment plants use the same physical and biological processes as those operating in both natural and constructed wetland systems. But whereas filtration, sedimentation, oxidation, reduction, and nutrient cycling occur in natural systems by the interaction of soils, water, vegetation, and microorganisms, these same processes occur in conventional plants only with substantially greater amounts of energy and chemical additives to compensate for the reduced space and time required to treat large volumes of effluent. Constructed wetlands generally fall in between the two extremes, depending on design and loading rates.

In any treatment system -natural, constructed, or conventional- a large number of variables can be manipulated to achieve pollutant reduction goals. While conventional plants use highly engineered, energy intensive systems to accommodate the microbial mineralization of organic carbon, natural wetland treatment systems are designed to take advantage of existing site and climatic conditions such as soils, plants, pH under submerged conditions, temperatures, precipitation, and flooding regimes. The primary management controls in the natural system are loading rates and residence times, though design of the distribution system can increase the number of outfalls and take advantage of or create gradients or slopes.

Our objective in this paper is to discuss the considerations for the use of wetland wastewater treatment in the coastal zone, with special reference to the coastal zone of Campeche. We first put the issue into a conceptual framework, that of restoration ecology. Then we develop a detailed analysis based on examples from a number of coastal areas followed by a discussion of the benefits and concerns of wetland treatment. Much of this paper is based on Breaux and Day (1993).

Before continuing further, we want to stress several points which are essential to our main hypothesis that wetland waste treatment is not only possible, it is desirable. First, mangrove wetlands are disappearing due mainly to pressure from agriculture and urban expansion. Coastal wetlands which are most amenable to wetland wastewater treatment are generally those which are most threatened, and we argue that wastewater application will benefit these wetlands. Thus, the nutrients and organic matter in the effluent are used as a resource rather than treated as a pollutant.

Second, there is surface water quality deterioration in the coastal zone of Campeche, mostly due to inputs of high levels of nutrients and non-toxic organic matter. Conventional treatment methods alone are often impractical or uneconomic. Most of the wastewater is generated in areas that are located adjacent to large tracts of wetlands so that water does not have to be transported over long distances. The City of Campeche is a good example of this with wastewater presently flowing into mangroves. Wetland wastewater treatment can be the most cost-effective means of treatment.

Figure 1. Conceptual model of the effects of treated effluent on wetland elevation. Addition of wastewater effluent stimulates wetland elevation both directly (through deposition of sediment) and indirectly (through increased plant production). In the Louisiana Coastal Zone wetland elevation is lowered due to sea level rise and subsidence, and thus continual accretion is necessary if plant communities are to be maintained

Finally, coastal wetlands are threatened by sea level rise. Conversely, effluent application can stimulate vertical accretion thus helping to offset waterlogging resulting from inundation. This accretion leads to rapid permanent burial of materials and thus wetland wastewater treatment systems will not become saturated. Since sea level rise is predicted to accelerate in the next century (Warrick and Oerlemans 1990), wastewater can be used as a resource to help offset the impacts of rising water levels (Fig. 1).

Restoration Ecology

Restoration ecology has been defined as the reassembly or partial assembly of an ecological system (Jordan *et al*., 1987). In attempting to restore and maintain coastal wetlands, the addition of sediments and nutrients to wetlands through effluent application constitutes a form of wetland restoration. The chief component of a restoration plan would be the selection of an adequate design and effective loading rates to ensure adequate hydrologic control and the health of the ecosystem. The success of wetlands as tertiary treatment systems has been amply demonstrated under conditions where populations are not large and natural wetland acreage is available (Nichols, 1983; Richardson and Nichols, 1985; Khalid *et al*., 1981; Best 1987)**.** Wetland wastewater treatment could be incorporated as a component of coastal management in Campeche where these conditions exist. The situation in Campeche presents the opportunity to investigate the assimilative capacity of wetlands to serve as more than tertiary systems (i.e., to treat effluent less than secondary). For example, in a recently completed a study of the use of wetlands to treat wastes from a potato chip factory in Louisiana, a system was designed to effectively treat less than secondary wastes (Breaux, 1992).

Wastewater application to wetlands does not usually lead to biological communities identical to those either preceding application or surrounding the receiving site, though such communities might be desirable. The ultimate aim of the discharge would be to make use of the assimilative capacity of the wetland to treat wastewater in order to maintain biological productivity and to offset sea level rise. Monitoring and research should be an integral part of any program that attempts to make use of wetland waste treatment to enhance the environment. Duplication of wetland functions is the important point. This is emphasized by Jordan *et al*. (1987) in their discussion of restoration ecology as both environmental technology and ecological technique:

> What is needed...is not rote copying, but imitation - the distinction being that copying implies reproducing systems item for item, while imitation implies creating systems that are not identical but that are similar in critical ways and that therefore act the same.

The authors state further that it is imitation that will ultimately provide the understanding critical for the reproduction of natural systems.

Wetland treatment systems in Campeche can be used to gain an understanding of the response application of sewage effluent. In so doing, knowledge of natural processes will be both expanded and refined. The natural processes investigated underlie the hypothesis that wetlands improve water quality and that added sediments and nutrients will benefit wetlands facing sea level rise. Maintaining coastal wetlands will prevent the loss of not only water purification functions and values but also flood control benefits, wildlife habitat and diversity, direct economic use, education, and research.

Benefits of Wetland Wastewater Treatment

The following are the primary benefits of wetland wastewater treatment in the coastal zone of coastal Campeche: **1**) improved surface water quality, **2**) increased accretion rates to balance subsidence, **3**) increased productivity of vegetation and improved habitat quality, and **4**) the financial savings of capital not invested in conventional tertiary treatment systems.

A number of factors associated with wetlands in general, and with Louisiana coastal wetlands in particular, lead to efficient reductions in biological oxygen demand, total suspended sediments, total organic carbon, and nitrogen and phosphorus levels contained in typical municipal or food processor effluent. These factors include **1**) a high rate of burial due to subsidence and **2**) high denitrification rates due to warm temperatures and wetland plants which enhance denitrification. Relatively high temperatures are also favor higher metabolic rates, and higher plant productivity in general. A third factor related to phosphorus removal is the adsorption and precipitation of inorganic phosphorus which is facilitated by reactions with iron and aluminum under the neutral conditions of saturated wetland soils (Nichols, 1983; Patrick, 1990). Phosphorus removal rates in the southeast are variable but potentially high. Nixon and Lee (1986), in a review of field studies of wetlands and water quality, found overall phosphorus removal rates in the southeast to range from 9% to 98% for a range of loading rates between 0.4 to 46 $gP/m^2/yr$. By using conservative hydraulic and nutrient loading rates and employing design criteria to optimize contact time, complete removal rates for all water quality constituents could be achieved.

Finally, the current mean relative sea level rise rate in the Mississippi Delta is about ten times that of eustatic sea level rise (Penland *et al*., 1988; Conner and Day, 1988; Baumann *et al*., 1984; Gornitz *et al*., 1982) This means that the Mississippi delta can serve as a model for the effects of sea level rise other coastal systems (Day and Templet 1989). Wetland restoration attempts through the stimulation of biomass in the rapidly subsiding Mississippi delta can, therefore, prove useful in the management of endangered wetlands and the creation of new wetlands beyond the reach of encroaching sea levels.

Potential Problems and Concerns

There are a number of potential concerns about the use of wetlands for wastewater treatment. We believe that proper design and operation of these systems in hydrologically altered areas in coastal Louisiana can overcome these concerns.

The main mechanism of phosphorus removal in wetland treatment systems is the adsorption and precipitation of iron, and aluminum complexes (Richardson, 1985). After long periods of effluent application, soils have become saturated and phosphorus removal efficiency has decreased (Faulkner and Richardson, 1989; Hemond and Benoit, 1988; Richardson, 1985; Nichols, 1983). Where natural soils do not contain sufficient amounts of iron, aluminum, or calcium to effectively remove phosphorus (Nichols, 1983), other techniques have been employed successfully in the field or lab such as the addition of an anaerobic zone in a section of the activated sludge system at the Walt Disney World treatment system (Knight *et al*., 1987). When phosphorus loadings are high or a wetland lacks the assimilative capacity to transform or remove it, Richardson and Davis (1987) suggest pretreatment using alum or iron, or aeration to decrease BOD and suspended solids. Khalid *et al*. (1982) found phosphorus removal from municipal wastewater to be enhanced both by the addition of calcium carbonate and by the pre-reduction of the soil/plant system. Finally, Louisiana wetlands can assimilate much higher levels of phosphorus than elsewhere due to the high rate of burial resulting from the high rate of subsidence. Because of this latter factor, properly designed treatment systems in the coastal zone will never become saturated.

Two other commonly voiced concerns over the issue of wetlands used as wastewater treatment systems include the suggestion of incomplete pathogen removal and the implications of treatment to wildlife populations. Questions have been raised by some researchers (e.g., Shiaris, 1985 and Grimes, 1985) about the effectiveness of wetland treatment in removing pathogens. At

the same time, however, successful pathogen removal by natural die-off has been reported by EPA (1987), and measured in the field or lab by Meo *et al*. (1975), and Gersberg (1987) among others. Kadlec (1989) reported that fecal coliforms are generally reduced to acceptable water quality standards after passage through wetlands, as are viruses and bacterial indicators such as fecal streptococcus. He found no reported incidents of adverse effects to animals or humans resulting from wetland wastewater treatment.

Finally, concerns for the potentially adverse effects of wastewater treatment to wildlife are sometimes expressed and the suggestion made that more artificial wetlands be built to serve as natural systems (e.g., Guntenspergen and Sterns, 1985). But others acknowledge that there is no substitute for a natural system, and that species diversity is usually lower in artificial systems (EPA, 1987). Many believe that the use of properly operated natural wetlands as treatment systems has benefited, and can continue to benefit, wildlife populations (e.g., Best, 1987). Wentz (1987) of the National Wildlife Federation also concluded that wetland waste treatment was not incompatible with wildlife management.

The fact that 1991 waterfowl survey figures for ten species of diving and dabbling ducks show a decline for nine of those species from the 1955-1990 average, with the northern pintail showing a decrease of 62% (US Fish and Wildlife Service 1991), emphasizes the need for full-scale habitat protection measures. The importance of Louisiana wetlands as waterfowl habitat, and the high wetland loss rates require efforts to increase and improve existing wetland acreage.

A careful design can combine the techniques of the engineer in terms of flow rates, holding ponds, stormwater diversions, and the pretreatment methodologies described above, with the impoundments, spoil banks, levees and sheer space available in the “natural” system to produce both effective wastewater treatment systems and productive wetlands. Wentz (1987) explains the benefit of and need for the carefully planned multiple use of wetlands: “We must take people beyond the idea that because wetlands are valuable they cannot and should not be `managed.’ It is very important that people understand that manipulation of wetlands is not necessarily a bad thing.” Indeed, manipulation of altered natural systems is essential in order to control the changes brought about by human interference. This is especially the case for Louisiana where human impacts threaten the very existence of the coastal zone. We believe that effluent application will enhance the long-term survival of coastal wetlands.

Current Political and Regulatory Climate

EPA

The US Environmental Protection Agency (EPA) has recognized the benefits and efficiency of wetland treatment systems. The Agency’s Report on the *Use of Wetlands for Municipal Wastewater Treatment and Disposal* states: “Wetlands appear to perform, to at least some degree, all of the biochemical transformations of wastewater constituents that take place in conventional wastewater treatment plants, in septic tanks and their drainfields, and in other forms of land treatment.” The report further states that both natural and constructed wetland treatment systems have been found to achieve high levels of removal from wastewater for nutrients, BOD, suspended solids, nutrients, heavy metals, trace organic compounds, and pathogens, as well as natural die-off of pathogens from wastewater (EPA, 1987).

While the Agency acknowledges that constructed wetlands are often more costly “and rarely achieve the same level of biological complexity as natural wetlands systems”, its stated policy is that “currently, use of constructed, rather than natural wetlands, is generally preferred by EPA when projects for wastewater treatment are proposed” (EPA, 1987). One reason for preferring constructed over natural wetland treatment systems is the reluctance to alter biotic communities of natural wetlands when using natural systems as treatment areas. The no action approach to wetland preservation in coastal Louisiana, however, is more likely than not to lead to the elimination of existing wetland species as they become increasingly and permanently inundated. Sediment and nutrient additions to the subsiding wetlands could help reverse the trend toward submergence.

An additional reason for encouraging the use of constructed over natural wetland systems is the presumed greater level of “control” in the former. Two points in regard to the issue of control need to be addressed here. First, in Louisiana’s case at least, it can be argued that the large number of isolated impounded or semi-impounded areas allow for as much control as might be available in a constructed wetland. Second, control in an artificially-created environment which lacks the diversity of a natural one, is not as instructive scientifically in terms of revealing the functions and processes of the wetland ecosystem. Again, Jordan *et al*. (1987) describe the situation appropriately with an emphasis on the value of control in natural systems, as opposed to artificial ones:

The essential idea is control -the ability not only to restore quickly, but to restore at will, controlling speed, decelerating change as well as accelerating it, reversing it, altering its course, *steering* it, and even preventing it entirely (which of course is actually a frequent objective of the ecological manager).

Louisiana's needs to control or prevent wetland loss and deal with surface water pollution suggest that wetland wastewater treatment would be beneficial. The use of hydrologically altered wetlands to treat wastewater will enable the testing of hypotheses regarding ecosystem response and land loss, and will contribute to the overall knowledge of wetland ecosystems.

EPA's preference for constructed over natural wetlands as treatment systems has undoubtedly influenced national policy. In 1987 the Agency itself acknowledged that "the lack of EPA water quality criteria for wetlands and the resulting absence of State water quality standards for wetlands is one of the most serious impediments to a consistent national policy on use of wetlands for wastewater treatment or discharge" (EPA, 1987). Florida is the only state to have instituted its own regulations for wetland treatment systems. Prior to the institution of those regulations in the mid-1980's, H.T. Odum (1978) used Florida as an example of a state who's regulatory authority lacked an appreciation of the environment's assimilative capacity: "An economy is vital when environment and economic developments are mutually reinforced and protected. Unfortunately, well-meaning efforts to draft laws to protect the environment have not always been made with an understanding of the ecological principles of symbiosis and recycling by which nature and humanity are best combined".

The regulations which Florida subsequently adopted allow for progressively stricter loading rates depending on the type of wetland to which effluent is discharged. The Florida plan allows for the following applications:

1. Hydrologically altered wetlands are allowed to receive a maximum of 75 $g/m^2/yr$ of total nitrogen and 9 $g/m^2/yr$ of total phosphorus;

2. Treatment wetlands are used to treat reclaimed water that has gone through secondary treatment with nitrification, and are allowed to receive 25 $gN/m^2/yr$ and 3 $gP/m^2/yr$;

3. Receiving wetlands are used to receive reclaimed water that has gone through advanced (tertiary) treatment, and can accept only wastewater treated to 3 mg/liter total nitrogen and 1 mg/liter total phosphorus (Harvey, 1988).

Florida's ranking of wetlands to treat wastewater is a response to environmental problems which include a high degree of water level reductions with relatively little subsidence. Discharge to treatment and receiving wetlands are generally prohibited in Class I and II waters and in non-cattail dominated herbaceous wetlands. Hydrologically altered wetlands in Florida are defined as those where upland vegetation has encroached and where substantial reductions in water levels have occurred. While Louisiana does have altered wetlands that fit this description due to drainage projects or deprivation of flows to some wetland areas, the problem of subsidence and rising water levels is a far more serious threat. Effluent with higher sediment and nutrient loads should be considered for discharge to submerging wetlands to increase accretion rates and productivity. While Florida needs to deal with the problem of wetland loss as a result of decreased water levels and the consequent transition to uplands, Louisiana needs to deal with the problem of wetland loss as a result of increased water levels, sediment starvation, and the consequent transition to open water.

An additional factor favoring wetland wastewater treatment in Louisiana is its relatively low population density and available land area. While Florida ranks first in the coterminous United States for total wetland acreage and Louisiana ranks second (Dahl, 1990), Louisiana has a substantially lower population density, with 97 persons per square mile of land area compared to 240 for Florida (US Bureau of the Census, 1991). In addition, the general tendency for populations in Louisiana to be distributed along natural levee ridges backed by wetlands facilitates use of those wetlands as treatment systems.

Since 1987, EPA has attempted to design standards that would be more appropriate for wetlands than the aquatic standards developed for surface water bodies. The Agency has recently published a manual describing numerical or narrative biological standards designed to prevent a decrease in wetland productivity or diversity (U.S. EPA, 1990). While the Agency is still willing to permit the use of wetlands as tertiary treatment systems in some Louisiana cases, it will not allow such use as a form of wetland "enhancement". The term was used in the report on wetlands to treat municipal wastewater (EPA, 1987) primarily as a possibility only in areas where insufficient water exists to maintain a wetland as occurs in the western United States, not in areas facing the possibility of conversion to open water as occurs in Louisiana. There appears to be a reluctance to admit, or a basic disagreement with, the

hypothesis that a natural but degraded wetland might adequately purify wastewater, while benefiting ecologically at the same time.

Consequently, EPA has discouraged wetland wastewater treatment in Louisiana as a form of "enhancement", and encouraged the state to approve wetland projects according to the "antidegradation" rule which requires that the state "provide for the protection of existing uses in wetlands..." (EPA, 1990). In Louisiana's case, where sea level rise is predicted to drown a vast expanse of coastal wetlands (Park *et al*., 1989; Day and Templet, 1989), such an emphasis on "present uses" appears short-sighted and designed to accommodate only those who use or will use the wetland areas directly over the next 2 to 3 decades or less.

The Louisiana DEQ has granted permission to discharge secondarily treated wastewater to wetlands near Thibodaux and is considering the same permission for Breaux Bridge, but only as a "naturally dystrophic waters" exception on the premise that dissolved oxygen levels are naturally lower than the EPA standard of 4.0 mg/l in estuarine waters. State DEQ personnel have generally sought to establish expedient permitting of wetland treatment systems, though working within the inflexible national framework of EPA policy has been a deterrent. A memo from one staff member to the Secretary emphasized the need for prompt consideration and processing of wetland treatment system permitting:

> If we are to make wetlands enhancement by wastewater application feasible in Louisiana, we must provide the regulatory structure to allow expedient permitting of such discharges. The establishment of appropriate wetland specific standards is the first step in providing the regulatory structure for permitting (Knox, no date).

Recently the state has developed a set of tentative standards for the Thibodaux wastewater treatment site which include the following prohibitions designed to protect wetlands from any adverse effects due to wastewater application:

1. No more than 20% decrease in naturally occurring litter fall or stem growth.

2. No significant decrease in the dominance index or stem density of bald cypress.

3. No significant decrease in faunal species diversity and no more than a 20% decrease in biomass.

Monitoring of the site after effluent application begins in the Spring of 1992 will test the validity of these criteria and serve as a basis for their expansion or refinement.

EPA has already acknowledged the capability of wetlands to effectively treat wastewater. It remains for the agency to review the potential for treated effluent to benefit Louisiana's wetlands in light of the unique problems of the state. If the basic premise that effluent can contribute valuable sediment and nutrients to the wetlands is accepted, then wetland wastewater treatment could be incorporated as a major component of an overall comprehensive plan to protect and restore the state's wetlands. Seven years ago Gosselink and Gosselink (1985) suggested that wetland wastewater treatment be incorporated into plans to divert freshwater from the Mississippi River to the coastal plain. Templet and Meyer-Arendt (1988) have emphasized that the wetland sediment deficit is a primary reason for Louisiana's land loss. Their suggested policy is to use Mississippi River water, sediments, and nutrients to revive and nourish coastal wetlands by helping to maintain surface elevations sufficient for plant growth. They state further that:

> The greater the number of conduits delivering water, sediments, and nutrients into the wetlands, the greater is the level of restoration of a formerly viable ecosystem.

Strategy: Provide maximum distribution of the waters of the Mississippi River across the deltaic plain by using the maximum number of distribution points to move water, sediment, and nutrients into the coastal wetlands.

Because of the dispersed nature of dischargers in the coastal zone, wide distribution to wetlands could easily be achieved. For example, 147 distribution points were identified as appropriate for discharge to subsiding wetlands in the Terrebonne and Barataria Basins in coastal Louisiana. These distribution points consist of dischargers of secondarily treated effluent, primarily from sewage treatment plants, oxidation ponds, subdivisions, schools, and trailer parks (Breaux, 1992). Total rural flow in the two basins is about 52 MGD, of which 38.1 MGD was appropriate in terms of effluent quality and total volume per discharger. Based on typical effluent composition of secondarily treated municipal wastewater of 25 mg/l suspended sediments, 20 mg/l total nitrogen, and 10 mg/l total phosphorus (Richardson and Nichols, 1985), and a total wetland area of approximately 783,000 ha in the study area (Louisiana Department of Environmental Quality, 1990), the following loading rates would be applied to the two basins: 0.17 $g/m^2/yr$ of suspended sediments; 0.13 $g/m^2/yr$ of total nitrogen; and 0.067 $g/m^2/yr$ of total phosphorus. Applied to the total wetland area, these additions of sediments and nutrients would be too small to make much of a difference to accretion.

Concentrated at only 148 receiving wetlands, however, they could be distributed in a manner that would help build up the wetland with sediment, and fertilize the vegetation with nutrients.

In sum, water, sediment, and nutrients from small industries and municipalities throughout the coastal region could enhance coastal management by increasing both the total volume and the maximum number of distribution points. Money saved from the construction of conventional or constructed wetland treatment systems, could be applied toward thorough preproject review of potential wetland treatment areas and a sophisticated monitoring and modeling system designed to prevent any detrimental impacts to natural areas.

In attempting to restore altered wetlands with added sediment and nutrients, a number of generic questions arise that pertain to the maintenance of virtually all Louisiana wetlands. Wetland wastewater treatment could be used as a component of a restoration plan to return nutrients and sediments to the wetland, but only after knowledge of the system and goals for its maintenance are established.

In addition to the question of exactly what were the historic hydraulic and nutrient levels that formed and nourished the wetland before it was altered, other questions that need to be addressed include: is the present vegetation identical or similar to previous types, or have different species established themselves? Are natural rates of succession occurring, or have human alterations sped up or changed the natural course? Where human intervention has brought about changes, then what is the ultimate goal - to revert to the previous system, maintain the present one, or manipulate the present one to achieve functional goals or aesthetic values deemed desirable by some segment or all of the present population? Clearly a comprehensive management plan is needed to save coastal Louisiana, and wetland wastewater treatment can be an integral part of such a plan. While the primary benefit of wetland treatment will be the improvement of water quality, it can contribute to the halting of wetland loss by increasing the number of sediment and nutrient distribution points to subsiding wetlands. Holding ponds, pretreatment techniques, rotating receiving areas, and multiple outlet distributions systems could be incorporated into wetland treatment systems in order to restore sediment and nutrients to the coastal plain.

Summary

Wetland wastewater treatment systems are widely used and have proven to be especially effective in warm regions such as the southern United States. When combined with careful designs and monitoring programs, wetland treatment systems show great promise for both enhancing the mangrove wetlands of Campeche and improving water quality. Specific benefits of wetland wastewater treatment include improved surface water quality, increased accretion rates to balance rising sea level, increased productivity as a result of the additions of nitrogen and phosphorus, and decreased financial outlays on conventional sewage treatment systems.

The sediments and nutrients contained in secondarily treated municipal effluent and in some types of industrial effluent (e.g., seafood processors) can be beneficially applied to wetlands in the coastal zone. The warm temperatures, relatively low population density and abundance of wetlands make the Campeche coastal zone an especially appropriate region for wetland wastewater treatment.

The use of natural wetlands as treatment systems conforms to the general principle of ecological engineering described by H.T. Odum (1978) who emphasized the challenge to modern culture as: “Recognizing the high values in existing landscapes and finding ways to fit man’s further developments without waste of the previous landscape values.

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The Relationship Between Shrimp Yields and Intertidal Vegetation (Mangrove) Areas: A Reassessment*

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Abstract

Three data sets (one from a worldwide survey, one from Indonesia and one using Philippine data) are combined to derive a single relationship linking penaeid shrimp yield, intertidal vegetation area (mainly mangrove) and latitude. This relationship, being logarithmic, cannot be used to compute precise estimates of shrimp fishery losses, given destruction or reclamation of a given surface area of intertidal vegetation. It gives support, however, to the widely held perception that intertidal vegetation plays a major role in penaeid shrimp recruitment.

Resumen

Tres juegos de datos (uno de investigaciones a nivel mundial, otro de Indonesia y otro usando datos de Filipinas) son combinados para derivar una relación simple vinculando capturas de camarones peneidos, áreas de vegetación intermareal (principalmente manglares) y la latitud. Estas relaciones, siendo logaritmicas, no pueden ser usadas para computar estimaciones precisas de pérdidas de capturas pesqueras, por destrucciones o usos alternativos de áreas de vegetacíon intermareal dadas. Sin embargo, justifica la noción ampliamente aceptada de que la vegetacíon intermareal juega un papel principal en el reclutamiento de camarones peneidos.

Introducción

Mangrove and other forms of intertidal vegetation have greatly increased in status in recent years. Once viewed as “wasteland”, the sole *raison d’être* of which was to be drained, filled, defoliated, burned or otherwise brought into the folds of “development”, they are now seen as a resource of their own, and the habitat of a variety of aquatic animals, especially the larvae and juveniles of commercially exploited stocks (Kutkuhn, 1966).

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Among the stocks which wholly depend on intertidal vegetation for their recruitment are various species of penaeid shrimps (Garcia and Le Reste 1981). The requirement of such commercially important species as *Penaeus duorarum* in the Atlantic and *P. monodon* and *P. indicus* in the Indo-Pacific for sheltered, estuarine conditions -e.g. as occur in mangrove swamps- has prompted several researchers to postulate, and later to demonstrate the existence, for various areas, of a correlation between penaeid shrimp yields and area of intertidal vegetation (MacNae, 1974; Turner, 1977; Martosubroto and Naamin, 1977).

The purpose of this paper is to expand on these earlier approaches, and more specifically:

- to demonstrate that earlier data (those of Turner 1977 and Martosubroto and Naamin 1977) can be combined into a single relationship;
- to show that data now available from various regions of the Philippines can also be incorporated into this single relationship;
- to show that the correlation between penaeid shrimp yields and intertidal vegetation can be increased by the inclusion of latitude as an explanatory variable; and
- to discuss some of the computational problems associated with both our and earlier approaches, notably with the use of logarithmic relationships.

Materials and Methods

Materials

Three sets of data on penaeid shrimp yields and intertidal vegetation area were used in the present study:

Data compiled by Turner (1977)

The data set consists of 24 pairs of estimated maximum sustainable yield (MSY) of penaeid shrimps and intertidal vegetation areas from 3 continents, together with the latitude corresponding to each area. All MSY estimates consist of the average landings in years with high, stabilized effort (see Turner, 1977). Turner's estimate of MSY were turned from "head off" to "head on" values through multiplication by a factor of 1.6 (Kutkuhn, 1962) to make them comparable with the "head on" values from Indonesia and the Philippines.

The surface areas of intertidal vegetation (salt marsh macrophytes, *Spartina* spp, *Juncus* spp, mangrove) were estimated by Turner (1977, Table 1, numbers 1-14) mainly by planimetry from high-scale maps. These data are reproduced in Table 1, numbers 15-24 and numbers 25-38. Turner's estimates for Indonesia and the Philippines (one data triplet each) have been omitted, much more detailed data being available from these two countries (see below).

Data compiled by Martosubroto and Naamin (1977)

The data set consists of 7 pairs of penaeid MSY and intertidal vegetation area (i.e. mangrove in this case). Both MSY and mangrove area were estimates as in Turner (1977) except for South Java where MSY was estimated from a plot of catch per effort on effort (Zalinge and Naamin, 1976). The Indonesian data are reproduced in Table 1 (#1-7), with latitudes added.

Original data from the Philippines

The data consist of 7 pairs of values of shrimp MSY and mangrove area from seven administrative Regions of the Philippines (Table 2). We used the same definition of MSY as Turner (1977). We have discounted shrimp landings from Region III (Manila Bay and adjacent waters and from Region IX to XII (Southern Philippines) for fear of over-reporting and under-reporting, respectively. The MSY estimates were obtained for each region by adding to the average "commercial" landings of the year 1974 to 1978 the average "municipal" (=artisanal) landings for the years 1977 and 1978 (Table 2). Gaps in the Philippine Fisheries Statistics prevented a more consistent approach.

The surface areas of intertidal vegetation are taken from Anon. (1979). They refer to mangrove areas as obtained using LANDSAT imagery, and differentiate between more or less untouched or "virgin" mangrove and logged-over or "exploited" mangrove (see Table 2). The summary data for the Philippines are given in Table 1 (#8-14).

Methods

Three approaches were used in the analysis of the data in Table 1.

Plotting $\log_{10}$ MSY/area *vs* $\log_{10}$ intertidal vegetation area, and plotting $\log_{10}$ MSY/surface area *vs* latitude, to demonstrate the effects of intertidal vegetation area and latitude on shrimp MSY;

Table 1. Data on penaeid shrimp yield (MSY) and its relationship to intertidal vegetation (mainly mangrove) and latitude *

Nr Area	Latitude ^{0}N or ^{0}S	Intertidal vegetation km^2 x 10^3	Shrimp MSY t x 10^3	MSY / area ** kg/ha
Indonesian Waters				
1 Northern Sumatra	2 N	1.29	9.57	74.2
2 Southern Sumatra	2 S	5.26	14.9	28.3
3 N-E Java Coast	6.5 S	0.587	5.21	88.8
4 South Java Coast	8 S	0.262	4.31	164
5 Kalimantan	0	6.97	11.9	17.1
6 Sulawesi	3 S	0.962	5.24	54.5
7 Western New Guinean & Moluccan	5 S	9.69	15.4	15.9
Philippine Waters ***				
8 Region I	16.5 N	0.010	0.340	340
9 Region II	18 N	0.0268	0.721	269
10 Region IV	15 N	0.406	5.29	130
11 Region V	13.5 N	0.163	4.75	291
12 Region VI	10.5 N	0.0972	3.40	349
13 Region VII	10 N	0.103	2.88	279
14 Region VIII	11 N	0.184	2.45	133
Misc. Asian Waters				
15 Sri Lanka	7 N	0.370	1.01	27.3
16 West Bengal	21 N	41.6	17.4	4.18
17 Malaysia	4 N	30.0	97.0	32.3
18 Pakistan	24 N	32.0	30.4	9.50
19 Thailand ****	10 N	16.4	124	75.6
20 Cambodia	10 N	2.15	1.38	6.42
21 South Vietnam	10 N	4.74	88.8	187
African Waters				
22 Madagascar	17 S	3.20	7.84	24.5
23 South Africa	18 S	1.35	0.845	6.26
24 Mozambique	15 S	8.58	5.28	6.15
American Waters				
25 Ecuador and Peru	2 S	4.00	9.98	25.0
26 Venezuela (Lake Macaraibo)	10 N	12.0	12.9	10.8
27 Trinidad	10.5 N	1.41	0.870	6.17
28 Nicaragua (Pacific Coast)	12.5 N	1.50	2.30	15.3
29 Nicaragua (Atlantic Coast)	12.5 N	21.2	7.97	3.76
30 El Salvador	13.5 N	6.5	5.76	8.86
31 Costa Rica (Pacific Coast)	9 N	3.85	3.81	9.90
32 Guatemala (Pacific Coast)	14.5 N	1.83	3.39	18.5
33 Louisiana to Texas (USA)	29 N	122	65.7	5.39
34 West Florida to Missisippi (USA)	29 N	4.05	22.4	55.3
35 East Florida	28 N	6.15	2.21	3.59
36 Georgia (USA)	31.5 N	14.8	3.08	2.08
37 South Carolina (USA)	33 N	17.6	2.22	1.26
38 North Carolina (USA)	35.5 N	6.43	2.03	3.16

* See text for sources of data; ** To convert kg/ha to tonnes/km^2, divide kg/ha by 10; *** See also Tables 2; **** Probably includes shrimp caught outside Thailand, as is also known to occur with “Thai” fish landings

Table 2. Data on shrimp landings of commercial and artisanal fisheries for 1974-1978 and mangrove areas by regions

		Commercial fishing vessels ($t \times 10^3$)				Artisanal fisheries ($t \times 10^3$)		Virgin mangrove km^2	Exploited mangrove km^2 *
Region	**1974**	**1975**	**1976**	**1977**	**1978**	**1977**	**1978**	(adapted Anon. 1979)	
I	0.055	0.0641	0.0827	0.058	0.051	0.389	0.167	-	9.89
II	-	-	-	-	-	0.695	0.747	6.47	20.3
IV	2.29	4.06	1.73	0.941	1.10	3.89	2.62	346	59.6
V	4.22	4.59	4.42	2.91	0.633	1.37	1.41	101	61.6
VI	3.01	2.70	2.59	1.68	1.08	1.21	1.17	39.0	58.2
VII	2.71	2.18	2.32	1.32	3.74	0.585	0.296	72.1	31.3
VIII	0.527	0.686	0.713	0.667	0.236	2.20	1.56	139	45.3

* Exploited mangrove consists of logged-over areas and low density areas

Plotting $\log_{10}$ MSY *vs* $\log_{10}$ intertidal vegetation area and latitude by means of a multiple regression, and comparing the results with those obtained without taking logarithms, to demonstrate that the relationship between MSY and intertidal vegetation area is not linear;

Calculating the residuals of the best fitting multiple regression and ranking these residuals (r= differences between actual and predicted values) to identify outliers.

Results

The relationship between $\log_{10}$ MSY/ha and $\log_{10}$ intertidal vegetation in km^2 can be described by the equation:

$$\log_{10}\text{MSY/area} = 1.603 - 0.569\log_{10}(\text{int.veg.}) \quad \text{...1)}$$

with R= 0.752, which is significant (P< 0.01). The relationship between MSY/area and latitude (N or S) is, similarly:

$$\log_{10}\text{MSY/area} = 1.861 - 0.03372(\text{lat.}) \quad \text{...2)}$$

with R= 0.452, which is significant (P < 0.05).

The linear plot of MSY (in metric tonnes) on intertidal vegetation area (in km^2) and latitude is described by the equation

$$\text{MSY} = 19.9 + 0.734(\text{int. veg.}) - 0.8292(\text{lat.}) \quad \text{...3)}$$

with R= 0.510, which is significant (P< 0.01). Using logarithms, i.e. plotting $\log_{10}$ MSY on $\log_{10}$(intert. veg.) and latitude, leads however to the equation

$$\log_{10}\text{MSY} = 0.874 + 0.484\log_{10}(\text{int.veg.}) - 0.021(\text{lat.}) \quad \text{...4)}$$

and a much improved fit (R= 0.725), explaining 53% of the variance in the dependent variable (Fig. 1).

Discussion

Our results suggest that the data sets of Turner (1977), that of Martosubroto and Naamin (1977) and the one from the Philippines we present here are, as a whole, mutually compatible and can be incorporated into a single relationship. However, the analysis of the residuals suggests that the values of MSY and/or mangrove areas for Thailand and possibly Malaysia may be erroneous (MSY too high).

The residuals for the Philippine data all have negative signs, i.e., the actual MSY values are lower than predicted by equation (4). Possible reasons for this may be found in the fact that we have not differentiated between virgin and exploited mangrove, that reported shrimp landings were underestimated, or both. The frequency distribution of all residuals is normally distributed (P <0.01), as assessed through a Kolmogorov-Smirnov test (Siegel, 1956). This justifies the use of the statistical model implied in equation (4). (See Blalock 1972, p. 464 footnote).

The problem with a relationship such as (4), however, is that as a logarithmic relationship, it cannot be used in a predictive mode, as is illustrated in the example below:

Figure 1. Plot of observed shrimps MSY (from Table 1) *vs* values predicted by Equation (4). Note relatively good correlation (r=0.725) in spite of some possible outliers (and see text for reason why Equation (4) cannot be used for predictive purposes)

Let us assume a country, located at 1° latitude, south with 3 shrimping grounds, each with associated mangroves as follows:

area A	300,000 km^2
area B	100,000 km^2
area C	50,000 km^2
Total	450,000 km^2

Equation (4) provides estimates of log_{10}(MSY) of 3.50, 3.27 and 3.13 for areas A, B, and C respectively; the sum of their antilogs (6,407 t-year^{-1}) is much more than the value of 3,883 t-year^{-1} that would have been obtained, had the total area of 450,000 km^2 been inserted into equation (4).

This dilemma cannot be avoided: it is due to the fact that large areas of intertidal vegetation have, on a per area basis, a smaller impact on fish yields than small areas, a fact reflected by the much improved fit of eq. (4) over eq. (3).

When reviewing aspects of this shrimp/mangrove relationship, the Standing Committee on Resource Research and Management of the Indo-Pacific Fisheries Commission (Anon. 1980 p. 6) wrote that:

"there appears to be a logarithmic relationship between the recruitment of shrimps in a given stock and the area of mangrove. [...]. If the logarithmic relationship holds, the impact of a given reduction of mangrove area on shrimp production will become greater as the remaining area is reduced".

We have demonstrated that the logarithmic relationship holds (even if it cannot be used directly for predictive purpose) and that, therefore destroying intertidal vegetation will affect shrimp fisheries, especially in those areas that have little of such vegetation.

Postscript (by Daniel Pauly, September 1993)

The above text is a slightly edited reprinted of a paper I presented in 1986 at a Workshop held in Campeche, Mexico, and which was subsequently included in the proceedings of that workshop, a "supplement" to IOC Workshop Report No. 44, edited by A. Yáñez-Arancibia and myself [shortly before publication of that document, in 1988, our names were deleted by an OIC staff who shall

remain anonymous, and who presumably felt that denying us credit would somehow elevate him or his organization...]

This paper was reasonably well-cited, e.g. by Turner and Boesch (1988) and Chua *et al*. (1989), although apparently not for what we thought were its key points. Thus, it seems appropriate to reiterate here what José Ingles and I thought were our key results, i.e., that establishing empirical relationships between intertidal vegetation (including mangroves) and shrimp yields is essentially useless, at least since the contributions of Turner (1977) and Martosubroto and Naamin (1977) because:

(**i**) such relationships only "prove" the obvious, i.e. that penaeid shrimp and intertidal vegetation have similar ecological requirements;

(**ii**) the non-linear character of such relationship and hence the non-additivity of estimate derived from them preclude precise prediction as required for mitigation purposes (e.g., to evaluate the losses of shrimp yields that would result from a certain less of intertidal vegetation).

Item (**ii**) implies that approaches other than empirical relationships should be considered if the shrimp *vs* intertidal vegetation issue is to be tackled. Of these approaches, the one most likely to provide results usable for mitigation is the investigation of the mechanisms by which *specific* life history stages of shrimp use *specific* features of *specific* intertidal plants.

This approach may eventually lead to a new class of generalizations, superior to the empirical relationships discussed above, and providing a further rationale against the reclamation of wetlands, which generally provide more services to humans when left untouched (Ruddle 1987).

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Social and Economic Value of Mangroves. A Method for Estimation and an Example

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Abstract

From a social and economic point of view, mangroves are important to the extent they can provide a flow of goods, services and perform important ecological functions which directly or indirectly satisfy human needs of present and/or future generations. As such, they are valued by individuals and society. Several methodological approaches and methods have been developed to determine the value of natural resources like mangroves but very few have been applied to conditions prevailing in developing countries. Moreover, the social, economic and ecological importance of mangrove forest and ecosystems, have not been fully recognized and as a consequence, they are being increasingly converted to alternative use, namely, shrimp-ponds, salt-ponds, port facilities, agriculture land, etc. High returns to investment on mangrove converted shrimp mariculture and the little recognition of forgone benefits from mangrove attributes and ecological functions are the main driving force behind this process.

In this chapter, the need to account for all value components and forgone benefits from non-sustained use of mangrove ecosystem is argued. A methodological framework where the main ecological social and economic characteristics and significance of mangrove ecosystems are discussed to provide the analytical basis for the valuation process within the Integrated Functional Coefficients (IFCM). Problems related to the dynamics of mangrove forest, data availability, identification of externalities and values of ecosystem functions are also discussed. A model to determine the economic (private) and social value of mangrove structured in terms of IFCM is developed and a simplified application to mangroves of Ecuador is presented as an example.

Resumen

Desde un punto de vista social y económico, los manglares son importantes por lo extenso del flujo de bienes, servicios que proporciona y por llevar a cabo importantes funciones ecológicas, las cuales satisfacen directamente las necesidades humanas actuales y/o de generaciones futuras. Como tal, son valoradas por los individuos y la sociedad. Diferentes aproximaciones metodológicas y metodos han sido desarrollados para determinar el valor de los recursos naturales como los manglares, pero muy pocos han sido aplicados a las condiciones prevalecientes de los países en

desarrollo. Además, al no ser completamente reconocidas la importancia social, económica y ecológica del ecosistema de manglar están siendo convertidos cada vez mas a usos alternos, como estanques para camaronicultura, salinas, instalaciones portuarias, tierras agricolas, etc. Las altas ganacias al invertir en la conversión de manglares para camaronicultura y el poco reconocimiento de privarse de los beneficios de los atributos del manglar y sus funciones ecológicas son las principales causas que están detrás de este proceso.

En este capitulo, se argumenta la necesidad de tomar en cuanta todos los componentes de valor y beneficios perdidos por un uso no sustentable de los ecosistemas de manglar. Un esquema metodológico donde son discutidas las principales características sociales y económicas y el significado de los ecosistemas de manglar que proporcionan la base analítica para el proceso de valoración dentro del Método Integrado de Coeficientes Funcionales (MICF). Son discutidos los problemas relacionados a la dinámica de los manglares, la disponibilidad de datos, la identificación de externalidades y el valor de las funciones del ecosistema. Se desarrolla un modelo para determinar el valor económico (privado) y social de los maglares, estructurado en términos del MICF y se presenta un ejemplo de una aplicación simplificada en los manglares de Ecuador.

Introduction

Mangroves are natural renewable resources located in the inter-tidal and supra-tidal coastal area of the tropics. Approximately 90 % of total world mangrove forests, estimated at about 24 million hectares, are located in tropical developing countries of which some 6 million hectares are in Latin America and the Caribbean. South America accounts for about 75 % of the total mangrove areas of the region. (Kapestsky 1985; Snedaker and Getter, 1985, Snedaker *et al*., 1986; Rollet, 1986; Day *et al*., 1988; Bossi and Cintron, 1990).

Mangroves perform important ecological functions in the coastal ecosystem like preserving water quality, regulating climate, preventing erosion, maintaining biodiversity, retaining nutrients, protecting and stabilizing shorelines, etc. In addition, they can generate a wide variety of valuable products and services which satisfy important human needs like timber, charcoal, fish, birds, navigation pathways, shelter, etc.[1]

The social, economic and ecological importance of mangroves forests and ecosystems and all the benefits they can generate, are not yet fully recognized and as a consequence, they are being increasingly converted to alternative uses[2], namely, shrimp-ponds, salt-ponds, port facilities, agriculture land, etc. (UNESCO, 1980; Ponds and Fiselier, 1991).

Conversion of mangroves into shrimp ponds is currently one of the preferred options, now taking place in several tropical developing countries, like Indonesia, Philippines, Thailand (Soerianegara *et al*., 1989, Macintosh *et al*., 1991), Colombia (Von Prahl, 1990; Zapata, 1992) and Ecuador (Gonzalez, 1993), etc.

Several factors are responsible for this continued process of mangrove conversion to alternative uses. First, policy makers and communities themselves seem to place little attention to the various non-market and indirect uses of mangrove ecosystems; in addition, as timber and related outputs from mangroves result from biological processes that take long periods of time to crystallize, they are rarely accounted as foregone benefits (costs) by current decision-makers (or generations) when conversion is being considered. Second, attractive returns on private investment seem to provide necessary incentives to engage in alternative uses of mangrove areas as the cost of foregone mangrove ecosystem is generally not considered or prices do not reflect their true scarcity value. Third, Governments of developing countries in collaboration with multilateral development agencies and investors from developed countries have encouraged and promoted this process because of the increased foreign exchange earnings and employment opportunities they generate and the high returns foreign investors can obtain (Bayley, 1988; Ruitenbeek, 1990).

These circumstances can thus be summarized, in theoretical terms as: *market* and *policy failures* (Andersson and Bojo, 1990).

1. For a list of products, services and functions of mangroves see: Hamilton and Snedaker, 1984; Yáñez-Arancibia, 1986; Snedaker *et al*., 1986; Dixon, 1989; Hamilton *et al*., 1990; Bossi and Cintrón, 1990; among others.

2. Conversion is the process by which the main features of the mangrove forest are disrupted and the benefits they generate can no longer be enjoyed. In the same process, other features are crated in its place which in turn produce alternative benefits.

Market mechanisms fail to account for all relevant costs/benefit components involved in the use (exploitation) or conversion of mangrove ecosystems. Generally, only market or explicit costs are taken into account. The unaccounted costs/benefits, better known as "externalities" [3], are foregone goods, services, resource attributes and functions which mangrove resources generate but because their outputs are generally not traded in the market or borne/enjoyed directly, they are not accounted by producers as costs/benefits when mangroves are exploited or converted. As most of these unaccounted costs are borne by society in general but not accounted by private producers, a divergence between social and private costs/benefits arises.

In addition, the public good and generally open access nature [4] of most mangrove ecosystems provide misleading signals to policy makers and the community in determining appropriate exploitation rates or management interventions. However, inappropriate interventions are due not only to market failures but also, to the conscious pursuit of policies that serve vested interests of those directly or indirectly engaged in the use/conversion of mangrove ecosystems.

Thus, at the root of these problems are people's behavior and the institutional setting in which the use and exploitation of mangrove ecosystems takes place. As it has been widely demonstrated in the resource economics literature, whenever the property rights/access system is not clearly defined and attractive cost/price ratios for resource output prevail, there is great incentive to over-exploit the resource; in this case, to cut and clear mangrove areas for their alternative use. This behavior is characterized by a pervasive tendency of individuals and commercial organizations to overexploit and misuse the resource. The classical example presented by Hardin in his article the Tragedy of the Commons (Hardin, 1868) clearly illustrates this situation.

Economic values of forests, in general, either as complete ecosystems or as composites of specific output flows, have not been measured with precision and generally not at all (Aylward and Barbier, 1991)). Available data on the actual yearly value of mangroves is equally imprecise and limited, although some estimates reported by Hamilton and Snedaker (1984) are available, showing considerable dispersion in the value placed on complete mangrove ecosystems (US$ 500 per ha/year in Trinidad as compared to US$ 1,550 ha/year in Puerto Rico in 1973-74 period).

In any case, as a recent economic analysis of tropical forest conservation initiatives prepared by the World Wide Fund for Nature, (Ruitenbeek, 1990) shows, the economic benefits attributable to the conservation initiatives in West Africa, exceeded those for a scenario which involved continued unsustainable exploitation and eventual deforestation. Similar results for other parts have been obtained such as by Gupta and Foster (1975) in the USA, Peters (1989) for the Amazonian rainforest, Barbier *et al.* (1991) for wetlands in Nigeria, etc.

The unaccounted divergence between social and economic costs and returns from mangrove conversion use has serious policy implications related to economic efficiency, equity and sustainability. The end result of this accounting failure (market failure) is resource misallocation, inequitable distribution of benefits (over time and people), unsustainable patterns of resource exploitation and the dissipation of potential resource rents. Moreover, when not all costs are accounted for and the produce of mangrove conversion is exported to other countries or regions, like shrimps exported to Japan or USA markets for example, a transfer of resource rent from producing countries (tropical under-developed) to importing countries (rich, industrialized) takes place with strong equity implications between developed and developing nations.

Corrective actions and management interventions to improve the social and economic efficiency (welfare) of coastal ecosystems like mangroves require information and understanding not only of the various biological, physical or ecological processes but about the social and economic factors as well. Furthermore, the dynamics of the various renewable resources needs to be linked with policy interventions as they affect at the same time, the performance of the entire coastal system.

3. The salient characteristics of externalities is that they are costs not borne or benefits not realized, by those tha generate them and consequently, not accounted by them. A "negative externality" reflects a cost imposed on others (directly or inderectly) and not accounted by the agent producing it. Externalities are classified in two groups: "technological or real" and "pecunary or monetary" (Scitovsky…). They may affect few or many individuals belonging to present or future generations; they may have a local, regional or global impact and their effects may be within or between sectors.

4. Furthermore, when mangroves are converted into shrimp ponds, only the market value of land they take is paid. Sometimes, a nominal fee is charged by the government to those retaining exclusive rights of use. However, "user's cost", or the value of mangrove *in situ* is rarely considered and therefore, considerable undervaluation of costs is incurred by producers. Undervaluing total costs implies overvaluing net returns.

A quantitative assessment of the various impacts and cross- effects of alternative actions over the mangrove ecosystem is thus required to account for all relevant costs and returns components. This involves an estimation of the value of each mangrove component and its change and the aggregated impact over the rest of the ecosystem; that is, an economic valuation of coastal resources and the ecosystem.

The dynamic, interdependent, renewable and fragile nature of mangrove ecosystems makes their economic and social valuation a complex venture; therefore, it must be conducted within an ecosystem, quantitative, dynamic and integrated approach to account for all relevant costs and returns components.

Although several methods exits today to conduct economic valuation of individual coastal resources, very few if any, are global, quantitative and integrated in nature.

In this chapter, a general methodological framework where the main ecological, social and economic characteristics and significance of mangrove ecosystems are discussed to provide the analytical basis for the valuation process within the Integrated Functional Coefficients Method (IFCM) (Agüero, 1993). Problems related to the dynamics of mangrove forests, data availability, identification of externalities and value of ecosystem functions are also discussed. A model to determine the economic (private) and social value of mangroves structured in terms of IFCM is developed and an simplified application to mangroves of Ecuador is presented as an example.

A Conceptual Framework for Socio-economic Valuation of Mangroves

From a social and economic point of view, mangroves are important to the extent they can provide a flow of goods, services and perform important ecological functions which directly or indirectly satisfy human needs of present and/or future generations. As such, they are valued and compared by individuals and society according to various criteria and indicators used for this purpose. Several methodological approaches have been developed and methods used to determine the value of natural resources.

Approaches and Methods for Economic Valuation

Various approaches exist to conduct economic valuation of natural resources like mangroves. On one side, within the traditional neo-classical economic analysis, the value of a particular resource is assumed to be determined by individuals and society according to the benefits they are perceived to provide[5]. Individual preferences are expressed through market transactions (or bidding) measured through alterative indicators like prices, willingness to pay (WTP) measures, costs, etc [6]. It is therefore, an homocentric, utilitarian and instrumentalist approach in the sense that natural and environmental resources are treated as instruments to satisfy human needs and valued (by humans) according to the benefits (utility) they provide (Randall, 1987). On the other hand, an emerging transdiciplinary field called *ecological economics*, addressing the relationships between ecologic and economic systems in the broadest sense and within a systems approach, proposes alternative methods to those based on traditional economics (Costanza, 1991). One of this method is the ecological-energetic approach or Emergy Analysis (Odum 1988) which assigns value according to physical measures, that is, units of a single energy type, like solar energy - solar joules- required to produce a given product. Thus, valuation of natural an environmental resources, although conducted by humans, is based on how costly they are to produce (in terms of energy); this cost is ultimately a function of how organized they are relative to their environment.

In general, these approaches differ in the way each one perceives the functioning of the ecologic and economic systems and the way they respond to changes. Nonetheless, whatever the instrument to measure, aggregate or assign values to a given resource, the fundamental problem lies on the concept of value behind the approach being used.

The concept of value

The concept of value as applied to natural resources, indicating worth, has also received different interpretations over time since the famous Tableau Economique with Quesnay in 1758 and the Phisiocrats, who placed the emphasis on the productivity of land as the main

5. However, these perceptions which may differ across individuals and change over time, are not always based on appropiate information and therefore, subject to error when individuals are asked to assign values.

6. Generally, individuals are not aware of the full range of benefits that mangrove provide nor have sufficient information to correctly estimate future benefits. Even so, they can not enjoy them all.

use and exchange value, placed the emphasis on labor as the main source of value. The neoclassicist utilitarian approach (Walras) and the latest concept of Total Economic Value prevail today among a significant number of resource economists (Randall and Stoll, 1983; Randall, 1987). It is becoming well-accepted now within this approach those individual preferences are the fundamental factor determining value (Randall, 1987). It is human beings that do the valuing and in so doing, they use their preferences to demand goods and services (resources) according to units of value assigned to successive units of resource. This behavior is measured or represented by the individual's willingness to pay, providing in this way, a measure of preferences or benefits (utility), and therefore of value (Pearce and Markandya, 1989)[7]. Willingness to pay is considered a better measure of utility than price which excludes consumer surplus [8] per unit.

A Total Economic Value approach

The concept of "total economic value", as applied in the Integrated Functional Coefficient Valuation Method (IFCOM) attempts to capture all source of value of a given resource. In this context, the total value of a given good (or service) can be defined as the maximum amount of money individuals are willing to pay for it (including consumer surplus). For a natural resource like mangroves however, the total economic value is composed of the "use value" plus the "non-use value" or "existence value" (Kristrom, 1990; Vanderpool, 1987). Use value refers to costs and benefits of a resource for which a market exist; be it directly used -in situ-like watching crocodiles, collecting wood or crabs in a mangrove area, etc, or indirectly (outside) via, for example, TV-programs about the life of mangrove communities. Direct use may be "consumptive" (its use deprives other from enjoying it) or "non- consumptive", meaning that others may also enjoy its benefits as well (Reveret *et al*., 1990). Furthermore, use value includes current use value and expected value of future use (including option and quasi-option value). Non-use" or "Existence value" refers to values generated independently of any current or future use of the resource; they are values "in and of themselves" (Vanderpool, 1987). Randall *et al*. (1990) distinguishes: bequest/heritage value, vicarious value, ecological value, cultural/heritage value and preservation/aesthetic value. However, in spite of the fine classification and distinctions of the various value components of total economic value presented above, as with any taxonomy, they are somewhat arbitrary and distinctions are rather fuzzy at the margin. They do provide in any case, criteria to identify value components beyond the simple consumptive use-value approach which has traditionally received all the attention in past research on the topic (Bishop *et al*., 1987). Consideration with respect to the value of future yield (output) of a given resource like mangroves are of vital importance; this issue is dealt with in the Integrated Coefficient Method through the use of sustained yield functions with appropriate discounting of costs and benefit streams during relevant periods of time.

The growing concern for environmental preservation and sustainable use of renewable resources like mangroves has highlighted the usefulness of the concept of non-use value. Although preservation and non-use values are not clearly attached to any particular component of a given resource, they tend to be associated with it as a whole (ecosystem). Thus, the role of a resource like mangrove ecosystems in preserving biodiversity or determining the uniqueness to culture and heritage contribute to the existence, bequest and option value that individuals place on preservation.

The mechanics of valuation

Social and economic valuation of mangrove and ecosystem resources is a process by which a quantitative assessment of their worth is made in units of value. Aggregation and comparison of heterogeneous elements is best done by using money as a numeraire. When money is used as a common denominator for value, it is then possible to rank, compare and make appropriate assessments of the relative convenience of one policy action over another. Thus, valuation of mangrove ecosystems should provide useful information required for policy design and management interventions when expressed in common and comparable units in which alternative options are also presented.

For valuation purposes, mangroves can be viewed as an exploitable resource from which a wide variety of goods, services and functions can be obtained, generating employment, foreign exchange, and personal wealth. All the these products can be extracted or enjoyed on sustained-yield basis provided extraction practices do not disrupt the functional capacity of the ecosystem. The value of these products (flows) whether in the form of goods, services, attributes or functions, in the long term, must be linked to the value of the mangrove ecosystem (Farnworth *et al*., 1981), although not all of them are traded in the market, used directly or enjoyed in the current period.

7. In the same way, it is implied that there would not be a willingness to pay for something which is not desired

8. Willingness to Pay= Expediture (price) + Consumer Surplus

Determining the value a of a renewable resource like mangroves is a complex and difficult task. Not only problems of sustainability and optimal use over space and time are at the heart of the matter, but equally important are the accounting of net benefits from all goods and services generated by the mangrove ecosystem, including the estimation of the value of ecological functions played by the mangrove system, its attributes and the non-tradable goods and services they generate.

Valuation methods

Several approaches have been developed to value natural renewable resources like mangroves. Several classifications exist which place the emphasis on various aspects of both the nature of the resource (i.e. renewable, non-renewable; private or public; etc) and the source of information about their value: direct, indirect or contingent methods. Moreover, several schools of thought with respect to the concept of value still prevail. Fig. 1 shows a schematic summary of the main economic valuation methods [9].

However, to date, very little efforts have been made in developing countries to measure the economic, social and environmental value of natural renewable resources like mangroves, within an integrated perspective. Although, calculations of value for some specific resources are found in the literature (mostly for Southeast Asia), they only reflect spot market valuations. No mention is made about “ecological”, “optional or quasi-optional”, “non-use”, “contingent” or “existence” values (Dasgupta and Goran-Maler, 1990). Similarly, no attempts have been made either to evaluate, in monetary or economic terms, the outcome of alternative exploitation strategies.

As a consequence, existing techniques and approaches developed to value environmental and natural renewable resources in industrialized countries have rarely been applied or adapted to the tropics. Alternative methods specially designed to conditions prevailing in tropical Latin America have not been developed either. Thus, the need for information required for this kind of exercises has not been acknowledged and so, little data/information or guidelines exist to determine the economic, social or environmental value of mangroves in tropical Latin America.

The nature and significance of mangrove ecosystems

Mangroves are highly diverse, complex, fragile and productive ecosystems. Their diversity results from the different environmental conditions in which they exist determining at the same time, their growth rates, density and distribution patterns over time and space. The intricate network of relationships among components of the ecosystem and their vulnerability to siltation/sedimentation, changes in salinity, temperature, hydroperiods and changes in physical/chemical properties of the substrate, make them a complex and fragile ecosystem. The use or exploitation[10] of mangrove by humans can also affect its dynamics and characteristics, adding complexity to the understanding of the ecosystem functioning.

Thus, for valuation purposes, mangroves are considered parts of an ecosystem where several interacting components of diverse nature, specific spatial distribution and temporal dynamics can be identified, determining its performance (yield).

Mangroves as complex and dynamic ecosystems

A clear and satisfactory definition of “mangrove ecosystem” or related terms like “mangrove community”, “mangal”, or “mangrove formation” for valuation purposes is not yet available (Barth, 1982). Moreover, because of the diversity of factors determining the characteristics and socio-economic performance of a particular mangrove area, it is important to determine the boundaries and hierarchy of the various system components as a first step in the valuation process.

In general, mangroves are defined as holophytic, woody, seed-bearing plants (Snedaker and Getter, 1985) ranging in size from tall trees to small shrubs. Although mangroves differ from one place to another in terms of their structure, composition and functioning, some basic components for valuation purposes can be identified in any mangrove ecosystem subject to use/exploitation. These basic components are:

9. For further details on these methods see: Hufschimidt *et al*., 1983; Reveret *et al.*, 1990; Dixon, 1990: Costanza, 1991; Munasinghe and Lutz, 1991; Agüero, 1993

10. The terms “use” and :exploitation” are utilized in their economic interpretation and therefore, as synonymus in this chapter

Figure 1. Economic valuation methods

* the natural and environmental resources base; including mangrove forest and associated flora and fauna (aquatic, terrestrial and aerial), the water bodies surrounding the forest and the substrate

* the technological system; methods of exploitation, means of production, infrastructure, factor endowments, etc.

* the socio-economic system; composed of human settlements, socio-cultural institutions, laws, regulations, market conditions, etc.

Figure 2 shows a schematic representation of the basic components and interactions of the mangrove ecosystem for valuation purposes.

In addition, several interrelated activities and processes take place within the ecosystem affecting the performance of the various components within the system and outside it. Among the most important ones, are:

* Resources dynamics; that is, how the various resources of the mangrove ecosystem and their dynamics change over time (natural equilibrium) and how they are affected by human interventions (use/exploitation or conversion).

* Human activities; the way mangrove resources are used or converted by human activities and the resulting net benefits from these interventions.

Figure 2. Schematic representation of basic components and interaction in mangrove ecosystems

* Technological processes or production processes; characteristics of the rate of output per unit of input and the instruments and factors required for each production process.

The interaction between the resource dynamics, human activities and the technological processes imply that, given the renewable nature of mangrove ecosystems, they are capable of providing a flow of output (good, services and functions), ad infinitum, if appropriate rates of exploitation (extraction) are respected. If exploitation rate is zero (preservation), a natural steady-state equilibrium will be reached which will be altered only if environmental or exogenous factors affecting it, change. However, if the rate of extraction is greater than the rate of regeneration or net growth, overexploitation takes place leading, if conditions persist, to extinction [11].

Figure 3 represents these relationships for typical renewable resource like mangroves in relation to time. In Fig. 4a different levels of sustained yield (Y) are related to various levels of Effort (E) at corresponding levels of biomass. In Fig. 4b sustained yield levels of effort (E) and costs (COPUE), while fig 4c and 4d, different levels of effort in relation to levels of sustained yield determine sustained yield (catch) per unit effort (CPUE).

The spatial distribution of mangroves is an important factor determining growth, yield, functional characteristics and opportunity costs associated to alternative uses of the land. As a consequence, for valuation purposes, a given mangrove ecosystem can be broken down or

Figure 3. Simplified relationships between sustained yield and effort for mangrove renewable resources

divided into various spatial areas if heterogeneity is a prevailing factor. Snedaker and Getter (1985) recognize five major mangrove forest-structure types: fringe, basin, riverain, overwash and dwarf. Although species zonation, created by gradients in topography and soil salinity, is an important factor determining their structural organization, differences in coastal landform, patterns of surface-water flushing and salinity are equally or more important factors as well for valuation purposes.

The yield of a renewable resource like mangroves under exploitation, can be represented by the change in time in a logistic growth function (sustained yield functions), in which different levels of resource exploitation (rate of extraction/transformation) under steady-state equilibrium represent different sustained yield levels, in number of individuals in weight/biomass.

Mangroves as a source of valuable goods, services and functions

For long, mangrove areas throughout the developing world were considered as an unhealthy, unproductive and useless environment (Blasco, 1991). Their ecological, social and economic importance was neglected

11. In this case, current yield is obtained at the expense of future yield, and is generally the case when exploitation takes place under conditions of open or uncontrolled acces. Conversions is thus an extreme case of over-exploitation with an infinitely large rate of extraction

Figure 4. Basic bio-techno-economic functional relationship in renewable resources

for centuries. Products and services which small scale hunters and fishermen harvested and obtained from the mangrove forests were taken for granted with no economic (market) value. This perception has changed over time and increasingly, the different value components of mangroves are being better understood and recognized.

Mangroves can generate a wide variety of products (like wood, charcoal, timber, mollusk, crustaceans, reptiles), and services (like tourism, water transport), etc. In addition, they play important ecological functions of diverse nature and have special attributes that bear significant economic or social values like cultural uniqueness, aesthetic effects, recreation, etc.

The value of products and services is generally realized directly through either consumption (destructive) or use (usually non-destructive). However, the value of attributes and functions performed by mangroves is not captured directly and thus, its estimation in quantitative terms is extremely difficult and needs to be determined indirectly through their contribution to the support of observable or measurable social or economic activities

Mangrove areas also have alternative uses which can be accessed by its conversion into aquaculture ponds, agricultural land, urban areas, salt flats, mining or other uses (Soemodiharno and Soeriaregare, 1989). Different uses of mangroves generate different kinds of goods, services and functions. For each alternative use there is an associated costs and benefits stream. Thus, the social and economic value of mangroves is determined by the amount of goods and services they can provide to satisfy human needs over time in their best alternative use, and the nature and intensity of their attributes and ecological functions they perform.

The mangrove management problem

The multiple-use nature of mangroves on the other hand, implies that choices need to be made with respect to the appropriate rate of exploitation for alternative resource uses. The selection criteria, from a socio-economic point of view, would undoubtedly be the attainment of the highest possible flow of net benefits over time (discounted), subject to constraints imposed by society [12].

Decisions are made regarding the use and exploitation of a particular natural renewable resource like mangroves, according to the expected flow of net benefits to be accrued from it over time. (Salm and Clark, 1982) Additional productive resources (labor, capital, technology) are allocated to their exploitation if expected net discounted benefits are positive and greater than alternative options. The standard procedure used to determine investment decisions is to conduct a cost-benefit analysis in which all costs and returns are included, evaluated and compared. Technical, economic and social feasibility are determined and appropriate actions identified. However, in poor developing countries, decisions are made based more on experience and short-run market signals or in the pursuit of self-vested interests than on complex, sophisticated and elaborated studies. As a consequence, decision makers (usually government officers or private investors) account only for what they perceive as costs and returns to their venture.

Under these circumstances, at least two reasons explain why mangroves are being misused throughout the developing world today. The first one relates to the apparent low (or zero) opportunity cost presently assigned to loosing mangroves. Users (destroyers) of mangroves do not need to pay foregone benefits from mangroves to society, and when relative high prices of shrimps in the international market or other commercial or agricultural products from mangrove prevail, investment in mangrove conversion becomes an attractive financial venture. The second reason is found in the open access nature of most mangrove areas in poor developing countries, where coastal dwellers with little alternative employment opportunities, engage in mangrove resources exploitation. Under this situation, especially relevant in densely populated countries like Indonesia or Philippines, millions of small, independent, uncontrolled and uncoordinated decisions are made regarding resource use. The aggregate results of these minor and individual decisions, which do not take into account the effect of their own decision on the rest of the system (externality), are major impacts on the ecosystem and resources base, generally characterized by ecological disruptions and resource abuse (unsustainable).

On the other hand, where market mechanisms guide decisions regarding resource use, and property rights are not clearly defined like in most developing countries, a strong incentive and bias towards conversion appears whenever prices of shrimps or other products are high relative to their exploitation costs. Taxes, fees, royalties or compensatory schemes besides access regulations are common practices and well known to economists and policy makers. Appropriate tools for effective implementation of these strategies exist. However, a major problem which needs to be solved in every case is to determine the real value (an therefore opportunity cost) of the mangrove subject to possible management interventions. Economic value of resources is therefore needed not only to determine whether a particular resource should be further exploited or converted, but to compare if additional resources should preferably be allocated to alternative uses.

Thus, whether misuse of mangroves is driven by inappropriate market signals failing to internalize foregone benefits or by growing rural poverty where market mechanisms fail to perform efficiently or by inappropriate policy interventions, the common problem is the existence of unrecognized externalities associated to unsustainable uses of mangroves.

12. One of the most important constraint in thi respect is sustainability; other important constraints may be: the establishment of protected areas or fishing periods, banning the use of certain exploitation techniques like the use of dynamite-fishing or trawling in near-shore areas, etc.

However, management interventions can affect a limited set of factors or control variables, while most of the relevant determining ones are exogenous or uncontrollable (constraining parameters and variables). Thus, multiple trade-off's need to be considered in determining the best (optimal) management strategy for the use and exploitation of a mangrove ecosystem aiming to maximize the net social benefits (welfare) that society can obtain from it on sustained basis.

Solution to the mangrove misuse problem seems to be relatively simple: regulate exploitation activities and/or control access. However, where population is not only large but relatively poor and widely scattered like in Indonesia (150 million people in 15.000 islands) or Philippines (50 million people in 7.000 islands), effective control to limit indiscriminate use or access is almost impossible within reasonable costs. In this case, a community-based management approach seems to be the most appropriate option, as externalities and environmental costs are internalized by the community and therefore have a better chance of being properly accounted for over time.

A Socio-economic Valuation Model for Mangrove Ecosystems

The integrated functional coefficients methods (IFCM) is a general method designed to determine the socio-economic value of coastal resources with emphasis on the characteristics and conditions prevailing in developing countries (Agüero, 1993). It adopts a quantitative, monetary, homocentric, integrated and total value approach to model the coastal ecosystem, its functioning and value accounting procedure. The application of this method to determine the socio-economic value of a particular mangrove ecosystem is made by constructing a specific model, structured in terms of a mathematical programming problem and solved using a microcomputer-based software, specially designed for this purpose called OPUS I (See ECLAC/ICLARM Technical Report, 1993).

Basic Procedure for Constructing the Valuation Model

The following summarized steps are required to construct the socio-economic valuation model:

1. Characterize the mangrove ecosystem, determining the intrinsic characteristics of the resource base and ecosystem dynamics (renewable and non-renewable resources; population dynamics, causal relationships, etc)

2. Characterize the socio-economic system, determining basic behavioral conditions (rates of resource use; supply and demand flows for inputs and outputs; employment rates; etc), parameters (like unit costs, prices, etc) and socio-institutional constraints (prohibitions, legal and customary laws, regulations, etc).

3. Determine the technology vector and infrastructure endowment, identifying alternative feasible production processes and yields, input requirements, infrastructure and factor availability.

4. Determine relevant production sectors and economic activities (formal and informal)

5. Identify basic components and processes for each relevant activity

6. Establish causal/functional relationships among components for processes and activities

7. Verify convexity, additivity and other necessary mathematical conditions of relevant variables

8. Construct the input-output functional coefficients matrix (Functional integrated coefficients)

9. Determine the corresponding constraining vector

10. Construct the mathematical programming problem objective function within the concept of Total Economic Value

11. Construct the mathematical programming matrix (tableau)

12. Collect necessary data-information; construct the Data Base (DABS)

13. Feed the model; run the model; analyze results

14. Conduct sensitivity; interpret final results.

Basic Components for the Socio-Economic Valuation Model

The basic components of the socio-economic valuation model can be summarize in terms of a set of relevant interacting sub-systems, characterized by a set of control variables, parameters and integrated coefficients and a constraining vector.

- Interacting sub-systems:

Ecological, environmental and mangrove resource system

Technological and factor endowments

Socio-economic andinstitutional system

- Control variables

Output level for each resource component (sector/activity) of the mangrove ecosystem

Activity level for each transformation stage (process) of mangrove resources

Output level for each product obtained in alternative uses (conversion) of mangrove area

Activity level for each transformation stage of products from alternative uses

Output level for each externality process

- Parameters and Integrated Coefficients

Price vector for all alternative outputs from mangrove resources

Costs vector for all alternative inputs

Integrated coefficients for physical yields of resources and processes (effort)

Integrated coefficients for monetary yields of products, services and functions (output)

- Restrictive levels

Restriction on mangrove ecosystem (area) and resources use

Restriction levels for factors and infrastructure endowments

Legal, institutional and social restrictions

The Formulation of the Mathematical Programming Model

Approach

For modeling purposes, it is assumed that benefits from mangrove can be attained either by using it directly or by partial or total transformation of the mangrove system. Thus a continuum ranging from total preservation to total conversion can be used to represent the various feasible combinations.

The method makes use of mathematical programming techniques to account for all relevant flows of benefits (positive) and costs (negative) resulting from different levels and combinations of resource exploitation. The largest difference between total revenues minus total costs (including externalities) from mangroves determines the Net Social Benefits derived from its exploitation in its best alternative use, within the constraints imposed on access, production and consumption (See Fig. 5 for a summarized mathematical programming formulation).

The best option (or mix) will be the one providing the largest total net benefits properly discounted over time. However, a distinction needs to be made between financial/economic and social benefits. The former involves the accountability of costs and returns obtained from the use and enjoyment of all goods and services obtained from mangrove use. In the latter, the value of mangrove functions needs to be internalized in addition to those from goods and services.

For practical purposes, it will be assumed that conversion of mangroves into shrimp ponds is the best option (among all competing alternatives) and thus, measuring the economic value of the mangrove area in relation to this option implies all best alternatives (opportunity cost).

Structure

The various sectorial activities within the mangrove ecosystem, exploitation/use processes, resources and socio-economic dynamics, constraints and input-output functional relationships among the components of the mangrove ecosystem, are structured in terms of a mathematical programming model. This model contains an objective function to be optimized, a technical coefficient matrix relating activities with constraints in a functional way and a vector of constraining factors.

a. Objective Function:

The objective function, constructed in terms of a Total Value Approach, accounts for all sources of value (positive or negative) including externalities, non-market goods, services, attributes and functions to be accounted for if appropriate value indicators are available. These sources correspond to the control variables whose values need to be determined at the optimum.

It is generally represented as follows.

$$NSB = \sum (TR - TC \pm NM)$$

$$= \sum (\rho_{zro} * X_{zsaro}) - \sum (c_{zsaro} * X_{zsarotg}) \pm$$

$$\sum (e_{zsartg} * X_{zsarotg}) \pm \sum (OB_{zsaro} * X_{zsaro})$$

NSB : Net social benefits derived from the use of mangrove resources in their best alternative use over time.

TN : Total market revenues from mangrove resources use

TC : Total market costs from mangrove resources use

NM : Non-market benefits from mangrove resources and ecosystem

X_{zsaro}: Quantity of the o-th output produced using the rth resource at the ath activity in the sth economic sector of the zth location.

$X_{zsarotg}$: Quantity of the o-th output produced using the gth gear, tth technology level and the rth resource at the ath activity in the sth economic sector of the zth location

p_{zro} : Market price of the oth output (goods and services) obtained from rth resource in the zth location.

c_{zsaro} : cost of producing one unit of the oth output using the rth resource at the ath activity in the sth economic sector of the z-th location.

e_{zsartg}: Positive or negative externality generated by the gth gear, tth technology using the rth resource in the ath activity of the sth economic sector in the zth location.

OB_{zsaro} : Other positive or negative benefits derived from the rth resource in the sth economic sector in the zth location, and:

z: Spatial location of the resource (i.e.; country, region, zone, sub-zone).

s: Economic sector (i.e.; fisheries, tourism, forestry, mining, etc).

a: Economic activity (i.e.; logging, harvesting, processing, transporting, storage, marketing and consumption).

r: Mangrove resource (i.e.; fish, tree, reptiles, birds, etc.

o: Output (i.e.; dried fish, fresh fish, wood, charcoal, wood poles, shrimp, camping, hikes, etc).

t: Technology (i.e.; capital intensive or labor intensive)

l: Scale of production (i.e.; large, medium or small).

g: Gear or instrument (i.e.; boat, net, hook, harpoon, axe, sawdust, chainsaw, etc).

Further specifications to distinguish specific features of the resource products or markets can be made, like distinguishing between frozen shrimp (round or tails) or boxes (of 20; 60; 100 pounds each) or quality size (grade), etc; similarly, markets can be distinguished between local, domestic and foreign (Europe, Asia, and Africa); etc. There is practically no limit to the level of desired specification. However, the order of sequence is important to avoid inconsistencies. All positive signs indicate benefits and negative signs indicate costs. Therefore, if a minus sign is attached to other benefits (OB) implies a cost.

Intra and inter-sectoral functional relationships guiding and binding the alternative uses of mangrove ecosystems are represented by a set of vectors and matrices as follows.

$$[A\ X] \leq B$$

where:

A: Technical coefficients (integrated) matrix of size n * m, containing m functional relationships (restrictions) related to n processes.

X: Quantity of output vector of size n * 1.

B: Vector of resource availability, factor endowments, regulations, etc (RHS).

Some of the relevant restrictions in mangrove resources valuation are:

- coastal and mangrove resources availability;
- values according to relationships between extraction rates and yields (sustained yield functions for renewable resources);
- installed capacity, given by available factors for processing, harvesting, transporting, etc;
- yield coefficients, estimated relating output to input, technology and resource abundance;
- demand restrictions, determined by demand functions;
- balance equations, to transfer and balance quantities across the tableau;
- convex sets to assure compliance with convexity conditions;

b. Non-negativity constraints

Non-negativity constraints are a set of conditions to ensure well behaved mathematical functions in the model, and it is represented as follows.

$$Xj >= 0$$

Input-output relationships reflecting the response of each resource to varying levels of exploitation (effort) in relation to output (yield) are directly related to costs (costs per unit input) and associated externalities (impact coefficients). Basic input-output relationships in production are synthesized in “yield per unit of input coefficients”, while their economic counterpart are represented by “cost-revenue per unit of output coefficients” (See. Fig. 5).

Output per Unit of Effort		
Integrated Coefficients	Sector	Resource
CPUE	Fisheries	Biomass
LPUE	Forestry	Biomass/Area
EPUE	Tourism	Site / Infrastructure
EIPUEi	Environmental	Carrying Capacity

Cost per unit of Output		
Integrated Coefficients	Sector	Functional relationships
CPUC	Fisheries	f(inputs, techn., extern., biomass)
CPUL	Forestry	f(inputs, techn., extern., biomass)
CoPUE	Tourism	f(inputs, techn., extern., population)
CPUEli	Environmental	f(carrying cap./Nat.Funct., techn., effort)

Figure 5. Basic interactions in the mangrove ecosystem; integrated functional coefficients. CPUE- catch per unit of effort; LPUE= logging per unit of effort; EPUE= enjoyment per unit of effort; EIPUEi= environmental impact per unit of effort of the ith activity; CPUC= cost per unit of catch; CPUL= cost unit of logging; CoPUE= cost per unit of enjoyment; CPUEIi= cost per unit of environmental impact of the ith activity

Parameters and coefficients of associated costs (COPUE), revenues (prices) and production functions (technological coefficients) are exogenous to the model (determined outside) and obtained by means of various statistical and econometric techniques.

A schematic representation of generalized objective function and table is presented in figure 5.

Optimal Value, Economic Values and Social Values

The optimization process, i.e., the search for the best (optimal) value of the control variables (output and activity levels) within the feasible set of alternatives, determines the economic value of each resource in its best alternative use/exploitation over time. The vector of shadow prices indicates how the net social benefits changes when one additional unit of mangrove area is made available, reflecting in this way, the social value of a unit of resource ecosystem area.

The mathematical programming problem is solved by means of the simplex algorithm (Revised Simplex Method) using OPUS, a computer software package developed for this purpose.

Data from various sources is collected, stored, processed and retrieved in/from a Data Base System (SISRECO V.1) which is part of OPUS software.

Valuing Mangroves in Ecuador. An example

In this section, an application of the Integrated Functional Coefficients Method for socio-economic valuation of coastal resources is presented as an example, applied to value mangrove resources in the Guayas Province of Ecuador.

First, the characteristics of mangroves in Ecuador and the Guayas Province are summarized to provide the basis for the modeling exercise. Then, a simplified socio-economic valuation model is specified and main results obtained are presented and discussed.

An Overview of Mangroves in Ecuador and Guayas Province

Ecuador is located in the Southwest Coast of Latin America, between Colombia and Peru (See Fig. 6). Its coast is approximately 530 km. long and has a varying width ranging between 20 and 200 km.

There are four coastal administrative provinces in Ecuador: El Oro, Guayas, Manabi and Esmeraldas. The total coastal area is approximately 314,000 ha of which 51.6 % (or 162.055 ha) correspond to mangrove areas, 46.4 % to shrimp ponds and 2 % are salt flats (CLIRSEN, 1992).

The Guayas Province, represents about 34 % of the national coastal area, and has the largest mangrove area in the country with 116.065 ha (or 66 % of the national's total).

Between 1969 and 1991, approximately 41,570 ha of mangrove areas in Ecuador were destroyed/converted to alternative uses, of which about 39,000 ha were cleared for shrimp mariculture. In the Guayas Province, conversion in that same period was about 15,600 ha, representing 37 % of the country's total convertion (CLIRSEN, 1992). In Guayas, the entire converted area was used to build shrimp ponds.

There are about 56 species of mangrove world-wide. Eight of these species are found in Ecuador (Cintron *et al*., 1981) corresponding to the *Rhizophora* spp, *Avicennia* spp, *Laguncularia* spp, *Conocarpus* spp and *Pellicera* spp genera. In the Guayas Province there are basically *Rhizophra* spp, *Avicennia* spp, and *Laguncularia* spp with an average density of 185 trees/ha (Twilley, 1989).

The coastal area of Ecuador is characterized by warm (>25 ^{o}C), and low salinity (<35 ‰) tropical waters. The area is also characterized by two clearly differentiated seasonal periods: summer (Jan-Apr) and winter (Jul-Oct) and the presence of El Niño Phenomena, bringing a periodic influx of unusually warm waters (29-30 ^{o}C) in the pacific coast particularly off Ecuador and Peru. Its occurrence produces dramatic changes in the local meteorological, oceanic and biological regimes having, as a consequence, great socio-economic impact on the coastal region (Cucalon, 1989).

Shrimp mariculture is the most important economic activity in the coastal area of Ecuador and the largest national source of foreign exchange after oil. In 1990, the country produced 76 % of the total shrimp production in the western hemisphere.

Total production of shrimp of Ecuador in 1991 was approximately 100,000 ton with an industry composed of 1,500 farms and 120 hatcheries. Total exports of shrimp generated US$ 420 million dollars of foreign exchange providing employment to about 250,000 people distributed in the various activities of the industry (Fitzgerald, 1992).

Although mangroves can provide a wide variety of products, in Ecuador, they are mostly used for shrimp ponds. Only about 1,500 ha have been used for urban expansion. There are few salt ponds; rice production is not a good option (Hornna *et al*., 1980) and coconut plantations are minimal (CLIRSEN, 1986). Finally, they are rarely used for recreational or tourism purposes.

Mangrove forest are logged and converted into woodpoles, charcoal and timber. It is generally a small scale type of activity conducted by family groups. Production of tanino is minimal due to bad market conditions. Agriculture is also of small significance due to the poor quality of the soil. As in most tropical countries, the preferred alternative use of mangrove ecosystems in Ecuador has been for shrimp mariculture. This process has been induced by attractive market conditions which in the average, has yield very high returns to private investors engaged in the industry (Agüero and Gonzalez, 1992).

Shrimp production systems in Ecuador, are classified according to the stocking density and feeding strategy into: intensive, semi-intensive and extensive system. Intensive systems are those with very high stocking densities (80,000 to 500,000 juveniles per ha) requiring supplemental feeding and mechanical water exchange and aeration (this system is used on experimental basis only in Ecuador and represents about 1 % of the national production) with yields ranging between 2,200 and 7,300 kg/ha/year; Semi-intensive systems have high stocking densities (40,000-120,000 juveniles per hectare) also requiring some

Figure 6. Map of Ecuador, source (Twilley (1989)

supplemental feeding and mechanical water exchange with yields ranging between 500 and 2,200 kg/ha/year; extensive systems are those with low stocking densities (10,000- 40,000 juveniles per ha) with no or minimal supplemental feeding and relying mainly on tidal water movements for in-pond water exchange and shrimp larvae; their yield is also low ranging between 100 and 500 kg/ha/year.

According to DGP statistics for 1989, there were about 88,000 ha of land allocated for shrimp farming in the Guayas Province. About 29,600 ha of this area were located in the inter-tidal ("beach") zone. A total of 827 shrimp farms (about 50 % of the total number of farms in Ecuador) were operating and producing an estimated production of 28,000 m ton.

For valuation purposes, shrimp farming in the Guayas can be decomposed into several basic activities like: culture, processing, storage, transport and marketing.

Culture activities in Guayas Province are characterized by a two-phase nursery and grow-out pond system; shrimp post-larvae are stocked in nursery ponds (0.5 to 1 ha) at very high densities (1 million post -larvae per ha) and nursed until larvae reach 0.5 to 1 gram in body weight; then they are transferred to stocking ponds. In semi-intensive production systems (like those in Guayas Province), shrimps are raised in regularly-shaped earthen ponds with flat bottom and water depths ranging from 1 to 1,5 m; 10 to 20 % of the water is mechanically exchanged daily and supplemental feeding is added when individuals reach 8 to 10 grams in weight (Chua and Kungvankij, 1990). At harvest time, ponds are drained and shrimps are caught at the drainage exit by nets.

Mayor inputs required are water, feed and electricity. Major productive factors are shrimp post-larvae and juveniles, land and labor. Villalón *et al*. (1989) estimated that shrimp survival from nursery pond to harvesting in semi-intensive production systems is about 49 %.

After harvesting, shrimps are transported by trucks to packing plants where they are usually cleaned, headed-off, classified, packed and frozen; whole shrimps are also packed and frozen for export (CPC, 1989). Yield from whole shrimp to head-off product, at packing plant is estimated at about 67 % (FEDECAM, 1989) with an average loss of 2 %.

Guayas Province contributes with about 81 % (770,560 lb/day) of the country's cold storage capacity. It involves three different technologies: freezing tunnels plated and brine freezing which are 65 %, 29 % and 6 % of the total province capacity respectively (Falconi and Miranda, 1989).

Approach, structure and components of the valuation model

Approach and methodological considerations

The socio-economic value of mangrove ecosystems in Guayas Province is assumed to be determined by the total output they can produce, that is, the quantity of goods and services they can generate and the functions they can perform during a given period of time. Mangrove areas on the other hand, have important alternatives uses which can generate valuable goods like shrimp products. Thus, the value of mangroves is related to the quantity of goods and services (yield) they can generate including the functions they perform and the amount of benefits each output (goods, services and functions) provides. Different uses of the mangrove areas generate different combinations of output; in turn, different output combinations determine different streams of costs and benefits and therefore, of total value (See Fig. 7a, 7b, 7c).

Value of goods and services generated by mangroves are determined by people, generally through market transactions and according to the amount of benefits they are perceived to provide. Prices, are generally taken as representing the value people assign to the benefits a given good or service provides. However, not all valuable output from mangroves are traded in the market and therefore, their value, i.e. price, is not readily available. Most of the ecological functions of mangroves belong to this category. Surrogate prices, opportunity costs or simply hypothetical values assigned to these outputs, will be used for this exercise.

For valuation purposes, a mangrove area is divided in homogenous geographical units (hectare) and therefore, assumed that the entire mangrove ecosystem can be used in various ways simultaneously. Then, a mix of different uses which maximizes total net benefits to be obtained from the entire ecosystem can be identified. This would represent on one hand, the best use of the mangrove area and at the same time, the one providing the highest amount of net benefits to society. Its value is thus determined by the maximum amount of benefits it can provide over time. Benefits obtained from the use and exploitation of mangroves whether directly or through its conversion, are generally realized within a given socio-cultural and institutional environment, which places constraints in the way the exploitation process takes place (laws, regulations, prohibitions, etc). Furthermore, renewable resources like mangroves have their own dynamics over time (population dynamics) which imposes further constraints on the amount of output to be obtained under different exploitation strategies.

The socio-economic valuation problem can then be casted in terms of the identification of the best use option (mix) that provides the largest (maximum) total net benefits (value) to society, properly discounted over time. Since not all costs and benefits are accounted for by market transactions, a distinction needs to be made between "economic" and "social" value. For practical purposes, the first will refer to the value of total net benefits as accounted using market prices while the second, will include non-market values and externalities.

Structure and model specification

The problem of identifying the optimal mix of resource use can be solved by means of mathematical programming optimization techniques. A Net Social Benefit Function (NSBF), representing the aggregate net value of all relevant sources of costs and benefit, including externalities and other non-market outputs is maximized over time subject to biological, ecological, technological, social, economic and institutional constraints.

Input-output relationships reflecting the response of each resource (fish stocks, forest biomass, shrimps, etc) to varying levels of exploitation (effort) in relation to output (yield), are directly related to costs (cost per unit of input) and associated externalities (impact coefficients) using integrated coefficients. Factor endowments, resource dynamics, market conditions and institutional setting are imposed as "constraints" binding the optimization process so that the optimal value is determined within the feasible set of options.

$$BSN = \Sigma X_B * P_B + \Sigma X_S * P_S + \Sigma X_F * B_F - \Sigma X_B * C_B - \Sigma X_S * C_S + \Sigma X_C * P_C - \Sigma X_C * C_C - \Sigma X_I * C_I$$

Figure 7a. Benefits and costs from alternative uses of mangrove area

Figure 7b. Alternative uses: preservation; sustainable use; conversion. Source: adapted from Snedaker and Getter, 1985

Figure 7c. Goods services and functions of mangrove ecosystems. Source: adapted from Snedaker and Getter, 1985

The mathematical programming optimization problem is solved using the simplex algorithm (revised simplex) by means of a microcomputer based software called OPUS I.

The following is a reduced form specification of the mathematical valuation model for mangroves of the Guayas Province:

$$MAX\ NSB = \sum_{b}^{B,S,F} NBM_b + \sum_{b}^{B} NBC_b$$

where:

NBM = Net Benefits from mangrove use/conservation

NBC = Net Benefits from converted mangrove area

B,S,F= Goods, Services and Functions

Components

The reduced form specification of the valuation model presented above can be further specified in terms of the following components:

a) Objective function (Net Social Benefit Function), **b)** Production Matrix (Integrated Functional Coefficients Matrix), **c)** Constraints vector (Factor endowment, non-negativity constraints balance equations, etc) and **d**) Non-negativity constraints.

a. Objective function

Thus, the Objective function to be maximized can be specified as:

$$NSB = \sum_a \sum_b \sum_c \sum_{A_j=1}^{t} \sum_{Nk=1}^{u} \sum_{l=1}^{v} \sum_{m=1}^{w} \sum_{n=1}^{y} X_{abc5A_jNklmn} * P_{abc5A_jNklmn}$$

$$-\sum_a \sum_b \sum_c \sum_{i=1}^{s} \sum_{A_j=1}^{t} \sum_{Nk=1}^{u} \sum_{l=1}^{v} \sum_{m=1}^{w} \sum_{n=1}^{y} X_{abciA_jNklmn} * C_{abciA_jNklmn}$$

where:

a = Use of mangrove area; a= {C,M}

C = mangrove area used as shrimp ponds

M = mangrove area for conservation or sustainable use/exploitation

b = Mangrove resource; b = {B, S, F, VF}

B = resources used for production of goods

S = resources used for production of services

F = resources' natural/ecological functions

VF = other non-market uses/values

c = Productive sector c = {F, P, C}

F= Forestry Sector

P= Fisheries Sector

C= Aquaculture

i = Activity level; i ={ 1,..s}

Aij = Location for the ith activity. (only for extractive activities)

A1 = inland zone

A2 = coastal zone

A3 = salt-flats

A4 = adjacent lands

A5 = channels and estuaries

A6 = coastal fishing area

Nk = Mangrove area conversion level (segment)

l = Technology (extensive and semi-intensive systems; small scale and industrial).

Aquaculture or Shrimp production; l = {E,I}

E = extensive culture system

I = semi-intensive culture system

m = effort (logged trees; stocking density, etc)

n = mangrove natural resource/product

Forestry Sector:

L = firerwood from *Avicennia*

P = wood-poles form *R. mangl*e

T = tanino from *R. mangle*

Fisheries Sector:

M = mollusks

G = crabs

L = postlarvaes

C = adult shrimps

P = fish

b) Production Matrix
(Integrated Functional Coefficients matrix)

The different relationships between biological, technological and socio-economic factors and their corresponding impact on the environment are represented and introduced into the model through integrated functional coefficients.

Physical input-out coefficients are sinthetased in the following integrated coefficients:

Fisheries Sector: CPUE = Catch per unit of Effort

Forestry Sector: LPUE = Logging per unit of Effort (ha)

Tourism Sector: EPUE = Enjoyment per unit Effort (visit)

Environment Sector: EIPUEi= Environmental impact per unit of the ith activity

while their economic counterparts are sinthetized in:

Fisheries Sector: CPUC = Cost per unit of Catch

Forestry Sector: CPUL = Cost per unit of logging (ha)

Tourism Sector: CoPUE = Cost per unit of enjoyment (visit)

Environment Sector: CPUEIi= Cost per unit of environmental impact of the ith activity.

c) Constraints vector

The following is a summary of the basic constraints:

* Land availability, per type of land:

$$\sum_b \sum_c \sum_{Nk=1}^{u} \sum_{l=1}^{v} \sum_{m=1}^{w} \sum_{n=1}^{y} (X_{Mbc1AjNklmn} + X_{Cbc1AjNKLMN}) \leq Aj$$

for all types of land j= {1...4}

* Forest carrying capacity:

$$\sum_{l=1}^{v} \sum_{m=1}^{w} X_{MBF_1AjNklmn} \leq R_{FAjNklmnY} * Aj$$

where:

$R_{FAjNklmn}$ * Aj = maximum biomass for specie n
$R_{FAjNklmnY}$ = Resource density for specie n.

* Fisheries carrying capacity

$$\sum_{l=1}^{v}\sum_{m=1}^{w} X_{MBF_1AjNklmn} \leq R_{FAjNklmnY} * Aj$$

where:

$R_{PAjNklmn}$ * Aj = maximum biomass for specie n
$R_{PAjNklmn}$ = Resource density

* Post-laveae availability

$$\sum_{Aj=1}^{t}\sum_{Nk=1}^{u}\sum_{l=1}^{v}\sum_{m=1}^{w}\sum_{n=1}^{y} X_{CBC1AjNKlmn} \leq PLM(Aj,Nk) + CPL$$

where:

CPL= Installed capacity for laboratories (hatcheries for pl)

PLM(Aj,Nk)= availability of natural seeds (mangrove function)

* Labor availability for each sector

$$\sum_{i=1}^{s}\sum_{l=1}^{v}\sum_{m=1}^{w}\sum_{n=1}^{y} X_{MBcijlmn} * R_{cinY} \leq MMOc$$

where

MMOc = Labor force for sector c.

Rcin = Labor productivity (coefficient) in activity i

* Effort availability per sector. Equipment, gears, boats, etc.

$$\sum_{i=1}^{v}\sum_{m=1}^{w}\sum_{n=1}^{y} X_{MBc1lmn} * R_{c1nY} \leq MCEc$$

where:

MCEc = Effort

Bc1lmn = catchability coefficient (or extraction rate) per unit of effort

* Processing capacity

$$\sum_{Al=1}^{t}\sum_{Nk=1}^{u}\sum_{m=1}^{w}\sum_{n=1}^{y} X_{CBC1AjNklmn} * R_{CAjNklmnY} \leq KCL$$

where

Rc2lmn = Production rate for technology m

CPc2n = Installed plant capacity

* Storage capacity (cold)

$$\sum_{i=1}^{v}\sum_{m=1}^{w}\sum_{n=1}^{y} X_{MBc3lmn} * R_{c3nyY} \leq CPc3c$$

where

Rc3lmn = packing capacity

CPc3n = Storage capacity

* Capital availability

$$\sum_{Aj=1}^{t}\sum_{Nk=1}^{u}\sum_{m=1}^{w}\sum_{n=1}^{y} X_{CBC1AjNklmn} * R_{CAjNklmnY} \leq KCL$$

where

RCAjl = Initial investment (área Aj) using production system

KCl = Available credit

Several operational constraints are also included like:

balance equations, to move products from one activity to another in the tableau, accounting at the same time for losses due to spoilage, yield, etc

distributional equations, to distribute products to alternative activities (from harvesting to different final product types) convexity restrictions to ensure that in the linearization process only one (or two adjacent) segment/ activity is chosen, etc.

Results and concluding remarks

Net social benefits per year from the mangrove ecosystem of Guayas Province were estimated at 173 million dollars, of which 106 million correspond to goods, services and functions obtained from sustained use of mangroves and 67 million from aquaculture/ shrimp production (implying some conversion).

The average value of an hectare/year of mangrove area is approximately US$ 1,500 although, as shown by the dual value of an hectare in different locations, significant differences exist between the intertidal and supra-tidal (interior) zones of the mangrove. The basic reason for this difference is the greater ecological importance (functions) of the mangrove inter-tidal zone.

Analysis of results show also that only the supra-tidal area of the mangrove (area 2) should be converted as the value of the inter-tidal area is higher. The above figures require that 49,000 ha. of shrimp ponds are constructed, of which 5,500 ha are in the supra-tidal area of the mangrove, 31,000 ha are salt-flats and 12,000 ha are in the interior zone. Extensive system should be used in approximately 75 % of the area, while around 65 % of total production should be produced with semi-intensive systems.

Annex 1. Economic valuation model; mathematical programming formulation

$$
\begin{aligned}
NSB &= \sum (TR - TC) \pm NM \\
&= \sum (X_{zsaro} * P_{zro}) - \sum (X_{zsaro} * C_{zsarotg}) \pm \\
&\quad \sum (X_{zsaro} * e_{zsartg}) + \sum (X_{zsaro} * OB_{zsaro})
\end{aligned}
$$

Where:

Sectors (s)	Fisheries / Aquaculture	Logging	...	Environmental
Activities (a)	Preparation Stocking Harvesting Processing Transporting Marketing / Storing	Reforestation Growing Loging Transporting Marketing	...	Transformation (Depletion & Regeneration)
Resource (r)	Specie 1 Specie 2 - - Specie r	Site 1 Site 2 - - Site r	...	Function 1 Function 2 - - Function r
Outputs (o)	Fresh Shrimp Frozen Frozen head-off Cured, Smoked, Salted Other	Charcoal Firewood Wood poles	...	Scenery Clean air & water Sediments Noise / waste Other

Subject to:

$\leq$ Resource abundance (sustained yield function)

$\leq$ Infrastructure (boat,plant,storage size/capacities,etc))

$\leq$ Capital stock (indebtedness capacity)

$\leq$ Labor supply

$\leq$ Environmental carrying capacity

$=$ Coefficients (prices, values, cost, yields)

Results obtained from the valuation model closely reflect reality as the values of relevant variables obtained from the model are similar to those obtained from national statistical sources. These results are shown and compared in the figure 3 shows the dual value for the different areas of the mangrove and for the various resources, denoting great differences between them. Thus, a spatial and resource discriminating policy is likely to yield higher social and economic benefits than non-discriminatory regulations.

The availability of land was subject to sensitivity analysis, as it provides a good indication of the value of a wide variety of good, services and functions. Changing the availability of land in zone 2 up to 90 % of its total, showed little impact in the total net benefit value. The slope of the curve shown in Fig...represents the shadow price or dual value for land in zone 1 and 2. When availability is very large, the scarcity value of land is very low (flat portion) and thus, the marginal increase in net benefits is minimal; the inverse analysis holds with opposite signs, that is, as availability becomes smaller, the shadow price of an hectare increases and thus, its scarcity value per hectare.

Several alternative scenarios were evaluated to observe the performance of the model. In general, changes in control variables (prices, costs, output level, etc) produced changes in activity levels as expected from pure theoretical basis. Once the model has been structured, a wide variety of alternative options can be easily “simulated” and analyzed. The shadow price vector showed consistency with theoretical principles and provided useful insights into the analysis of policy alternatives

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Mangrove Ecosystem Analysis *

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Introduction

The extensive land development activities in South Florida have been accompanied by progressive loss of natural resources and deterioration of environmental quality. Governmental agencies, in response to public concern, have initiated studies of regional ecosystems whose objectives are to describe, quantitatively, the patterns and mechanisms of man's impact on the structure and function of the landscape units. One if the regional studies is the South Florida Ecological Study coordinated by the United States Department of the Interior. An objective of this study is to survey knowledge of the ecology of South Florida, identify major gaps, and initiate research necessary to bridge these gaps. Models of energy flow were used to identify research needs in the study, and are reported elsewhere (Lugo *et al*., 1971). The concept was to use qualitative ecosystem models as planning tools for research such that data to be collected would be quantitative and in a form amenable to computer simulations. The original planning model for the mangrove research is depicted in Fig. 1. This model served to identify major compartments, flows, and forcing functions believed to be important in the local and regional functions of the mangrove ecosystem. Research was then designed to obtain baseline data expressed per unit area for the storages, and per unit time for the flows and forcing functions. Emphasis, in general, was placed on those data that were not available for south Florida mangrove ecosystems.

This paper reports a first attempt to simulate some of the information collected prior to and during the first phase of the study. As research progresses, results from these simulations will be validated and the model will be refined. Therefore, this report should be considered preliminary.

Regional Role of Mangrove Ecosystems

Since the early studies of Davis (1940), mangroves have been recognized for the value they contribute to regions in which they grow. Davis, for example, discussed their role as land builders and protectors of coastal areas during periods of high tides and strong winds caused by hurricanes. Golley *et al*. (1962) described the role of mangroves exporters of labile organic matter to adjacent bays. More recently, Heald (1969) and Odum (1969) measured and traced this organic output to the food webs supporting fisheries of the southern coastline of Florida. Sastrakusumah (1971) described the role of mangrove estuaries as nursery grounds for the pink shrimp (*Penaeus duorarum*), and Clark (1971) did the same for juvenile fish species in Everglades National Park.

The regional importance of mangroves, and the fact that they occur in desirable locations for development, creates a dilemma within certain sectors of society. Criteria for decisions concer-

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Figure 1. Planning model for mangrove research in South Florida. Symbols are those of the energy language described by Odum (1972). The model id from Lugo et al. (1971), and it depicts the mayor energy flows and interactions belived to be operating in mangrove forests in South Florida

Figure 2. Map of South Florida depicting areas where mangrove research has been conducted. Our research sites are Rookery Bay, Faka Union Bay and Fakahatchee Bay. Also shown are the research sites of Heald (1969) and Odum (1969) in Shark River, those of Miller (1972) on Key Largo and Cape Sable where Davis (1940) described the largest stands of mangroves in Florida (from Lugo *et al*., 1975)

ning the development or protection of these areas are needed in order to optimize their value to man. Questions that need to be answered to manage mangroves for maximum regional service are related to the sensitivity of mangrove ecosystems to environmental factors which control their structure and function. In the planning model (Fig. 1), these factors are illustrated as forcing function and include oxygen, rainfall, terrestrial runoff, tides, turbulence, sun, and heat. These were considered to be the major energy sources to which mangrove ecosystems respond with structural and functional adaptations. Many of these factors interact with each other and Fig. 1 summarizes the pathway that they any control.

In the early phases of this study, a field survey was made to describe the extant mangrove types in the Ten thousand Island area of south Florida (Fig. 2). It was determined from this survey that the earlier phytosociological classifications (e.g. Davis, 1940), based on zonation and species composition, were not applicable to the mangrove area of interest.***** Instead, distinctive physiognomic patterns (irrespective, to a large extent, of species composition) were observed to be closely associated with the following:

1. location with respect to the mainland coastline;

2. topographic irregularities and the total area uniformly covered with mangrove; and,

3. integrating these two, characteristic of surface water movement resulting from tides and seasonally high water.

Based on these observations, four mangrove forest types (basin, fringe, riverine, and overwash) were described and will be reported on in detail elsewhere. This paper focuses specifically on the mangrove overwash type, although generalizations are extended to encompass mangroves in general.

Mangrove overwash forests are dominated by the read mangrove (*Rhizophora mangle*) and contain an occasional black mangrove (*Avicennia nitida*) synonymous with *A. germinans*] or white mangrove (*Laguncularia racemosa*). They occur as small islands, usually very long and narrow, with uniform elevations of approximately 30 cm above mean sea level. The sustrate is organic peat with a variable ash content of around 6 %. The distribution and spatial arrangement of these islands (Fig. 2) serve to restrict water flow in and out of the relatively large estuarine bays contiguous with the mainland. The low elevations, however, permit them to be overwashed at high tide. Surface flushing by incoming and retreating tide water carries with it loose debris and detritus into the estuarine bays. This result in a much reduced standing stock of organic debris as compared with mangrove islands (fringe forest) which are inundated but not overwashed at high tide (1565 $\pm$ 245 g/m^2 versus 5165 $\pm$ 295 g/m^2, x $\pm$ 1 s.d.).

* The Ten Thousand Island area is characterized by a low, essentially level, topographic relief, and thus the "zones" are broad as to be unrecognizable

Figure 3. Simulation model showing expressions that describe each pathway and changes in state level of each compartment in the mangrove forest model. $\boldsymbol{Q_1}=k_1 I Q_3Q_1 - k_3Q_1^2 - k_2Q_1$; $\boldsymbol{Q_2}= k_2Q_1 - k_4Q_2Tk_5Q_2 - k_6O_2Q_2 = k_{10}Q_2$; $\boldsymbol{Q_3}= k'_5Q_2 + k'_6O_2Q_2 + J_1 - k_8Q_3 - k_9IQ_3Q_1$. Symbols are described by Odum (1972)

To initiate interpretation of the available data, and for purposes of this simulation, we chose to study the relative importance of terrestrial runoff and tidal flushing in nutrient cycling and organic production in the overwash forest type. The simulation model id shown in figure 3 and described below. The objectives of the simulation were:

1. to study the relative effects of terrestrial runoff and tides on nutrients cycling and productivity in mangrove forests;

2. to study the effect of tidal flushing on accumulation and export of detritus in and from mangrove forests;

3. to study the role of mangrove on water quality; and

4. to asses the usefulness of modeling for research planning.

Description of the Model

In this model, the radiant energy of sunlight *I* interacts with nutrients Q_3 and mangrove biomass Q_1 and is converted through the process of gross photosynthesis into organic matter. Some of this gross production is respired by the forest, some is stored as a net increase in forest biomass, and some is deposited in the forest floor as detritus. The detritus Q_2 may be exported from the forest floor to the estuary by tidal action. Some of it is grazed in situ by mangrove consumers, and some is decomposed or accumulated as peat. Decomposition may occur under influence of the oxygen-saturated waters of incoming tides, or by atmospheric oxygen when the forest floor is exposed to the air. Decomposition of detritus within the mangrove system represents a source of nutrients for photosynthesis. Other nutrient sources are from terrestrial runoff, tidal waters, rainfall, and sediments storage. Of these, terrestrial runoff is the most significant. In the model, they are all grouped as a single source. Some nutrients Q_3 are nor used and are lost from the system; the rest are sequestered through plant photosynthesis, thus completing the cycling in the model.

Model Structure and Computer Program

Each flow or pathway in figure 3 can be described by an equation that indicates the flow to be a linear or nonlinear relationship with storage or forcing function in the model. An example of a linear relationship is the flow from mangrove biomass to detritus, k_2Q_1. Gross photosynthesis flow into biomass is an example of a nonlinear relationship, $k_1IQ_3Q_1$. Nonlinear interactions in this model were assumed to be multiplicative and are identified by the multiplier symbol. The expressions for each pathway are

Table 1. Rate coefficients used for flows in the mangrove model [a]

Coefficient	Value [b]
k_1	
High metabolism, low nutrients	2.55×10^{-9} m^4/kcal g nutrients
High metabolism, high nutrients	4.25×10^{-11} m^4/kcal g nutrients
Mean metabolism, low nutrients	1.32×10^{-9} m^4/kcal g nutrients
Mean metabolism, high nutrients	2.20×10^{-11} m^4/kcal g nutrients
k_2	8.4×10^{-2} y^{-1}
k_3	
High metabolism	1.68×10^{-5} m^2/g C y
Mean metabolism	1.25×10^{-5} m^2/g C y
k_4	512 m^{-1} y^{-1}
k_5	1.80×10^{-2} m^2/g C y
k_5'	1.44×10^{-3} m^2/g C y
k_6	1.02×10^{-2} m^3/g O_2 y
k_6'	8.20×10^{-2} m^3/g O_2 y
k_8	
High metabolism, low nutrients	3.5×10^{-1} y^{-1}
High metabolism, high nutrients	5.8×10^{-3} y^{-1}
Mean metabolism, low nutrients	188 y^{-1}
Mean metabolism, high nutrients	3.13×10^{-2} y^{-1}
k_9	
High metabolism, low nutrients	2.05×10^{-10} m^4/kcal g nutrients
High metabolism, high nutrients	3.40×10^{-12} m^4/kcal g nutrients
Mean metabolism, low nutrients	1.05×10^{-10} m^4/kcal g nutrients
Mean metabolism, high nutrients	1.75×10^{-12} m^4/kcal g nutrients
k_{10}	3.68×10^{-1} y^{-1}

[a] Figure 3 identifies the pathway in the model where these constants are used. [b] noted that y= year

shown in figure 3. Also shown in the figure are the differential equations describing rates of change in mangrove biomass, detritus, and nutrient levels. The rate coefficients (*k*'s) were assumed to remain constant throughout the simulation. Table 1 contains all the rate coefficients used in the various simulations. Tables 2-4 summarize the data that were used. The following equations, Eqs. (1)-(3), demonstrate a sample calculation:

$$\textit{gross photosynthesis} = k_1 I Q_3 Q_1, \qquad \textbf{(1)}$$

where

$$I = 1{,}46 \times 10^6 \text{ kcal m}^{-2}\text{ y}^{-1}$$

$$Q_3 = 100 \text{ g nutrients m}^{-2}$$

$$Q_1 = 10{,}500 \text{ g C m}^{-2}$$

Using a high estimate of gross photosynthesis (3920 g C m^{-2} y^{-1}),

$$k_1 = 3920 \text{ g C m}^{-2}\text{ y}^{-1} / (1.46 \times 106 \text{ kcal m}^{-2}\text{ y}^{-1})(100 \text{ g nutrients m}^{-2})(10{,}500 \text{ g C m}^{-2}) \qquad \textbf{(2)}$$

or

$$k_1 = 2.55 \times 10^{-9} \text{ m}^4 \text{ kcal}^{-1} \text{ g nutrients}^{-1} \qquad \textbf{(3)}$$

Equations (4)-(6) following demonstrate the procedure for analog computer scaling, as detailed by Patten (1971). The scaled for mangrove biomass, detritus, and nutrients are shown in Eqs. (6)-(8), respectively.

For mangrove biomass Q_1,

$$dQ_1/dt = k_1 I Q_3 Q_1 - k_2 Q_1 - k_3 Q_1^2 \qquad \textbf{(4)}$$

Inserting numerical values of the rate coefficients (Table 1) and dividing and multiplying each variable on the right by its assigned maximum values gives:

$$\frac{dQ_1}{dt} = 2.55\times10^{-9}(3.65\times10^6)\left|\frac{I}{3.65\times10^6}\right|(800)\left|\frac{Q_3}{800}\right|3\times10^4\left|\frac{Q_1}{3\times10^4}\right| -0.084(3\times10^4)\left|\frac{Q_1}{3\times10^4}\right| - 1.68\times10^5(3\times10^4)^2\left|\frac{Q_1}{3\times10^4}\right|^2 \quad \textbf{(5)}$$

Dividing both sides the assigned maximum value for mangrove biomass gives the scales equation

$$\frac{dQ_1/dt}{3\times10^4} = 7.45\left|\frac{I}{3.65\times^6}\right|\left|\frac{Q_3}{800}\right|\left|\frac{Q_1}{3\times10^4}\right| -0.084\left|\frac{Q_1}{3\times10^4}\right| - 0.504\left|\frac{Q_1}{3\times10^4}\right| \quad \textbf{(6)}$$

Similar equations for detritus and nutrients are shown in Eqt. (7) and (8), respectively:

$$\frac{dQ_2/dt}{10^4} = 0.252\left|\frac{Q_1}{10^4}\right| - 10.24\left|\frac{Q_2}{10^4}\right|\left|\frac{T}{2}\right| - 0.018\left|\frac{Q_2}{10^4}\right| -0.0816\left|\frac{Q_2}{10^4}\right|\left|\frac{Q_2}{8}\right| - 0.368\left|\frac{Q_2}{10^4}\right| \quad \textbf{(7)}$$

$$\frac{dQ_3/dt}{10^4} = 0.018\left|\frac{Q_2}{10^4}\right| + 0.082\left|\frac{Q_2}{10^4}\right|\left|\frac{Q_2}{8}\right| + 0.455 -0.035\left|\frac{Q_3}{800}\right| - 22.4\left|\frac{I}{3.65\times10^6}\right|\left|\frac{Q_3}{800}\right|\left|\frac{Q_1}{3\times10^4}\right| \quad \textbf{(8)}$$

The model with the data presented in Fig 4, and Fig 5 is the analog computer program.

FIELD DATA

Field studies were conducted in the Ten Thousand Island area in southwestern Florida from August (1971) to February 1973. Metabolic data were collected in a zoned mangrove forest located at Rookery Bay, near Naples. Biomass data were obtained in a mangrove overwash forest in Faka-Union Bay some 20 miles to the east (Fig. 2).

Photosynthesis and respiration rates were obtained with a Beckman infrared carbon dioxide gas analyzer, powered by gasoline and diesel generators, and located in a tent inside the mangrove forest. These metabolic rates were measured on a diurnal basis as described by Odum *et al*. (1970). The apparatus was assembled with solenoids valves, timers, blowers, pumps, and so forth, so that four forest compartments could be monitored in sequence at 15-min intervals. Over 50 diurnal records of photosynthesis and respiration (sun and shade leaves, tree stems, prop-roots, pneumatophores, and seedlings of each mangrove species) were obtained during the period of study. A detailed account of the procedures and results of these measurements will be reported elsewhere.

Figure 4. Simulation model with data values utilized for scaling the analog computer. Symbols are described by Odum (1972)

Figure 5. Analog computer diagram of the simulation model

Biomass determination was based on replicated 5 x 5 m clearcut harvests in a mangrove overwash forest. The particular study site was considered to be representative of the overwash type of mangrove stands in the Ten Thousand Island area. For each species in each harvest area, leaf, steam (by size class), detritus, prop root, and fruit and flower biomass levels were determined. In addition, leaf, prop root, and trunk area indices were calculated by species for each site.

Leaf fall was determined from 20 litterfall baskets located at Rookery Bay and emptied periodically during the study. Water quality of incoming and outgoing tides, river runoff, swamp waters, precipitation throughfall, and of adjacent canals was determined seasonally at Rookery Bay. In addition, concurrent studies by the Environmental Protection Agency and the University of Miami's Rookery Bay Project provides monthly data on water quality, water flows, tidal characteristics of the large area outside Rookery Bay, and also provided data on periphyton productivity on mangrove prop roots. Rates for detritus export into the bays and its decomposition in the forest were obtained from the literature. This included work of Golley *et al*. (1962) in Puerto Rico, and Heald (1969) in the Shark River estuary, southeast of the present study site (Fig. 2). Nutrient uptake associated with photosynthesis was calculated from photosynthetic rates, assuming a 3 % ash content plus a 1 % nitrogen content in mangrove biomass. Table 2 summarizes the metabolic data that were obtained, Table 3 characterizes the structure and biomass data for the overwash study site, and Table 4 depicts all values used in scaling equations for the analog computer simulation. The simulation was done on an Electronic Associates, Inc. Miniac analog computer.

Table 2. Photosynthesis and respiration of the experimental mangrove forest in south Florida [a]

Site 3[b]	Red Mangrove					White mangrove					R_{24} trunk and root	Periphyton		Total	
	LAI	Leaves P_{net}	R_{night}	P_{gross}	R_{24}	LAI	Leaves P_{net}	R_{night}	P_{gross}	R_{24}		P_{net}	R_{24}	P_{gross}	R_{24}
High estimates															
Plot 7	2.05	5.88	0.88	6.76	1.76	1.80	2.52	0.54	3.06	1.08	1.33	0.9	0.9	10.72	5.07
Plot 8	3.65	10.47	1.57	12.04	3.14	-	-	-	-	-	1.33	0.9	0.9	12.94	5.37
Mean estimates															
Plot 7	2.05	2.82	0.48	3.30	0.96	1.80	1.04	0.30	1.34	0.60	1.33	0.9	0.9	5.54	3.79
Plot 8	3.65	5.03	0.85	5.88	1.70	-	-	-	-	-	1.33	0.9	0.9	6.78	3.93

[a] Values in g C/m^2/day. High estimates are based on an optimal day. Mean estimates represent the mean of all determinations made for that ecosystem component. Net daytime photosynthesis is P_{net}; gross photosynthesis is P_{gross}; nightime respiration is R_{night}; and 24-h respiration is R_{24}. Leaf area index is LAI.
[b] Overwash mangrove forest

Table 3. Structural indices and biomass characteristics of a mangrove overwash forest in South Florida

Parameter	Mean	Std. error mean
Area indices		
Basal (m^2/ha)	14.68	0.33
Leaf (m^2/m^2)	3.74	0.12
Trunk (m^2/m^2)	0.15	
Prop root (m^2/m^2)	1.31	
Biomass [a]		
Leaves	710.0	22.0
Fruit	12.8	15.3
Wood	7043.0	7.0
Prop roots	4695.0	711.0
detritus	1565.0	234.5

[a] grams per dry weight organic matter per square meter

Table 4. Values used in simulations of the mangrove model for initial conditions of forcing functions, state variables and flows

	Initial value	Maximum value
Forcing functions		
Sunlight, I	4,000 kcal/m^2/day	10,000 kcal/m^2/day
Tide, T	10cm	2 m
Dissolved oxygen, O_2	4 g/m^3	8 g/m^3
State variables		
Mangrove biomass, Q_1	10,500 gC/m^2	30,000 gC/m^2 (current values)
Detritus, Q_2	300 gC/m^2	30,000 gC/m^2 (successional conditions)
Nutrients, Q_3	780 gC/m^2	10,000 gC/m^2
	100 gC/m^2	800 gC/m^2 (low nutrients)
		8,000 gC/m^2 (high nutrients)
Flows		
Gross photosynthesis, $k_I Q_1 Q_1$		10.72 gC/m^2/day (high value)
		5.54 gC/m^2/day (mean value)
Respiration of mangroves, $k_1 Q_1^2$		5.07 gC/m2/day (high value)
		3.79 gC/m^2/day (mean value)
Litterfall, $k_2 Q_1$		2.41 gC/m^2/day
Export detritus by tidal flushing, $k_4 Q_2 T$		1.1 gC/m2/day
Decomposition of detritus when mangroves are dry, $k_5 Q_2$		0.16 gC/m^2/day (only 3 months of year)
Decomposition of detritus when mangroves forest floor is water-covered, $k_6 Q_2 Q_2$		0.12 gC/m^2/day (during 3 months of dry season)
		0.30 gC/m^2/day (during 6 months of wet season)
Grazing on detritus and others losses, $k_{10} Q_2$		0.786 gC/m^2/day
Nutrients derived from decay of		0.0128 gC/m^2/day (only 3 months of dry season)
detritus, $k_5 Q_2$		0.0336 gC/m^2/day (only 3 months of dry season + 6 months of wet season)
detritus, $k_6 O_2 Q_2$		
Nutrients from others sources, J_1		0.940 g nutrients/m^2/day
Nutrients uptake by mangroves, $k_9 I Q_3 Q_4$		0.846 g nutrients/m^2/day
Nutrients not used by mangroves, $k_8 Q_3$		0.094 g nutrients/m^2/day

Results

Simulation results are presented in Figs 6-17. For convenience, the results are presented under four headings: mangrove development under current (initial) conditions, effects of tides on mangrove production and export, effects of mangrove succession on nutrient content and adjacent water, and effects of nutrient runoff on mangroves.

A. Mangrove Development Under Current (Initial) Conditions

Three simulations were done utilizing the measured standing crop, and high and mean estimates of metabolic rates (gross photosynthesis and total respiration for 24-h period) as initial conditions. For each run, the temporal patterns of gross photosynthesis, mangrove and detritus standing crop, and detritus export were studied. These result are depicted in Figs. (6-8).

Figure 6. Standing crop of biomass and detritus storage in mangrove forests with (a) starting conditions at present levels of mangrove biomass and (b) early successional levels of mangrove biomass. Each simulation was run ay high and mean rates of metabolism. Initial gross photosynthesis as follow (gC/m^2/day): (1) detritus, 10.72; (2) detritus, 5.54; (3) mangrove biomass, 5.54. Table 4 contains all values used for initial conditions

Figure 7. Rates of gross photosynthesis and detritus export for mangroves undergoing succession, with initial conditions of current biomass levels and (a) high and (b) mean metabolism rates. Tidal depth 10 cm. Table 4 contains all values used for initial conditions

Figure 6a suggests that the overwash mangroves in the Ten Thousand Islands are about 10 y from reaching steady state with respect to standing crop, gross photosynthesis, and detritus export. The steady-state standing crop is dependent on initial metabolism rates, reaching a maximum of 16,200 g C m^{-2} and 13,100 g C m^{-2} at high and mean estimates, respectively. The rate of detritus accumulation in the forest also depends on metabolism of the stand, with steady-state values of 1230 and 1000 g C m^{-2}, high and mean estimates, respectively. These detritus values, however, do not appear to be as sensitive to changes in metabolism as is the total standing crop of the system. Figures 7a and b compare the ratios of gross photosynthesis to detritus export with high and mean initial rates of metabolism. At high rates of metabolism this ratio reaches a steady-state value of 8.7 compared to a value of 5.3 for the mean metabolic rate.

Figure 8. Rates of gross photosynthesis and detritus export for mangroves undergoing succession with initial conditions of 300 gC/m^2 of mangrove biomass and (a) high and (b) mean rates pf metabolism. Tidal depth 10 cm. Table 4 contains all values used for initial conditions

If one sets the initial conditions of standing crop to a value similar to those measured for successional plots in the study area, one observes the rate of mangrove successions at mean and high metabolism rates. These simulations are depicted in Figs. 6B and 8. Figure 6b shows the changes in mangrove standing crop and detritus storage in the forest at mean and high metabolism rates. It is clear that steady-sate conditions are retarded by the lower metabolic rate. At the initial mean metabolism rates the system takes about 23 y to reach steady-state conditions compared to 12 y at high metabolic rates.

The mean rates of gross photosynthesis and respiration seem to depict a more realistic picture of the true development of mangrove systems. This is not surprising since mangroves are not expected to metabolize at optimal rates every day of the year throughout their development. The ratio of gross photo-synthesis to detritus export is depicted in Fig. 8 for both high (8a) and mean (8b) metabolic rates. High rates of metabolism caused an overshoot in the gross photosynthesis curve. This overshoot was not observed when initial mean rates were utilized but was observed in several runs with high rates of metabolism. It appears that overshooting is a property of a fast-growing system exhibiting surges of high production during short time periods. The initial decrease in detritus export shown in this simulation (Fig. 8) is due to the time lag in establishment of a system with sufficient production for export. Table 5 summarizes the levels and steady-state values obtained from this first set of simulations.

Table 5. Steady-state levels of biomass, detritus and nutrients; ratio of gross photosynthesis to detritus export and time required to reach steady state in four simulations with different starting conditions of biomass and metabolism rates

Initial Conditios [a]	Ratio of P_{gross} to detritus export	Level at steady state (g/m^2)			Time to steady state (years)		
		biomass	detritus	nutrients	biomass	detritus	nutrients
1	8.7	16,200	1230	90	7.5	6	5
2	5.8	16,200	1230		10	8	
3	8.7	13,100	1000		12.5	8	
4	6.0	13,100	1000		23	19	

[a] mangrove biomass (gC/m^2)	P_{gross} (gC/m^2 /day)	Respiration (gC/m^2 /day)
1 10,500	10.72	5.07
2 10,500	5.54	3.79
3 300	10.72	5.07
4 300	5.54	3.79

Figure 9. Rates of gross photosynthesis and detritus export in a mangrove forest submitted to several tidal amplitudes and high rates of metabolism. Table 4 contains all values used for initial conditions

B. Effects of Tides on Mangrove Production and Export

Figure 9 depicts the effect of different tidal levels on the rate of detritus export and gross photosynthesis in a mangrove forest with initial conditions of high metabolism and measured standing-crop. It is clear that tides have less effect on gross photosynthesis as compared to their effects on the rate of Florida study area. In the simulations in figures 14 and 16 the initial conditions of nutrient levels were raised from 100 g m-2 to 6000 g m^{-2}.

The model was sensitive to nutrient availability. Figures 15 and 16 show that, when nutrient runoff was set at zero, mangrove biomass decreased steadily. The steady-state level depends on the fertility of the site as shown in figure 16, where the initial nutrient levels were set at 6000 g m^{-2}. At higher rates of nutrient runoff, however, the steady-state value of biomass was independent of the initial nutrient conditions although the transient patterns of biomass growth were different for each initial setting. Figure 14 shows changes in nutrient levels in the forest associated with different rates of nutrient runoff and the metabolic behavior of the forest. In Fig. 17, the pattern of gross photosynthesis is shown to be sensitive to the efficiency of nutrient uptake from surrounding waters. This suggests a role for a mechanism that would concentrate nutrients.

These simulations demonstrate the dependency of mangrove ecosystems on nutrient inputs derived from the land.

Decomposition within the forest and inputs from the sea do not seem to be enough to maintain the observed rates of metabolism in these systems. Table 8 summarizes the relative importance of nutrient sources to the mangrove forests, and Table 9 summarizes the results of this set of simulations.

Figure 10. Level of detritus storage in a mangrove foest submitted to several tidal amplitudes (a) high and (b) mean rates of metabolism. Table 4 contains all values used for initial conditions

Table 6. Steady-state and time required to reach steady-state of gross photosynthesis, detritus export and standing drop in nine simulations with different starting conditions for tidal levels and mangrove biomass

	P_{Gross} (gC/m^2/day)		Rate of detritus export (gC/m^2/day)		Detritus (gC/m^2/day)	
Initial conditions tide level (cm)	**Time to steady-state (years)**	**Level at steady state**	**Time to steady-state (years)**	**Level at steady state**	**Time to steady-state (years)**	**Level at steady state**
A[a]						
0	5	16.3	0	0	10	2,600
5	2.5	16.1	8	1.26	8	1,650
10	5	15.9	7.5	1.84	7.5	1,200
20	5	15.8	7.5	2.36	5	800
40	5	15.7	7.5	2.77	3	450
B[b]						
0					15	2,170
5			8	1.0	12	1,350
10	8	8.9	10	1.53	10	1,000
20			8	1.89	8	650
40			8	2.19	5	400

[a] Mangrove biomass. 10,500 (gC/m^2/day); P_{Gross} 10.72 (gC/m^2/day); respiration 5.07 (gC/m^2/day)
[b] Mangrove biomass. 10,500 (gC/m^2/day); P_{Gross} 5.54 (gC/m^2/day); respiration 3.79 (gC/m^2/day)

Figure 11. Rates of gross photosynthesis and detritus export at several tidal depths from a mangrove forest at initial conditions of mean metabolism. Table 4 contains all values used for initial conditions

Initial biomass (g C m^{-2})

Gross photosynthesis		Nutrients	
1	10.500	4	10,500
2	5250	5	5250
3	2625	6	2625

Figure 12. Effects of mangrove biomass level on nutrient level in mangrove forests with high metabolism. Table 4 contains all values used for initial conditions

Initial biomass (gC m^{-2})

	Nutrients		Gross photosynthesis
1	10,500	4	10,500
2	5250	5	5250
3	2625	6	2625

Figure 13. Effects of mangrove biomass level on nutrient level in mangrove forests with mean rates of metabolism. Table 4 contains all values used for initial conditions

Table 6. Steady-state levels of gross photosynthesis and nutrients in water in eight simulations with different initial conditions for mangrove biomass and metabolism rates

Initial conditions	P_{Gross} (gC/m^2/day)		Nutrients g/m^2	
	Time to steady-state (years)	Level at steady state	Time to steady-state (years)	Level at steady state
A[a]				
Mangrove biomass				
10,500 g C/m^2	2.5	16.2	6	90
5,250 g C/m^2	5	16.2	7.5	90
2,625 g C/m^2	5	16.2	8.5	90
300 g C/m^2	5	16.2		
B[b]				
Mangrove biomass				
10,500 g C/m^2	8	8.9	7.5	120
5,250 g C/m^2	15	8.9	15	120
2,625 g C/m^2	18	8.9	18	120
300 g C/m^2	20	8.9		

[a] P_{Gross} 10.72 (gC/m^2/day); respiration 5.07 (gC/m^2/day)
[b] P_{Gross} 5.54 (gC/m^2/day); respiration 3.79 (gC/m^2/day)

Figure 14. Rates of gross photosynthesis and level of nutrients in mangrove forests with initial conditions of high nutrient level (6,000 gC/m^2), mean rates of metabolism and three rates of nutrient runoff. Gross photosynthesis, 5.54 gC/m^2/day

Figure 15. Mangrove biomass at current initial conditions, mean rate of metabolism and three levels of nutrient runoff. Initial photosynthesis, 5.54 gC/cm^2, initial nutrients, 100 gC/m^2

Figure 16. Mangrove biomass with high initial conditions of nutrients, mean rate of metabolism and three levels of nutrient runoff. Initial nutrients, 6,000 g/cm^2, gross photosynthesis, 5.54 g/m^2/day

Figure 17. Gross photosynthesis and nutrient levels as affected by variations in efficiency of nutrient uptake at mean rates of metabolism. Gross photosynthesis (nutrients unused): (1) 188 g/m^2/y. (3) 376 g/m^2/y, (5) all nutrients used. Nutrients (nutrients unused): (2) 188 g.m^2/y, (4) 376 g/m^2/y (6) all nutrients used

Table 8. Phosphorus and nitrogen inputs into Rookery Bay, Naples, Florida [a]

source	Wet season kg/day	Dry season kg/day
River runoff	6.99	52.8
Total flow	0.3	4.9
rainfall	0.0001	

[a] Values were obtained by multiplying the concentration of nutrients by water flow in a wet a dry month (November and March respectively)

Table 9. Steady-state levels and time required to reach them for mangrove biomass, gross photosynthesis and nutrients in simulations with different initial conditions for nutrient runoff, nutrient levels and efficient use

Initial conditions		P_{Gross} (gC/m^2/day)		Nutrients g/m^2	
		Time to steady-state (years)	Level at steady state	Time to steady-state (years)	Level at steady state
A[a]					
Nutrient input of	240 g /m^2/year	2	7.67	2	74
	480 g /m^2/year	2	16.0	5	92
	720 g /m^2/year	2	24.1	5	116
Nutrient losses	0 g /m^2/year	2	17.0	5	94
	35 g /m^2/year	2	16.0	5	92
	70 g /m^2/year	2	14.8	5	89
B[b]					
Nutrient input of	240 g /m^2/year	5	3.84	5	78
	480 g /m^2/year	8	8.9	10	126
	720 g /m^2/year	13	15.5	12	160
Nutrient losses	0 g /m^2/year	7.5	17.3	8	164
	188 g /m^2/year	8	8.9	10	126
	376 g /m^2/year	5	4.66	5	93

[a] P_{Gross} 10.72 (gC/m^2/day); respiration 5.07 (gC/m^2/day); initial nutrients, 100 g/m^2

[b] P_{Gross} 5.54 (gC/m^2/day); respiration 3.79 (gC/m^2/day); initial nutrients, 100 g/m^2

Discussion

A. Steady-State Biomass and Metabolic Rates

The validity of the model was tested by comparing some of the simulation results with values reported in the literature for other stands. In figure 6 the model predicted a maximum biomass at steady-state of 16,200 to 13,100 g C m^{-2}, depending upon the initial rate of metabolism. These values are higher than our own biomass estimates in the other plots that were harvested (Table 10). However, all the experimental plots were under the influence of recent hurricanes and, thus, presumably below steady-state conditions. The descriptions of Davis (1940) and Craighead (1971) of mature stands in Cape Sable suggest higher possible biomass levels for Florida. The biomass predictions based on mean metabolic rates are closer to measured values than those based on the high metabolism estimate. Of interest is the length of time required to reach a steady-state condition with respect to biomass. When metabolism rates are set at the high value, the forest reaches steady state in 7.5 y. However, when the mean values are used, steady state takes 10 y from the present and 23 y from an early stage of succession. Literature reports on the age of mangrove stands seem to indicate that most mangroves reach maturity at about 20-25 y (Davis, 1940; Craighead, 1971). These estimates agree with the model predictions based on a mean rate of metabolism. Wadsworth (1972) reports a growth rate for mangroves of 3.0 m in 18 months and indicates that stands are usually 25 years old with a few large individuals exceeding 50 years.

Table 10. Comparison of the mangrove model's prediction of steady-state levels of mangrove biomass, detritus, standing crop, gross photosynthesis and detritus export with independence field determinations of the same parameters

Model Prediction			
Ecosystem parameter	**High metabolism rate**	**Mean metabolism rate**	**Observed values**
State variable Mangrove biomass	16,200 gC/m^2	13,100 gC/m^2	8,700 gC/m^2 on riverine forest in Florida (Snedaker *et al*., unpublished) 14.000 gC/m^2 in Panama (Golley, 1968)
Detritus	1,230 gC/m^2	1,000 gC/m^2	782 ± 123 to 2,582 ± 147 gC/m^2 (Snedaker *et al*., unpublished)
Flow (process variable) Gross photosynthesis	15.9 gC/m^2	8.9 gC/m^2	8.7 gC/m^2 (Lugo *et al*., unpublished); Mean for the study sites
Detritus export	1.84 gC/m^2	1.5 gC/m^2	1.1 gC/m^2 (Golley *et al*., 1962) 0.67 gC/m^2 (Heald, 1969)

These represent the survivors from previous hurricanes. Examination of hurricane frequencies in Puerto Rico and our study area reveal a probable mean frequency of 24 and 20 y, respectively (Table 11). Thus, it appears that mangrove ecosystem are adapted to rapid growth following hurricane disturbance and are thus capable to regaining steady-state conditions during the time period between hurricanes. The model prediction of a steady state in 10 y with current initial conditions also agrees with the 20 years hurricane cycle as the last hurricane in the area was Hurricane Betsy in 1965.

In figures 7 and 8 the model predicted steady-state values for gross photosynthesis of 8.9-15.9 g C m^{-2} day-1, depending on initial conditions. These values are within the range of our metabolic studies in south Florida mangroves (Table 10). This is also true for the detritus storage and export values (Table 10). The conclusion at this point is that the simulations using mean rates of metabolism as initial conditions provide a closer estimate of observed processes than those obtained with high rates of metabolism. This indicates that mangroves operate at a maximum metabolic rate for short time periods and that our metabolism estimates are in line with real world values.

B. Metabolic Basis of Mangrove Vigor and Zonation

For a long time the zonation and vigor of mangrove stands has been related to gradients of salinity (Davis, 1940). A good reason for this is the impressive array of adaptations to a saline environment. However, no one has suggested nutrients as another important factor in determining the vigor of mangrove ecosystem. Figures 9 and 11 suggested that the gross photosynthetic rate of a stand was not affected much by tidal fluctuation, but that the amount and rate of detritus export was not affected much by tidal fluctuation, but that the amount and rate of detritus export was a function of tidal action. In Figs, 14-17 it was shown that the amount of nutrients available to mangroves and the efficiency of their use were the main determinants of succession rates and biomass levels that could be developed at steady state. Table 8 demonstrates that most of the nutrients available to mangroves are of terrestrial origin. In addition, description of mangrove stands by Davis (1940), Craighead (1971), Macnae (1967), and Walsh (1867) indicate that the largest and most vigorous mangrove stands are always associated with riverine conditions where detritus accumulation is low. These observations have been confirmed by the writers reporting on mangroves in several locations in Puerto Rico, Florida, Costa Rica, and Venezuela.

Thus, it appears that nutrient availability for photosynthesis is an important determinant of the vigor of a mangrove stand and that salinity adaptations may represent the energetic cost of tapping these nutrient sources where competition is controlled (i.e., reduced) by other factors. The overall gain in nutrients is greater than nutrient losses (in detritus) to the estuarine bays. This is demonstrated in our simultaneous measurements of photosynthesis bad respiration for a given day.

Table 11. Comparison of hurricane frequencies in two mangrove areas and the predictions of two simulations for the time required by mangroves to reach steady-state [a]

Model predictions	High metabolism	Mean metabolism
Time to reach steady-state biomass level Current initial conditions	7	10
Initial conditions of low biomass (300 gC/m^2)	10	23

[a] Literature reports related to steady-state mangroves. Frequency of hurricanes: in the study area, 20 years (Brunn *et al*., 1962); in southern Puerto Rico, 24 years (Anon., 1972)

Red mangroves exposed to riverine inputs exhibits maximum rates of photosynthesis which are twice as high as white mangroves growing more inland, away from the riverine input. Similarly, these red mangroves had s higher metabolic rate than black mangroves growing inside the swamp. The black mangroves had a higher metabolism rate than a red mangrove growing in the same habitat, Night respiration rates in the leaves were the same in all trees.

C. Implications for Nutrients Recycling

Figures 12 an 13 implied that successional development in mangroves was associated with their control of regional water quality. The role of mangrove forest as nutrient sinks has been described by Hesse (1961) and by Harriss (pers. comm.) for heavy metals. In the present study area a proliferation of molluscs and other filter feeders, and periphyton on prop roots and pneumatophores was observed. The metabolic work of these organisms represents mechanisms for nutrient recycling and uptake and seems to be coupled to proliferation of fine absorptive mangrove roots growing in close proximity. These adaptations would increase the efficiency of nutrient uptake from tidal or riverine waters passing over the swamp. As suggested in Fig. 17, increasing the efficiency of nutrient uptake would enhance the capability of the swamps to maximize productivity and biomass.

D. Implications for Mangrove Development

In spite of biological adaptations for the maximization of nutrient uptake and recycling from flowing waters, the simulations in Figs. 15 and 16 demonstrate that *in situ* decomposition in mangrove forest is not enough to mantain observed high rates of gross photosynthesis and biomass storage. This is partially due to detritus export to the bay which drains part of the nutrient currency of the system. Thus, mangroves require a steady input of terrestrial nutrients in order to maintain their characteristic rates of growth. Many of the land developments in south Florida include channelization of water flows and diversion of terrestrial runoff to coastal areas. These waters are usually diverted for human consumptions or discharged through canals directly into the sea without exchange with mangrove stands in the estuaries. This strategy is not ecologically sound since the analog simulations suggest that under these conditions mangroves would have to utilize the sediment storage of nutrients which, over a period of time, is not adequate to maintain the original growth rates. The result is loss of mangrove vigor and selection for smaller stands. Mangrove management requires maintenance of terrestrial runoff patterns, and perhaps these forests could be used for tertiary sewage treatment. This strategy would require periodic stresses similar in intensity to hurricanes in order to crate growing conditions leading to surges in nutrient uptake.

Summary and Conclusions

It appears that the use of model for planning research is a valuable tool for programs involving one or many researchers attempting to understand the regional relationships among ecosystem types. A preliminary model of a mangrove forest in south Florida has yielded the following information that was not apparent from examination of data prior to the present study.

1. Mangrove forest appears to reach a steady state, with respect to their biomass, in phase with the frequency of tropical hurricanes in regions where they occur.

2. The storage of organic detritus in the forest and its export to be bays is a function of tidal amplitude, but tides do not seem to affect gross photosynthetic rates as much as they do detritus accumulation versus export.

3. Gross photosynthesis appears to be sensitive to terrestrial input of nutrients, and the development of mangrove biomass is dependent on the quantity of nutrients and the efficiency of nutrient uptake.

4. Mangrove zonation and vigor may thus be a function of nutrient availability rather than solely salinity as previously thought.

5. During succession, mangroves exert significant control over the amount of nutrients in adjacent waters but, if terrestrial runoff is reduced, they do not have the capacity to maintain themselves at the same level of production. This is due to loss of nutrients in detritus export to the bays and suggests that there must be selective pressure for mechanisms of recycling within the mangrove forest.

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