

United States
Department of
Agriculture

Forest Service

**Pacific Southwest
Research Station**

General Technical
Report PSW-118



Mangroves of the Pacific Islands: Research Opportunities

Ariel E. Lugo



Lugo, Ariel E. 1990. **Mangroves of the Pacific islands: research opportunities.** Gen. Tech. Rep. PSW-118. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 13 p.

The perception of mangroves by people in the Pacific islands and throughout all the world has changed in the past decades. Today, the economic, social, ecologic, and esthetic values of mangroves are well recognized. Past research on these ecosystems is responsible for the change in perception. However, a review of eleven subjects relevant to the management of Pacific mangrove forests revealed numerous gaps in quantitative understanding of mangrove functions and values. These gaps must be filled if the gains in public perceptions of mangrove values are to be institutionalized through enlightened management. The subjects reviewed were diversity of mangrove habitats; primary productivity; nutrient cycling; food chains; birds, fisheries, and other wildlife; silviculture; response to stressors; restoration; basic biology; values; and changes in sea level. A proposal for mangrove research in the Pacific islands calls for programs with holistic focus, a hierarchical classification of mangrove habitats, a long-term perspective, sensitivity to human and cultural issues, and use of modern research tools such as geographical information systems, networking of permanent research plots, modeling, and team research.

Retrieval Terms: coastal ecosystems, mangrove ecosystems, Micronesia, tropical forests

Acknowledgments

This manuscript was prepared in response to a request from the Pacific Southwest Research Station. I thank Craig D. Whitesell, Marjorie Falanruw, Edwin Q.P. Petteys, Leonard Newell, and Sandra Brown for reviewing the manuscript. The work was done in cooperation with the University of Puerto Rico.

THE AUTHOR:

ARIEL E. LUGO is project leader in charge of tropical American forest management research and director at the Institute of Tropical Forestry, Southern Forest Experiment Station, Río Piedras, Puerto Rico.

Publisher:

**Pacific Southwest Research Station
P.O. Box 245, Berkeley, California 94701**

March 1990

Mangroves of the Pacific Islands: Research Opportunities

Ariel E. Lugo

CONTENTS

Introduction	1
Methods	1
Mangroves of the Pacific Islands	2
Mangrove Habitats	5
Primary Productivity	5
Nutrient Cycling	6
Food Chains	6
Birds, Fisheries, and Other Wildlife	8
Silviculture	8
Responses to Stressors	9
Restoration	9
Basic Biology	9
Values	9
Change in Sea Level	10
Proposed Focus for Research	10
References	11

INTRODUCTION

In Micronesia the mangrove swamps have, at present, little economic importance, except that some of the trees are occasionally used for timber, as in Sonneratia on Kusaie.

Usually the mangrove belt is passed by as dreary, uninteresting, and mosquito-infested by the tropical traveler, but to the botanically inclined, or even to the seeker of beauty, this region well repays closer acquaintance.

(Fosberg 1947, p. 138)

One of the earliest descriptions of the mangroves in the Pacific islands focused on the botanical diversity of the swamps and their extreme beauty (Fosberg 1947). Since that time, two dramatic changes have taken place in the perception of mangroves by people. First, mangroves are understood to have multiple economic values (Hamilton and Snedaker 1984, Saenger and others 1983), and secondly, mangroves now attract the attention of many sectors of society, not just the adventurer or botanically inclined. In fact, mangroves are now 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 developments) and those who advocate complete preservation of the ecosystem even at the exclusion of people. As the Pacific islands continue to develop economically, their governments must balance the various uses of mangroves and other coastal areas. Already it is obvious that the first quote from Fosberg is no longer applicable to Micronesian mangroves. Today, fishing alone makes the Micronesian mangroves extremely important to the export economy of these islands.

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.

I recommend research that will advance current understanding of mangrove ecosystems and that will also be useful to the

management of the mangroves in the Pacific islands. Such research focuses on maximum benefit to people while conserving the integrity and biological diversity of mangrove forests. This report describes some of the early work on the mangroves of the Pacific islands and suggests topics that offer the best research opportunities in the region 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). I then grouped those areas that have shown the greatest progress since 1962 when functional studies of mangroves began (*table 1*). By

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

Area of research	Key sources
Species richness, community structure, and physiognomy	Chapman 1976
Anatomy, morphology, and taxonomy	Tomlinson 1986
Classification of mangrove habitats	Cintrón and others 1986, Lugo and Snedaker 1974, Thoml 1975, 1982, 1984
Zonation and succession	Chapman 1976, Lugo 1980, Macnae 1968, Snedaker 1982
Ecosystem function including ecophysiology	Chapman 1976, Clough 1982, Lugo and Snedaker 1974, Walsh 1974,
Regional importance of mangroves	Carter and others 1973, Odum 1970, Snedaker and Lugo 1973, Turner 1977
Leaf dynamics production, turnover, and detritus dynamics	Twilley 1985, Twilley and others 1986
Mangrove stressors	Lugo 1978, Lugo and others 1981
Management and conservation	Hamilton and Snedaker 1984, Watson 1928,

comparing what is known about mangroves from different parts of the world with information from the Pacific island region, I identified gaps in knowledge. Such gaps are, in fact, research needs in the region. These were then grouped into the following categories: (1) diversity of mangrove 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.

The mangroves of interest to this review are referred to in the literature as mangroves from the Pacific islands, Micronesia, or Oceania. The mangrove flora from this vast area originates from the Indo-west Pacific mangrove flora (*sensu* Macnae 1968). Although I will refer to the Pacific island mangroves, the focus will be in those of Micronesia as defined below by Fosberg (1975).

MANGROVES OF THE PACIFIC ISLANDS

On a global scale, Pacific island mangroves constitute a small fraction of the total mangrove area (Saenger and others 1983). However, on individual islands mangrove forests can be an important fraction of the total forest resource (*table 2*). For the

five Caroline Island groups for which information is available, the fraction of total forest area that is mangroves ranges from 15 percent in Palau to 31 percent in Truk. Such a large fraction of mangroves in an island is impressive and unusual. For Puerto Rico, a Caribbean island with comparable data, mangroves constitute only 1.5 percent of the island's forested area. It is highly probable that, in continents and other Caribbean islands with larger total areas of mangroves, the fraction of the forest resource that is mangroves is much smaller than in these Pacific islands. In addition, because of land use history and human pressure on the land, the mangroves of these islands represent the best examples of relatively undisturbed forests in the region.

The basal area and wood volume in the mangroves of Pohnpei, the island in *table 2* with the largest mangrove area, compare favorably with those in Malaysia, Florida, Venezuela, and Puerto Rico for which comparative information is available (*table 3*). Net wood volume in Pohnpei and Kosrae is much higher than in Truk and Yap (*table 3*). Results from forest surveys in the Pacific islands suggest that most stands have more than 70 percent canopy cover, and the diameter at breast height of trees is generally larger than 12.5 cm but smaller than 30 cm (Cole and others 1987, Falanruw and others 1987a, b, MacLean and others 1988a, Whitesell and others 1986). Tree heights of up to 30 m appear common. Detailed timber inventory data are reported in MacLean and others (1988b).

In some islands a large fraction of mangrove forests are stunted. This was reported for Pohnpei (MacLean and others 1988b), Yap (Falanruw and others 1987a), and Palau (Cole and others 1987). These stunted forests are usually found inland (probably basin forests, *sensu* Lugo and Snedaker 1974), and are associated with low water circulation and a firm surface (Falanruw and others 1987a, MacLean and others 1986), or an organic hard pan (Cole and others 1987). In the island of Kosrae, less developed mangroves also occur, but these grow behind a protective strip of coastal strand vegetation which protects the mangroves from direct contact with ocean waves and currents (Whitesell and others 1986).

Table 2—Area of forests, upland forests, mangrove forests, and other wetlands in the Caroline Islands, annual rainfall, and the total area of the islands

Island group	Other wetlands							
	Annual rainfall	Total land	Total forests	Upland forests	Mangroves	Swamp forests	Marsh	Source
	<i>mm</i> ----- <i>Area (hectares)</i> -----							
Palau ¹	3,730	41,619	31,259	21,891	4,708	1,680	634	Cole and others 1987
Yap	3,028	9,716	3,882	2,556	1,171	155	171	Falanruw and others 1987a
Truk ²	3,650	4,170	986	677	306	2 ³	234	Falanruw and others 1987b
Pohnpei	4,820	35,493	19,683	12,548	5,525	214 ³	178	MacLean and others 1988b
Kosrae	5,000-7,000	11,186	7,066	5,090	1,562	345	25	Whitesell and others 1986

¹The largest island in this group, Babelthuap, has an area of 36,733 ha and 26,473 ha of forest lands (including 3,566 and 1,613 ha of mangrove and other wetlands, respectively; MacLean and others 1988c).

²Includes only the islands of Moen, Dublon, Feban, and Eten.

³Ivory nut palm forests on edge of wet areas.

¹The largest island in this group, Babelthuap, has an area of 36,733 ha and 26,473 ha of forest lands (including 3,566 and 1,613 ha of mangroves and other wetlands, respectively; MacLean and others 1988c).

²Includes only the islands of Moen, Dublon, Feban, and Eten.

³Ivory nut palm forests on edge of wet areas.

Table 3—Stand characteristics of mangrove forests in the Caroline Islands, Eastern Caribbean Islands, Florida, Venezuela, Malaysia, and the Philippines

Location	Number of species	Basal area	Gross volume	Net volume ¹	Source
		<i>m</i> ² / <i>ha</i>	— <i>m</i> ³ / <i>ha</i> —		
Palau, Micronesia	6			58	MacLean and others 1988b
Pohnpei, Micronesia	6	20.4 ²	100 ^{2,3}	76	MacLean and others 1988b,
Pohnpei, Micronesia	5	32.1 ⁴	217 ^{3,4}		Petteys and others 1986
Kosrae, Micronesia	4			76	MacLean and others 1988a
Truk, Micronesia	1			19	MacLean and others 1988a
Yap, Micronesia	3			62	MacLean and others 1988a
Florida, North America	5	6.0-38.5			Pool and others 1977
Puerto Rico, Caribbean	4	6.9-35.0			Pool and others 1977
Venezuela, South America	3	10.0-39.0	197 ± 33		Taninos y Maderas Venezolanas 1971
Malaysia, Asia			162-223		Christensen 1983
Philippines, Asia			160		FAO 1984

¹Excluding rotten wood.
²Stratum 1—trees at least 12 cm dbh but less than 30 cm.
³84 percent bole.
⁴Stratum 2—trees with a dbh of 30 cm or greater.

In addition to mangroves, these Pacific islands have significant areas of other types of wetlands (*table 2*). I included both saline and freshwater marshes in the marsh category. The total area of mangroves and forested and nonforested wetlands represents a significant fraction of the island's landscape (13-17 percent). The high rainfall in the region (over 3,000 mm/yr, *table 2*) in combination with poorly drained soils most likely accounts for the large fraction of wetland area. However, these estimated areas are probably less than the true area of wetlands, because many forests without standing water but with saturated soil are classified as upland forests (c.f. Laird 1983 for description of the soils of Truk). Descriptions of freshwater forested wetlands are available in Hosokawa (1952a, b).

The species composition of the mangroves in the Pacific islands was described by Fosberg (1947) who noted important differences among islands. Fosberg focused on the islands of Micronesia which included the Mariana, Caroline, Marshall, and Gilbert islands. There are other peripheral islands in Micronesia, but according to Fosberg, they had no natural mangrove stands. He noted that the island of Palau had the largest number of mangrove species and the most diverse mangrove forests in the region (Fosberg 1947, 1975). A total of 29 plant species were listed for the mangroves of Micronesia of which 17 were identified as "core" mangrove species because they were associated mainly with mangrove communities, and 12 were identified as "associated" mangrove species because they also occurred in other communities (*table 4*).

The flora of the Micronesian mangroves is a depauperate and attenuated extension of the vast areas of mangrove vegetation of Malaysia (Fosberg 1975). The number of mangrove species in the islands decreases northward and eastward of Palau. Fosberg pointed out that this distribution could not be attributed to dispersal because (1) mangroves had been in the region since the Miocene (70 million years ago; even in islands that today have no mangroves), (2) the species that dominated the stands had excellent dispersal mechanisms, and (3) there was ample time for dispersal. Instead, he and Chapman (1975, 1976) attributed the biogeographical distribution of mangroves in the Pacific island region to the availability of suitable habitats.

Micronesian mangroves in high rainfall conditions (Yap, Palau, Truk, Pohnpei, and Kosrae) harbor a rich epiphytic flora of about 18 species (Chapman 1976). These epiphytic communities are shared with adjacent rainforest ecosystems and grow in the sunny and dry places at the base of the crowns, and sometimes on the upper parts of stems. The higher the rainfall, the greater the number of epiphytes. The number of epiphytic species varies from island to island, from one species in Saipan to 11 species in Palau. Epiphytes may play an important role in intercepting rainwater, capturing nutrients in rainfall, and recycling them through the mangroves. Epiphytes also boost the primary productivity of stands and contribute additional carbon to the forest floor and herbivorous and detrital food chains. Detailed accounts of epiphytes in Micronesian freshwater swamps are given by Hosokawa (1952a, b).

Table 4—Mangrove species arranged in order of breadth of geographic distribution in Micronesia (Fosberg 1975)

Mangrove species	Growth form	Panotropical	Indo-Pacific	Palau	Yap	W. Caroline Atolls	Truk	Pohnpei	E. Caroline Atolls	Koror	Guam	Rota	Tinian	Saipan	N. Mariana	S. Marshall Atolls	N. Marshall Atolls	N. Gilbert Atolls	S. Gilbert Atolls	Nauru
A. Core species																				
<i>Bruguiera gymnorhiza</i>	t		x	x	x	x	x	x	x	x	x			x		x	x	x	x	x
<i>Lumnitzera littorea</i>	t		x	x	x	x	x	x	x	x	x					x		x		
<i>Sonneratia alba</i>	t		x	x	x		x	x	x	x						x		x		
<i>Rhizophora mucronata</i>	t		x	x	x	x	x	x	x	x	x					x		x	x	
<i>Rhizophora apiculata</i>	t		x	x	x		x	x	x											
<i>Derris trifoliata</i>	l		x	x	x		x	x	x	x	x									
<i>Nypa fruticans</i>	t-s		x	x	x		x	x		x	x									
<i>Dalbergia candanensis</i>	l		x	x	x		x	x		x	x									
<i>Xylocarpus granatum</i>	t		x	x	x		x	x		x										
<i>Xylocarpus moluccensis</i>	t		x								x	x	x							
<i>Smythea lanceata</i>	l		x	x			x	x	x	x										
<i>Avicennia alba</i>	t			x	x						x									
<i>Ceriops tagal</i>	t		x	x	x															
<i>Dolichandrone spathacea</i>	t		x	x	x															
<i>Scyphiphora hydrophyllacea</i>	s		x	x	x															
<i>Acanthus ebracteatus</i>	s		x	x																
<i>Rhizophora mucronata</i> var. <i>stylosa</i>	t		x								x									
B. Peripheral species																				
<i>Pemphis acidula</i>	s-t		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
<i>Hibiscus tiliaceus</i>	t	x		x	x	x	x	x	x	x	x	x	x	x	x	x				
<i>Cyperus javanicus</i>	h		x	x	x	x	x	x	x	x	x	x	x	x	x			x		
<i>Nephrolepis acutifolia</i>	eh		x	x				x	x	x	x					x				
<i>Acrostichum aureum</i>	h	x		x	x	x	x	x		x	x	x	x	x	x	x				
<i>Paspalum distichum</i>	h	x		x	x	x	x	x		x	x	x				x	x	x		
<i>Barringtonia racemosa</i>	t		x	x	x	x	x	x	x	x	x	x								
<i>Cerbera manghas</i>	t		x	x	x		x	x	x	x										x
<i>Heritiera littoralis</i>	t		x	x	x		x	x		x	x			x						
<i>Phragmites karka</i>	h		x	x	x		x	x		x	x		x	x						
<i>Excoecaria agallocha</i>	s-t		x	x	x		x													
<i>Lepiniopsis trilocularis</i>	t		x	x			x													
Explanation of symbols for growth forms t = tree; s-t = shrub or tree; h = herb; eh = epiphytic herb; l = liana; t-s = tree or shrub; s = shrub.																				

Chapman (1975, 1976) called attention to several environmental features of mangroves in the Pacific islands region that, in his view, were critical to understanding these ecosystems. Specifically he argued that wind direction (and hence wave action) was critically important because mangrove development was more extensive in the leeward than windward coasts (e.g., Palau and Pohnpei). Wave action is modified by the presence and type of coral reefs offshore and by the fetch of lagoons fringed by mangroves. Physiography is also critical because it limits the opportunities for mangrove establishment and the potential area of the mangrove habitat. Salinity, drainage, and soil type are additional factors considered by Chapman as critical to the distribution of mangroves in Pacific islands. During my visit to these islands I did not observe high soil salinity, as is common in arid environments or in climates with prolonged dry seasons.

Fosberg (1947, 1975) was the first to describe the wide diversity of mangrove habitats in Pacific islands. He discussed the following mangrove environments: riparian along tidal rivers, fringes on bays, ocean fringes, on coral atolls where the land dips below maximum water level, and depressions of clear, salty water with rocky bottoms (mangrove depressions). Substrates

vary widely from calcareous, volcanic, or metamorphic origins and may either be muddy, rocky, or of fine sand. Chapman's (1976) review of the work of Hosokawa lists three mangrove habitats in these islands: (1) *Sonneratia alba* forests on the seaward environments with coral material as substrate, (2) *Rhizophora mucronata* forests on stream banks, river mouths, and shallow inlet areas, and (3) *Bruguiera gymnorhiza* forests on the landward portions of the mangrove habitat with low salinity. The relation between species composition, ecosystem function, and the presence of these environments and substrates has not been studied.

In addition to the biogeographic and natural history research conducted in the region (see reviews by Chapman 1976, Macnae 1968, Percival and Womersley 1975, and Woodroffe 1987), there is little additional work on the mangrove ecosystems of Pacific islands (Anonymous 1978). Fosberg (1975) described three principal gradients that in his view required additional study but are yet to be analyzed. These were (1) a reduction of salinity along rivers in high islands (associated with dramatic changes in vegetation), (2) climatic change from seasonally wet to constantly wet west to east along the equator, and increasing dryness both northward and southward from the equatorial wet

belt, and (3) an east-west topographic gradient characterized by increasing distance from the species-rich Malaysian source area. Only the last gradient is unique to the region. The first two gradients occur in other parts of the world. For this reason, the design of new research programs must take advantage of the information that is transferable from mangrove studies elsewhere in the world.

Mangrove Habitats

The forest surveys of Pacific islands (MacLean and others 1988a, b, c, Petteys and others 1986) are extremely valuable for assessing total forest area, forest distribution, and stand composition of mangroves. 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.

Research in Australia has led the world in showing the geomorphological basis for mangrove stand classification (Semeniuk 1985a, b; Thom 1975, 1982, 1984). These researchers have carefully documented how growth conditions in mangroves are a function of the geomorphology of their physical habitats. In the Pacific islands, Fosberg (1947, 1975) and others have noted the diversity of mangrove habitats, but there is no systematic description of these mangrove habitats. How many types of mangroves are there in the islands? Which are the most important? How well do mangrove ecosystem structure, composition, and dynamics relate to mangrove habitats classified according to geomorphology?

Recently Woodroffe (1987) reviewed the distribution and environmental setting of Pacific island mangroves. He used the eight environmental settings of Thom (1982, 1984) and reduced them to four for Pacific islands: (1) Deltaic estuarine mangrove swamps, (2) Embayment/harbor/lagoon mangroves, (3) Reef flat mangroves, and (4) Inland mangroves and depressions. These categories are very useful for organizing information for Micronesian mangroves. The only modification that I suggest is to eliminate the term "estuarine" from the Deltaic mangroves because all mangroves are technically estuarine (i.e., freshwater mixes with seawater at some point in time during the life history of stands).

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 man-

groves 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). 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. At 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 smallest scale 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 classifications 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 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

I could not find a single estimate of the primary productivity of mangroves in Pacific islands. Only an article by Woodroffe and Moss (1984) measured litterfall in a "restricted" forest (probably a basin mangrove *sensu* Lugo and Snedaker 1974) in the island of Vaitupu, Tuvalu, south Pacific (7°28'S, 178°42'E). The forest, dominated by *R. stylosa*, although stunted, had a similar rate of litter production as that of mangroves in other locations (7.8 Mg/ha.yr). The monthly pattern of litterfall had little seasonality (probably reflecting the high rainfall in the

island (3,000 mm/yr), and 84 percent of the total production was leaves followed by 13 percent in stipules. Woodroffe and Moss remarked that the rates they obtained compared favorably with rates measured elsewhere in the world.

Litter production in mangroves is fairly well understood (Bunt 1982, Lugo and Snedaker 1974, Twilley and others 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 produced litter at the same rate as those of Malaysia, it is unlikely that they would match Malaysian mangroves in the production of wood or roots. However, Pacific island mangroves 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. Studies of primary productivity of Pacific island 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 and others 1982a, b, Manan and Khan 1984, Putz and Chan 1986). As noted earlier, crown epiphytes as well as epiphytes on roots may play an important role in the primary productivity of high rainfall Pacific island 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 25 sites in the world for which at least one chemical analysis of a vegetation or soil sample was reported (*table 5*). None were from the Pacific islands. Furthermore, 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.

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.

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. However, information about the islands was limited to general statements on the flora. 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 and others 1973, Lewis and others 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 through the Micronesian islands it becomes obvious that fish exports are increasing from islands 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 and others 1988). This 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 the mangroves of Pacific islands. As a minimum, this information will indicate which food chain model (if any) of those already described in other parts of the world applies to the Pacific island region.

Table 5— Identification and characteristics of sites used for describing the chemical properties of mangrove ecosystems

Site	Type of mangrove	Location	Latitude	Longitude	Tidal amplitude (m)	Annual rainfall (mm)	Mean annual Temperature (°C)	Source
A 1	Many, including fringe and basin	Hinchinbrook Island, Missionary Bay Australia	18°20'S	146°10'E	2 - 3	2,000-3,000		Bunt 1982
A 2	Fringe-basin transect, 9 sites	Hinchinbrook Island, Missionary Bay Australia	18°13'S	146°11'E	>1.2			Boto 1982, Boto and Wellington 1983, 1984
A 3	Fringe	Western Port Bay, Victoria, Australia			2.8			Clough and Attiwill 1975
A 4		Barker Inlet, Gulf of St. Vincent, South Australia	34°S	138°W	2.5			
B 1	Managed stands	Matang Mangrove Reserve, Port Weld Perak, Malaysia	4°50'N	100°35'E	< 2			Ong and others 1982a, b
B 2	Riverine	Sungai Merbok Estuary, Kedah, Malaysia						Ong and others 1980b, 1981
B 3	Unknown	China						Rodin and Bazilevich 1967
B 4	Fringe	Matang Mangrove Reserves, Pulau Kecil, Malaysia	4°48'N	100°35'E				Putz and Chan 1986
B 5	Unknown	India						
C 1	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
C 2	Fringe	Joyuda Lagoon, Puerto Rico	18°8'N	67°14'W				Levine 1981, Musa 1986
C 3	Basin	Joyuda Lagoon, Puerto Rico	18°8'N	67°14'W				Musa 1986
C 4	Fringe	Jobos Bay, Puerto Rico	18°N	66°15'W	0.4	884	26.4	Lugo and others 1987
D 1	Riverine	Darien, Santa Fe, Panama				2,000	25	Golley and others 1975
E 1	Basin	Rookery Bay, Florida	25°62'N	80°25'W	0.55	1,346	23.6	Lugo and Snedaker 1975, Twilley 1985, Twilley and others 1986
E 2	Dwarf	Turkey Point, Southeast Florida	25°20'N	80°60'W				Snedaker and Brown 1981
E 3	Hammock	Turkey Point, Southeast Florida	25°20'N	80°60'W				Snedaker and Brown 1981
E 4	Many in 11 stations	Turkey Point, Southeast Florida	25°20'N	80°60'W				Snedaker and Brown 1981
E 5	Unknown	Mostly from Florida						Walsh 1974
F 1	Riverine	Itanhaém, Sao Paulo, Brazil	24°11'S	46°47'W		1,717	21.9	Lamberti 1969
F 2	Many in 18 sites	Southeast Coast of Brazil	10°25'S-23°15'S					Lacerda and others 1986a
F 3	Fringe	Baia de Sepetiba, Rio de Janeiro Brazil	23°S	44°W				Lacerda and others 1985, 1986b
F 4		Brazil						Rodin and Bazilevich 1967
F 5		Catalao Island, Guanabara Bay, Brazil	22°46'S	43°17'W				Lacerda and others 1986b
F 6		Baia de Sepetiba, Rio de Janeiro, Brazil	23°S	44°W				Aragon and others 1986

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). 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 Pacific islands?

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 1986b). 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 and others 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 and others 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 resolution 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 Pacific islands? 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, molluscs, and crustaceans. 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 and others 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 and others 1977). Crabs consume wood (Lacerda 1981) and change the topography of the mangrove floor (Warren and Underwood 1986). Seed predators influence the distribution of tree species (Smith 1987a, b).

Wildlife management in mangrove forests requires a holistic understanding of the system. Wildlife research must be integrated into other types of mangrove research, which includes 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 and others 1975) and primary productivity point of view (Ong and others 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 Maderas Venezolanas C.A. 1971) and for those in Fiji (Marshall, undated, Baines 1979).

Are any of the available mangrove management systems applicable to Pacific islands? How much of the mangrove areas of Pacific islands and which stands are suitable for intensive silvicultural practices? Given the small area of forests in this part of the world, what is the minimal area of swamp that can be treated with a positive economic return? What alternative silvicultural systems can be developed for small islands 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 Pacific islands as in those of Malaysia where cutover sites are dominated by the fern *Acrostichum* (Hassan 1981)?

The evidence is conflictive regarding the effect of *Acrostichum* on mangrove regeneration. Chan and others (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. gymnorhiza* in the presence of *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 by Liew (1970), Srivastava (1980), and Yao (1986), Tang and others (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 and others 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, overexploitation, etc. Examples of these stressors and mangrove responses to them are given in Gordon 1987, Lugo and others 1981, 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 patterns of response of mangroves to stressors is fairly universal (Lugo and others 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 changes 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 which 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 1985a, b, Jiménez 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, wave runup protection, 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 and others (1986), Lugo and Brinson (1979), and Odum and others (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 developed and extended during the late Holocene. Aging of mangrove peats through the whole region yielded peats younger than $6,500 \pm 190$ yr. Today, there is public concern 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.

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 low-land areas.

PROPOSED FOCUS FOR RESEARCH

The proposed research program for mangroves of Pacific islands 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-à-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.

REFERENCES

- Anonymous. 1978. **Proceedings of the international workshop on mangrove and estuarine area development for the Indo-Pacific region**. Los Banos, Laguna, Philippines: Philippines Council for Agriculture and Resource Research; 201 p.
- Aragon, G.T.; Pires, V.S.; Lacerda, L.D.; Patchineelan, S.R. 1986. **Distribuição espacial de nutrientes e metais pesados em sedimentos e águas superficiais em um ecossistema de manguezal**. Acta Limnol. Brazil 1:365-385.
- Baines, G.B.K. 1979. **Mangroves for national development: a report on the mangrove resources of Fiji**. Nathan, Q. 4111, Australia: Institute of Applied Social Research, School of Australian Environmental Studies, Griffith University; 28 p.
- Banerjee, U.; Choudhury, P.K.R. 1986. **Preliminary studies on artificial regeneration of mangrove forests in the Sundarbans, west Bengal**. Indian Forester 112: 208-222.
- Bamett, T.P. 1982. **On possible changes in global sea level and their potential causes**. DOE/NBB-0022, UC-11, TR-001. Washington, DC: U.S. Department of Energy, Office of Energy Research, Office of Basic Energy Sciences, Carbon Dioxide Research Division; 36 p.
- Bianchi, T.S.; Dawson, R.; Sawangwong, P. 1988. **The effects of macrobenthic deposit-feeding on the degradation of chloropigments in sandy sediments**. Journal of Experimental Marine Biology and Ecology 122:243-255.
- Bismark, M. 1986. **Keragaman burung di hutan bakau, taman nasional Kutay (Kallmantan Timur)**. Buletin Penelitian Hutan 482: 11-22.
- Boto, K.G. 1982. **Nutrient and organic fluxes in mangroves**. In: Clough, B.F., ed. **Mangrove ecosystems in Australia**. Canberra, Australia: Australian Institute of Marine Sciences and Australian National University Press; 239-257.
- Boto, K.; Wellington, J.T. 1984. **Soil characteristics and nutrient status in a northern Australian mangrove forest**. Estuaries 7: 61-69.
- Boto, K.G.; Wellington, J.T. 1983. **Phosphorus and nitrogen nutritional status of a northern Australian mangrove forest**. Marine Ecology Progress Series 11: 63-69.
- Bunt, J.S. 1982. **Studies of mangrove litterfall in tropical Australia**. In: Clough, B.F., ed. **Mangrove ecosystems in Australia**. Canberra, Australia: Australian Institute of Marine Science and Australian National University Press; 223-237.
- Carter, M.R.; Bums, L.A.; Cavinder, T.R.; [and others]. 1973. **Ecosystem analysis of the Big Cypress swamp and estuaries**. EPA 904/9-74-002. Atlanta, GA: U.S. Environmental Protection Agency, Region 4.
- Cawkell, E.M. 1964. **The utilization of mangroves by African birds**. Ibis 106: 251-254.
- Chakrabarti, K. 1986a. **Generic and species diversity of animal vegetation dynamics of Sundarbans mangrove south Bengal laterite tracts of west Bengal and north Bengal forests—an ecological study**. Indian Forester 112: 407-416.
- Chakrabarti, K. 1986b. **Fish and fish resources in the mangrove swamps of Sundarbans, west Bengal—an indepth study**. Indian Forester 112: 538-542.
- Chan, H.T.; Husin, N.; Chong, P.F. 1987. **Is there a need to eradicate *Acrostichum speciosum* prior to planting *Rhizophora mucronata* in logged-over mangrove forest area?** Occasional paper. Kepong, Malaysia: Forest Research Institute of Malaysia; 7 p.
- Chapman, V.J. 1975. **Mangrove biogeography**. In: Walsh, G.; Snedaker, S.; Teas, H., eds. **Proceedings of international symposium on biology and management of mangroves**. Gainesville, FL: Institute of Food and Agricultural Sciences, University of Florida; 3-22.
- Chapman, V.J. 1976. **Mangrove vegetation**. J. Cramer. Vaduz, Germany. 447 p.
- Christensen, B. 1983. **Mangroves—what are they worth?** Unasylva 35(139): 2-15.
- Cintrón, G.; Lugo, A.E.; Martínez, R. 1986. **Structural and functional properties of mangrove forests**. In: D'Arcy, W.G.; Correa M.D., eds. **The botany and natural history of Panama: La botanica e historia natural de Panama**. Monographs in Systematic Botany 10. St. Louis, MO: Missouri Botanical Gardens; 53-66.
- Cintrón, G.; Schaeffer-Novelli, Y. 1984. **Methods for studying mangrove structure**. In: Snedaker, S.C.; Snedaker, J.G., eds. **The mangrove ecosystem: research methods**. Monographs on oceanographic methodology, 8. Paris, France: UNESCO; 91-113.
- Cintrón, G.; Schaeffer-Novelli, Y. 1985. **Características y desarrollo estructural de los manglares de Norte y Sur América**. Ciencia Interamericana 25: 4-15.
- Clough, B.F., ed. 1982. **Mangrove ecosystems in Australia. Structure, function, and management**. Canberra, Australia: Australian Institute of Marine Sciences and Australian National University Press; 302 p.
- Clough, F.; Attiwill, P.M. 1975. **Nutrient cycling in a community of *Avicennia marina* in a temperate region of Australia**. In: Walsh, G.; Snedaker, S.; Teas, H., eds. **Proceedings of international symposium on biology and management of mangroves**. Gainesville, FL: Institute of Food and Agricultural Sciences, University of Florida; 137-146.
- Clusener, M.; Breckle, S.W. 1987. **Reasons for the limitation of mangrove along the west coast of northern Peru**. Vegetatio 68: 173-177.
- Cole, T.G.; Falanruw, M.C.; MacLean, C.D.; [and others]. 1987. **Vegetation survey of the Republic of Palau**. Resour. Bull. PSW-22. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 13 p. + 17 maps.
- Costanza, R.; Daly, H.E. 1987. **Towards an ecological economics**. Ecological Modelling 38: 1-7.
- Dagar, H.S.; Basu, P. 1985. ***Bruguiera cylindrica* (L.) BL. (Rhizophoraceae) a rare mangrove in the Andaman-Nicobar Islands**. Journal of Economic and Taxonomic Botany 7: 653-654.
- Falanruw, M.C.; Whitesell, C.D.; Cole, T.C.; [and others]. 1987a. **Vegetation survey of Yap, Federated States of Micronesia**. Resour. Bull. PSW-21. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 9 p. + 4 maps.
- Falanruw, M.C.; Cole, T.G.; Ambacher, A.H.; [and others]. 1987b. **Vegetation survey of Moen, Dublon, Fefan, and Eten, State of Truk, Federated States of Micronesia**. Resour. Bull. PSW-20. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 6 p. + 3 maps.
- Farber, S.; Costanza, R. 1987. **The economic value of wetlands systems**. Journal of Environmental Management 24: 41-51.
- Food and Agriculture Organization. 1984. **Mangrove forests in Asia Pacific region. A summary of available information**. GCP/RAS/106/JNP Field Document No. 1. Bangkok, Thailand: Food and Agriculture Organization/United Nations; 40 p.
- Fosberg, F.R. 1947. **Micronesian mangroves**. Journal of the New York Botanical Garden 48: 128-138.
- Fosberg, F.R. 1975. **Phytogeography of micronesian mangroves**. In: Walsh, G.; Snedaker, S.; Teas, H., eds. **Proceedings of international symposium on biology and management of mangroves**. Gainesville, FL: Institute of Food and Agricultural Sciences, University of Florida; 23-42.
- Golley, F.B.; McGinnis, J.T.; Clements, R.G.; [and others]. 1975. **Mineral cycling in a tropical moist forest ecosystem**. Athens, GA: University of Georgia Press; 248 p.

- Gopalakrishnan, V. 1978. **Notes of the fish culture in mangrove areas of coral atolls.** In: Proceedings of the international workshop on mangrove and estuarine area development for the Indo-Pacific region. Los Banos, Laguna, Philippines: Philippines Council for Agriculture and Resources Research; 161-162.
- Gordon, D.M. 1987. **Disturbance to mangroves in tropical-arid western Australia: hypersalinity and restricted tidal exchange as factors leading to mortality.** Technical Series No. 12. Perth, Western Australia: Environmental Protection Authority; 36 p.
- Hamilton, L.S.; Snedaker, S., eds. 1984. **Handbook for mangrove area management.** Honolulu, HI: United Nations Environment Program and East West Center, Environment and Policy Institute; 123 p.
- Hannon, B.; Costanza, R.; Herendeen, R.A. 1986. **Measures of energy cost and value in ecosystems.** Journal of Environmental Economics and Management 13: 391-401.
- Hassan, H.H.A. 1981. **A working plan for the second 30-year rotation of the Matang mangrove forest reserve Perak. The first 10-year period 1980-1989.** Ipoh, Peninsular Malaysia: Perak State Forestry Department, 109 p.
- Hosokawa, T. 1952a. **A plant-sociological study in the mossy forests of Micronesian islands.** Memoirs of the Faculty of Sciences Kyushu University, Japan. Series E (Biology) 1: 65-82.
- Hosokawa, T. 1952b. **A synchronological study of the swamp forests in the Micronesian Islands.** Memoirs of the Faculty of Sciences Kyushu University, Japan. Series E (Biology) 1: 101-124.
- Jiménez, J.A. 1985a. **Rhizophora mangle silvics of forest trees of the American tropics.** SO-ITF-SM-2. New Orleans, LA: Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; 7 p.
- Jiménez, J.A. 1985b. **Laguncularia racemosa silvics of forest trees of the American tropics.** SO-ITF-SM-3. New Orleans, LA: Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; 4 p.
- Jiménez, J.A.; Lugo, A.E. 1985. **Avicennia germinans silvics of forest trees of the American tropics.** SO-ITF-SM-4. New Orleans, LA: Southern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; 6 p.
- Jiménez, J.A.; Lugo, A.E.; Cintrón, G. 1986. **Tree mortality in mangrove forests.** Biotropica 17: 177-185.
- Khan, M.A.R. 1986. **Wildlife In Bangladesh mangrove ecosystem.** Journal Bombay Natural History Society 83: 32-48.
- Lacerda, L.D. de. 1981. **Mangrove wood pulp, an alternative food source for the tree crab.** Biotropica 13: 317.
- Lacerda, L.D. de; de Resende, C.E.; Vilela Jose, D.M.; Fernández Francisco, M.C. 1986a. **Metallic composition of mangrove leaves from the south-eastern Brazilian coast.** Rev. Brasil Biol. 46: 395-399.
- Lacerda, L.D. de; de Resende, C.E.; Vilela Jose, D.; [and others]. 1985. **Mineral concentrations in leaves of mangrove trees.** Biotropica 17: 260-262.
- Lacerda, L.D. de; Jose, D.V.; de Rezende, C.E. [and others]. 1986b. **Leaf chemical characteristics affecting herbivory in a new world mangrove forest.** Biotropica 18: 350-355.
- Laird, W.E. 1983. **Soil survey of islands of Truk, Federated States of Micronesia.** Washington, DC: U.S. Department of Agriculture, Soil Conservation Service; 65 p.
- Lamberti, A. 1969. **Contribuição a conhecimento da ecologia das plantas do manguezal de Itanhaem.** Sao Paulo, Brazil: University of Sao Paulo; 218 p.
- Levine, E.A. 1981. **Nitrogen cycling by the red mangrove, Rhizophora mangle in Joyuda lagoon, on the west coast of Puerto Rico.** Mayaguez, Puerto Rico: University of Puerto Rico; 103 p. Master Thesis.
- Lewis, R.R.; Gilmore, R.G.; Crews, D.W.; Odum, W.E. 1985. **Mangrove habitat and fishery resources of Florida.** In: Seaman, W., ed. Florida aquatic habitat and fishery resources. Kissimmee, FL: Florida chapter of the American Fisheries Society; 281-336.
- Liew, T.C. 1970. **Research on mangrove forest In Sabah (1970).** Negeri Sabah, Malaysia: Laporan Penyelidik Hutan; 80-96.
- Liew, T.C.; Diah, M.N.; Chun, W.Y. 1975. **Mangrove exploitation and regeneration in Sabah.** Malaysian Forester 38: 260-270.
- Louis, M.; Hoai, T.L.; Lasserre, G. 1985. **Resultats preliminaires sur le recrutement en poissons dans deux lagunes des mangroves de Guadeloupe:** Belle-Plaine et Manche-a-Eau. Revue d'Hydrobiologie Tropicale 18: 249-265.
- Lugo, A.E. 1978. **Stress and ecosystems.** In: Thorp, J.H.; Gibbons, J.W., eds. Energy and environmental stress in aquatic systems. U.S. Department of Energy Symposium Series (CONF-77114). Springfield, VA: National Technical Information Services, 62-101.
- Lugo, A.E. 1980. **Mangrove ecosystems: successional or steady state?** Biotropica 12(supplement, 2): 65-72.
- Lugo, A.E. 1982. **Some aspects of the interaction among nutrient cycling, hydrology, and soils in wetlands.** Water International 7: 178-184.
- Lugo, A.E. 1987. **Avances y prioridades de investigación en manglares.** Simposio sobre ecosistemas da costa sul e sudeste Brasileira. Sao Paulo, Brazil: Academia de Ciencias do Estado de Sao Paulo; 59-76.
- Lugo, A.E.; Cintrón, G.; Goenaga, C. 1981. **Mangrove ecosystems under stress.** In: Barrett, G.W.; Rosenberg, R., eds. Stress effects on natural ecosystems. Sussex, England: John Wiley and Sons; 129-153.
- Lugo, A.; Laboy, E.N.; Cintrón, G. 1987. **Structure and dynamics of a mangrove fringe forest in the Jobos Bay National Estuarine Research Reserve.** National Oceanic and Atmospheric Administration Technical Report Series OCRM/DMEM. Washington, DC: U.S. Department of Commerce; 55 p.
- Lugo, A.E.; Brinson, M.M. 1979. **Calculations of the value of salt water wetlands.** In: Greeson, P.E.; Clark, J.R.; Clark, J.E., eds. Wetland functions and values: the state of understanding. Minneapolis, MN: American Water Resources Association; 120-130.
- Lugo, A.E.; Snedaker, S.C. 1974. **The ecology of mangroves.** Annual Review of Ecology and Systematics 5: 39-64.
- Lugo, A.E.; Snedaker, S.C. 1975. **Properties of a mangrove forest in southern Florida.** In: Walsh, G.; Snedaker, S.; Teas, H., eds. Proceedings of international symposium on biology and management of mangroves. Gainesville, FL: Institute of Food and Agricultural Sciences, University of Florida; 170-212.
- MacLean, C.D.; Cole, T.G.; Whitesell, C.D.; McDuffie, K.E. 1988c. **Timber resources of Babelthuap, Republic of Palau.** Resour. Bull. PSW-23. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 8 p.
- MacLean, C.D.; Cole, T.G.; Whitesell, C.D.; [and others]. 1988b. **Vegetation survey of Pohnpei, Federated States of Micronesia.** Resour. Bull. PSW-18. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 9 p. + 11 maps.
- MacLean, C.D.; Whitesell, C.D.; Cole, T.G.; McDuffie, K.E. 1988a. **Timber resources of Kosrae, Pohnpei, Truk, and Yap, Federated States of Micronesia.** Resour. Bull. PSW-25. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 8 p.
- Macnae, W. 1968. **A general account of the fauna and flora of mangrove swamps and forests in the indo-west-Pacific region.** Advances in Marine Biology 6: 73-270.
- Manan, D.H.O.B.A.; Khan, N.K.B.N. 1984. **Towards sustained yield management of mangroves: the Matang experience.** In: Ong, J.E.; Gong, W.K., eds. Productivity of the mangrove ecosystem: management implications. Penang, Malaysia: Universiti Sains Malaysia; 142-152.
- Marshall, C. (undated). **Sustained yield management of the mangrove salt-water swamp forest of Fiji.** Suva, Fiji: Department of Forestry; 19 p.
- Mukherjee, A.K. 1984. **The environmental Impact analysis for three mangrove species of Indian Sunderbans.** Bulletin of the Botanical Survey of India 26: 181-182.
- Mukherjee, A.K. 1986. **Adaptations in mangroves of Sunderbans.** Journal of Economic and Taxonomic Botany 8: 185-190.
- Mun, L.Y. 1984. **Energetics of leaf litter production and its pathway through the sesamid crabs in a mangrove ecosystem.** Penang, Malaysia: Universiti Sains Malaysia; 140 p. Thesis.
- Musa, J.C. 1986. **Influencia de Ins tributarios de agua dulce en la física-química del suelo, estructura, productividad, retorno y eficiencia de nutrientes (N, P, K, Ca) en el bosque de mangle de la laguna Joyuda, Cabo Rojo, Puerto Rico.** Mayaguez, Puerto Rico: University of Puerto Rico; 201 p. Dissertation.
- Naskar, K.; Bakshi, D.N.G. 1986. **On the verge of extinction of some important mangrove species from the Sunderbans delta in west Bengal.** Journal of Economic and Taxonomic Botany 8: 431-437.
- Odum, H.T.; Wang, F.C.; Alexander, J.F., Jr.; [and others]. 1987. **Energy analysis of environmental value.** Publication 78-17. Gainesville, FL: Center for Wetlands, University of Florida; 97 p.

- Odum, W.E. 1970. **Pathways of energy flow in a south Florida estuary.** Coral Gables, FL: University of Miami; 162 p.
- Ong, J.E.; Gong, W.K.; Wong, C.H. 1980. **Ecological survey of the Sungei Merbok estuarine mangrove ecosystem.** Penang, Malaysia: School of Biological Sciences, Universiti Sains Malaysia; 83 p.
- Ong, J.E.; Gong, W.K.; Wong, C.H. 1982a. **Studies on nutrient levels in standing biomass, litter and slash in a mangrove forest.** Penang, Malaysia: Mangrove ecosystem research group, School of Biological Sciences, Universiti Sains Malaysia; 44 p.
- Ong, J.E.; Gong, W.K.; Wong, C.H. 1982b. **Productivity and nutrient status of litter in a managed mangrove forest in Malaysia.** In: Proceedings symposium on mangrove forest ecosystem productivity in southeast Asia. Biotrop Special Publication No. 17; 33-41.
- Onuf, C.P.; Teal, J.M.; Valiela, I. 1977. **Interactions of nutrients, plant growth, and herbivory in a mangrove ecosystem.** Ecology 58: 514-526.
- Percival, M.; Womersley, J.S. 1975. **Floristics and ecology of the mangrove vegetation of Papua New Guinea.** Botany Bulletin No. 8. LAE Papua New Guinea National Herbarium, Department of Forests; 96 p.
- Petteys, E.Q.P.; Peter, S.; Rugg, R.; Cole, T.G. 1986. **Timber volumes in the mangrove forests of Pohnpei, Federated States of Micronesia.** Resour. Bull. PSW-19. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 2 p.
- Pool, D.J.; Snedaker, S.C.; Lugo, A.E. 1977. **Structure of mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica.** Biotropica 9: 195-212.
- Putz, F.E.; Chan, H.T. 1986. **Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia.** Forest Ecology and Management 17: 211-230.
- Ramos, M.I.S.; Nascimento, I.A.; de LL e Silva, J. 1986. **The comparative growth survival of Pacific oyster (*Crassostrea gigas* Thunberg, *C. gigas* var. *Kumamoto*) and mangrove oyster (*C. rhizophorae*) in Todos os Santos Bay, Brazil.** Ciencia e Cultura 38: 1604-1615.
- Robertson, A.I. 1986. **Leaf-burying crabs: their influence on energy flow and export from mixed mangrove forests (*Rhizophora* sp.) in northeastern Australia.** Journal of Experimental Marine Biology and Ecology 102: 237-248.
- Rodin, L.E.; Bazilevich, N.I. 1967. **Production and mineral cycling in terrestrial vegetation.** London, England: Oliver and Boyd; 288 p.
- Saenger, P.; Hegerl, E.J.; Davie, J.D.S., eds. 1983. **Global status of mangrove ecosystems.** The Environmentalist 3(supplement 3): 1-88.
- Semeniuk, V. 1985a. **Mangrove environments of Port Darwin, northern territory: the physical framework and habitats.** Journal of the Royal Society of Western Australia 67: 81-97.
- Semeniuk, V. 1985b. **Development of mangrove habitats along ria shorelines in north and northwestern tropical Australia.** Vegetatio 60: 3-23.
- Smith, T.J. 1987a. **Seed predation in relation to tree dominance and distribution in mangrove forests.** Ecology 68: 266-273.
- Smith, T.J. 1987b. **Effects of seed predators and light level on the distribution of *Avicennia marina* (Forsk.) Vierh. in tropical, tidal forests.** Estuarine, Coastal and Shelf Science 25(1): 43-51.
- Snedaker, S.C. [Letter to Ariel Lugo]. 1988 March 8. 1 leaf. Located at: Institute of Tropical Forestry, Southern Forest Experiment Station, Rio Piedras, Puerto Rico.
- Snedaker, S.C. 1982. **Mangrove species zonation: why?** In: Sen, D.N.; Rajpurohit, K.S., eds. Tasks for vegetation science. The Hague, Netherlands: Dr. W. Junk Publishers; 111-125.
- Snedaker, S.C.; Brown, S. 1981. **Water quality and mangrove ecosystem dynamics.** U.S. Environmental Protection Agency 600/4-81-022. Gulf Breeze, FL: Environmental Protection Agency; 80 p.
- Snedaker, S.C.; Lugo, A.E. 1973. **The role of mangrove ecosystems in the maintenance of environmental quality and high productivity of desirable fisheries.** Gainesville, FL: Center for Aquatic Sciences, University of Florida; 404 p.
- Srivastava, P.B.L. 1980. **Research proposals for mangrove vegetation in Malaysia.** In: Srivastava, P.B.L.; Kader, R.A., eds. Workshop on mangrove and estuarine vegetation. Serdang, Selangor: Faculty of Forestry, Universiti Pertanian Malaysia; 64-75.
- Sukardjo, S. 1987. **Natural regeneration status of commercial mangrove species (*Rhizophora apiculata* and *Bruguiera gymnorhiza*) in the mangrove forest of Tanjung Bungin, Banyuasin district, south Sumatra.** Forest Ecology and Management 20: 233-252.
- Tang, H.T.; Haron, H.A.H.; Cheah, E.K. 1981. **Mangrove forests of peninsular Malaysia—a review of management and research objectives and priorities.** Malaysian Forester 44: 77-86.
- Taninos y Maderas Venezolanas, C.A. 1971. **Plan de manejo forestal de la unidad norte de los manglares de la reserva forestal de Guarapiche.** Merida, Venezuela: Universidad de los Andes, Facultad de Ciencias Forestales.
- Thom, B.G. 1975. **Mangrove ecology from a geomorphic viewpoint.** In: Walsh, G.; Snedaker, S.; Teas, H., eds. Proceedings of international symposium on biology and management of mangroves. Gainesville, FL: Institute of Food and Agricultural Sciences, University of Florida; 469-481.
- Thom, B.G. 1982. **Mangrove ecology- a geomorphological perspective.** In: Clough, B.F., ed. Mangrove ecosystems in Australia. Canberra, Australia: Australian Institute of Marine Sciences and Australian National University Press; 3-17.
- Thom, B.G. 1984. **Coastal landforms and geomorphic processes.** In: Snedaker, S.; Snedaker, J.G., eds. The mangrove ecosystem: research methods. Monographs on oceanographic methodology, 8. Paris, France: UNESCO; 3-17.
- Tomlinson, P.B. 1986. **The botany of mangroves.** Cambridge, England: Cambridge University Press; 413 p.
- Tostain, O. 1986. **Etude d'une succession terrestre en milieu tropical: les relations entre la physionomie végétale et la structure du peuplement avien en mangrove Guyanaise.** Revue d'Ecologie (La Terre et la Vie) 41: 315-342.
- Turner, R.E. 1977. **Intertidal vegetation and commercial yields of panaeid shrimp.** Transactions of the American Fisheries Society 106: 411-416.
- Twilley, R.R. 1985. **Exchange of organic carbon in basin mangrove forests in a southwest Florida estuary.** Estuarine Coastal and Shelf Science 20: 543-557.
- Twilley, R.R. 1987. **Ecosystem analysis of the Guayas River estuary in Ecuador: implications for the management of mangroves and shrimp mariculture.** Report to the University of Rhode Island Coastal Resources Management Project. 50 p. + figs.
- Twilley, R.R.; Lugo, A.E.; Paterson-Zucca, C. 1986. **Litter production and turnover in basin mangrove forests in southwest Florida.** Ecology 67: 670-683.
- Walsh, G.E. 1974. **Mangroves: a review.** In: Reimold, R.J.; Queen, W.H., eds. Ecology of halophytes. New York: Academic Press; 51-174.
- Warren, J.H.; Underwood, A.J. 1986. **Effects of burrowing crabs on the topography of mangrove swamps in New South Wales.** Journal of Experimental Marine Biology and Ecology 102: 223-235.
- Watson, J.G. 1928. **Mangrove forests of the Malay Peninsula.** Malayan Forestry Records No. 6. Kuala Lumpur, Malaysia: Federated Malay States Government; 275 p.
- Whitesell, C.D.; MacLean, C.D.; Falanruw, M.C.; [and others]. 1986. **Vegetation survey of Kosrae, Federated States of Micronesia.** Resour. Bull. PSW-17. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 8 p. + map.
- Woodroffe, C.D. 1987. **Pacific Island mangroves: distribution and environmental setting.** Pacific Science 41: 166-185.
- Woodroffe, C.D.; Moss, T.S. 1984. **Litter fall beneath *Rhizophora stylosa* Griff., Vaitupu, Tuvalu, south Pacific.** Aquatic Botany 18: 249-255.
- Wright, J.M. 1986. **The ecology of fish occurring in shallow water creeks of a Nigerian mangrove swamp.** Journal of Fish Biology 29: 431-441.
- Yao, C. 1986. **Mangrove reforestation in Central Visayas.** Canopy International 12(2): 6-9.



The Forest Service, U. S. Department of Agriculture, is responsible for Federal leadership in forestry. It carries out this role through four main activities:

- Protection and management of resources on 191 million acres of National Forest System lands
- Cooperation with State and local governments, forest industries, and private landowners to help protect and manage non-Federal forest and associated range and watershed lands
- Participation with other agencies in human resource and community assistance programs to improve living conditions in rural areas
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

The Pacific Southwest Research Station

- Represents the research branch of the Forest Service in California, Hawaii, American Samoa and the western Pacific.

Persons of any race, color, national origin, sex, age, religion, or with any handicapping conditions are welcome to use and enjoy all facilities, programs, and services of the U.S. Department of Agriculture. Discrimination in any form is strictly against agency policy, and should be reported to the Secretary of Agriculture, Washington, DC 20250.