

Pacific Island Mangroves: Distribution and Environmental Settings¹

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ABSTRACT: Mangroves, absent from many small, "low" islands and from most of Polynesia, do not cover large areas on Pacific islands, and show rapid decrease in species diversity and stature across the Pacific. Preliminary data indicate that where they do occur they may be as productive, particularly in terms of detritus per unit area, as more luxuriant mangrove forests elsewhere. Oscillations of sea level during the Quaternary have disrupted the distribution of mangroves and present mangrove swamps are shown to have developed and extended substantially during the late Holocene in each of four environmental settings: i) deltaic/estuarine mangroves, ii) mangroves of embayments/harbors/lagoons, iii) mangroves of reef flats, iv) inland mangroves and mangrove depressions. These are ranked in order from i) to iv), from highest to lowest, in terms of landform and mangrove habitat diversity, rates of sedimentation, opportunities for freshwater nutrient input and enhanced productivity, and, it is argued, potential for organic carbon flux and trophic diversity. Structure and functioning of the mangrove ecosystem differs between settings. Restricted stands of mangroves, such as those inland on "low" islands or atolls, are unlikely to export quantities of organic carbon, but nevertheless are productive and support resources which can play an important role in the subsistence economy of the local inhabitants.

MANGROVE SWAMPS play several important roles in the coastal ecosystem. In particular they have been shown to be productive areas in which the rate of primary productivity is high, and, importantly, areas which contribute particulate and dissolved organic carbon to surrounding waters (Heald 1969, Odum and Heald 1972, Lugo and Snedaker 1974, Boto and Bunt 1981, Twilley 1985). Structurally and floristically mangrove swamps attain their greatest diversity in the Indo-West Pacific region (Macnae 1968), and there is a decrease in number of species with increasing latitude and location west into the Indian Ocean. Mangrove swamps do not cover a large area on islands in the Pacific Ocean; from west to east across the Pacific there is a

particularly rapid attenuation in the number of mangrove species and a general decline in mangrove forest stature.

Mangroves cover about 640 km² in the Solomon Islands, about 200 km² each in Fiji, New Caledonia and New Zealand, more than 4,000 km² in New Guinea, and nearly 12,000 km² in Australia (Saenger, Hegerl and Davie 1983). On other smaller island groups in the Pacific they may be far more limited in extent, covering about 10 km² in Tonga, and being rare or absent on the smallest and most isolated "low" islands, and absent from most of Polynesia. As a result of the restricted development of mangrove swamps and their often stunted growth forms on islands in the Pacific, the value of mangroves has not been widely appreciated (Baines 1981) and little legislation exists for their protection (Dahl 1980). Already, extensive areas have been reclaimed for urbanization or for agriculture (Straatmans 1954, Wildin 1965, Hassall 1980).

This paper examines the distribution of mangrove taxa on islands in the Pacific

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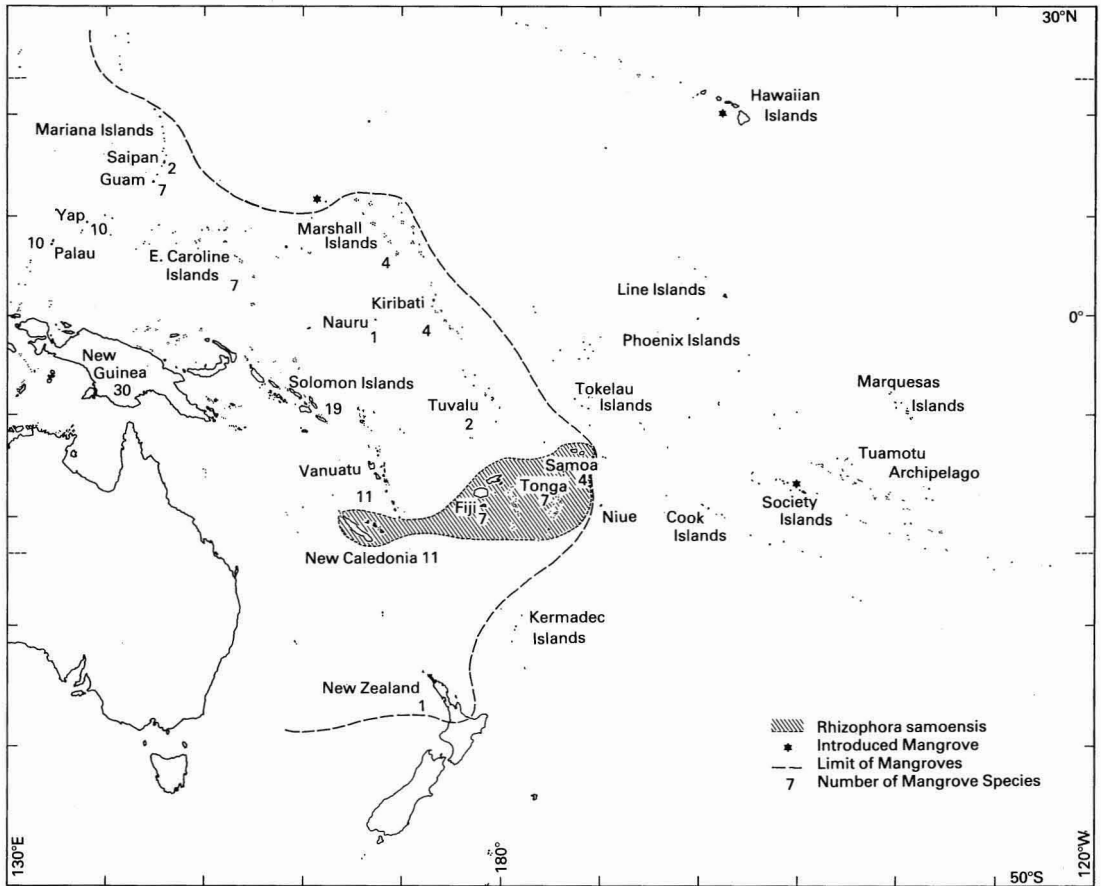


FIGURE 1. The distribution of mangrove taxa (species and hybrids) on islands or island groups in the Pacific (refer to Table 1 for details of genera).

Ocean, and identifies four environmental settings within which mangroves are found. The area examined lies east of longitude 130°E (Figure 1), but excludes New Guinea and Australia for which comprehensive accounts of floristics and geomorphology of mangrove swamps already exist (Percival and Womersley 1975, Clough 1982). Data on primary productivity of mangroves in and around the region are reviewed, and it is suggested that there is little reason to attach less importance to mangroves where they do grow in the Pacific than where they occur elsewhere in the world. However geomorphological processes, sedimentation patterns, and late Holocene history differ for each of the environmental settings and it is argued that biological func-

tioning and trophic structure are also likely to differ between settings.

DISTRIBUTION OF MANGROVE TAXA

The flora of many of the more remote islands of the Pacific is still poorly known and inadequately collected. The distribution of mangrove species is incompletely documented and confusion has arisen as a result of changes in nomenclature and perpetuation of errors of misidentification and mislabelling. The genus *Rhizophora* provides a good example. *Rhizophora mucronata* Lamk. was reported in Fiji in early accounts (Seeman 1867–1873, Guppy 1906) and the record was cited in subsequent treatments of the genus (Salvosa

1936, Ding Hou 1960). Richmond and Ackermann (1975) found no individuals of *R. mucronata* in Fiji and it now seems certain that it does not grow there and that the earlier record was of *R. stylosa* Griff. (Macnae 1968). Recently Tomlinson (1978) has recognized four species of *Rhizophora* in the Pacific region, *R. mucronata*, *R. stylosa*, *R. samoensis* (Hochr.) Salvosa and *R. apiculata* Bl., and two putative hybrids, *R. x lamarckii* Montr. (probably *R. stylosa* and *R. apiculata*) and *R. x selala* (Salvosa) Tomlinson (probably *R. stylosa* and *R. samoensis*). He has clarified taxonomy and distribution of these in the Southwest Pacific, recognizing *R. stylosa*, *R. samoensis*, and *R. x selala* from Fiji. Similar treatments might be extended usefully to *Avicennia*, *Bruguiera*, and *Sonneratia* throughout the Pacific.

In view of the confusion that exists at the specific level, Table 1 and Figure 1 indicate number of species (and hybrids) recorded in characteristic mangrove genera as reported in the literature. Chapman (1970) has recognized 16 genera which are restricted to mangrove swamps and of these, 13 are represented in the Pacific (*Aegialitis*, *Aegiceras*, *Avicennia*, *Bruguiera*, *Campostemon*, *Ceriops*, *Lumnitzera*, *Osbornia*, *Rhizophora*, *Scyphiphora*, *Sonneratia*, *Xylocarpus*, and the palm, *Nypa*), while *Kandelia* is found in Southeast Asia, Taiwan, and as far north as Kyushu, Japan.

These might be thought of as "true" mangroves, but there are other species, such as *Acanthus* spp. in New Guinea and Palau, and *Excoecaria agallocha* L. and *Heritiera littoralis* Ait. throughout much of the Pacific which, though also found on limestone cliffs, are widely associated with tidal forests. The fern *Acrostichum aureum* L. and the coastal shrub *Pemphis acidula* J. R. and G. Forst. and tree *Thespesia populnea* L. are often found growing with mangroves, though all have a more widespread distribution throughout the Pacific.

The number of species of mangroves (using Chapman's definition) declines from 30 in the complex tidal forests of New Guinea (Percival and Womersley 1975) and 19 in the Solomon Islands (Whitmore 1966, Tomlinson 1978) to 11 in Vanuatu (Marshall and Medway 1976) and New Caledonia (Guillaumin 1948, Balt-

zer 1969, Tomlinson 1978). There are seven species recorded in Fiji (Richmond and Ackermann 1975) and Tonga (Yuncker 1959, D. Hassall pers. comm.), and the eastern limit of mangrove forests in the Central Pacific is in Aunu'u in Eastern Samoa, where stands of *Rhizophora samoensis*, <5 m tall, and taller woodland of *Bruguiera gymnorrhiza* (L.) Lamk. have been described (Whistler 1980). Also recorded from Samoa are *Xylocarpus moluccensis* (Lamk.) Roem. (Christophersen 1935) and *Rhizophora stylosa* (Tomlinson 1978, in the text though not in Fig. 1 of that paper, Taylor 1979).

In Micronesia, Palau and Yap show the greatest diversity, with ten species of mangroves each and there is impoverishment to the east and to the north (Fosberg 1975). Only seven species are recorded from Truk, Ponape, Kusaie, and Guam and there is a rapid depauperization of mangrove flora north of Guam; no mangroves grow in the Bonin or Volcano Islands and on Saipan there is only a restricted mangrove swamp at Tana-pag, dominated by *Bruguiera gymnorrhiza* (Fosberg 1960), though *Lumnitzera littorea* (Jack) Voigt. is also recorded from the island (Hosokawa, Tagawa, and Chapman 1977). Similarly mangrove flora of the Marshall Islands is depleted. The four species recorded, *Bruguiera gymnorrhiza*, *Lumnitzera littorea*, *Rhizophora mucronata* and *Sonneratia alba* J. Smith are largely restricted to "mangrove depressions" in the surface of the atolls (Fosberg 1947). The same four species are found patchily distributed in Kiribati (Fosberg 1975), but only two species of mangroves, *Rhizophora stylosa* and *Lumnitzera littorea*, are found in Tuvalu (Woodroffe 1985a). On the more isolated islands, mangroves are absent, as in the examples of Wake and Kapingamarangi (Fosberg 1959, Fosberg and Sachet 1969, Niering 1963). *Rhizophora mangle* L. on Eniwetok and *Bruguiera gymnorrhiza* on Bikini are considered to have been introduced (Taylor 1950, St John 1960).

One species of mangrove, *Avicennia marina* (Forsk.) Vierh. var. *resinifera* (Forst.) Bakh. occurs in New Zealand (Chapman and Ronaldson 1958, Lynch 1973) where it reaches as far south as Ohiwa Harbor (38°S).

The limits of mangroves in the Pacific are

shown in Figure 1. No mangroves have been recorded in the Kermadec Islands, Niue or in the Cook, Tokelau or Phoenix Islands (Wilder 1931, Luomala 1951, Parham 1971, Sykes 1970, 1977). *Rhizophora stylosa* has been introduced to Tahiti, Moorea, and Bora Bora in the Society Islands (Taylor 1979). *Rhizophora mangle* and *Bruguiera gymnorrhiza* have been introduced and are established in the Hawaiian Islands, while *R. mucronata*, *B. parviflora* (Roxb.) Wight & Arn. ex Griff. and *Ceriops tagal* (Perr.) C. B. Rob. were introduced but are no longer established, and *Conocarpus erectus* L. is cultivated (Wester 1981).

This rapid attenuation in mangrove species numbers across the Pacific, and the absence of mangroves from the eastern Central Pacific, despite their occurrence on the west coast of Central and South America and in the Galapagos, has been ascribed by van Steenis (1962) to difficulties of dispersal away from an Indo-West Pacific center of origin. Several lines of evidence, however, suggest that the history of mangrove establishment may have been more complex.

Fossil evidence of mangroves from the Pacific is scarce, but pollen of *Rhizophora*, *Sonneratia*, *Avicennia*, *Lumnitzera*, *Scyphiphora*, *Ceriops*, and *Bruguiera* has been reported from Miocene deposits cored from Eniwetok, and of *Rhizophora*, *Ceriops*, and *Bruguiera* from the Miocene of Fiji (Leopold 1969). This indicates that these genera had evolved and dispersed into the Pacific at least by the Miocene, though we cannot be certain they were restricted to an intertidal habitat at that time. It is apparent also that as these genera are not all found in this part of the Pacific today, their distribution has contracted since the Miocene. Wider distribution of mangroves through the Pacific in the past does not support the idea of slow, on-going differential dispersal rates of different taxa (van Steenis 1962), but is more in accord with the vicariance theory of a fragmented widespread ancestral biota (McCoy and Heck 1976).

Also anomalous is the disjunction of the New World *Rhizophora* in the Pacific (Figure 1). In Fiji, Tonga, Samoa, and New Caledonia, though not on islands in the eastern Central Pacific, a form of *R. mangle* occurs, now

recognized as a separate species, *R. samoensis* (Tomlinson 1978). Several explanations have been offered for its occurrence. It has been suggested that propagules were carried by ocean currents from the New World. Though mangroves are viviparous, and their fruits appear well adapted to drift dispersal, Guppy (1906) discounted, on the basis of experimental evidence, the possibility of such a transoceanic crossing, and absence of the species in the eastern Central Pacific appears to support this view. Hemsley, (1895) upon initially encountering the New World *Rhizophora* in Tonga, suggested that it had been accidentally introduced with ballast, and Chapman (1970) proposed that it was deliberately introduced by primitive man who found its bark useful for tanning.

The considerable area covered by *Rhizophora samoensis*, its morphological differences from *R. mangle* (Breteler 1977, Tomlinson 1978), and its hybridization with *R. stylosa* (producing the hybrid, *R. x selala*) all suggest that a considerable period of time has elapsed since arrival of this form. For these reasons its introduction by man seems unlikely. As pollen grains of the New World *Rhizophora* can be distinguished from those of the Old World (Müller and Caratini 1977), it may be possible to resolve this question by palynological study of Holocene mangrove peat deposits.

Undoubtedly oscillations of climate and sea level during the Quaternary have had important consequences in terms of availability of suitable habitats for mangrove colonization. It is demonstrated below that in each of four environmental settings in which mangrove swamps are developed in the Pacific, there has been substantial extension of mangroves in the last 5,000 years. The two main reasons for this are available suitable topography and substrate, and relative sea-level stability. On many islands it is coincidence of present sea level with pre-existing platforms or topographic breaks of slope which provides extensive environments for mangrove development. Elsewhere Holocene reef growth or barrier formation over similar topography has provided a suitable habitat for mangrove establishment. On the other hand, when sea level was lower, or when it was changing

TABLE 2

ENVIRONMENTAL SETTINGS IN WHICH MANGROVES OCCUR AND THOSE RECORDED IN THE PACIFIC

	ENVIRONMENTAL SETTING (AFTER THOM 1982, 1984)	CHARACTERISTICS OF SETTING	PACIFIC ISLAND MANGROVE EQUIVALENT (THIS STUDY)
Terrigenous			
Setting I	River-dominated allochthonous	Deltaic/estuarine, microtidal	Deltaic/estuarine mangrove swamps
Setting II	Tide-dominated allochthonous	Deltaic/estuarine, macrotidal	—
Setting III	Wave-dominated barrier lagoon (autochthonous)	Barrier islands and spits, high wave energy	—
Setting IV	Composite river and wave dominated	Deltaic and lagoonal	—
Setting V	Drowned bedrock valley	Bedrock embayment	Embayment/harbor/lagoon mangroves
Carbonate			
Setting VI	Carbonate platform	Over lime mud on broad platforms	—
Setting VII	Sand/shingle barrier	In lee of rampart	Reef flat mangroves
Setting VIII	Quaternary reef top	Over reef flat or fossil reefal environments	
	—	—	Inland mangroves and depressions

comparatively rapidly, as it was for most of the Quaternary, the coastal physiography of many of the islands must have consisted of limestone cliffs and been unfavorable for development of even limited mangrove swamps.

Thus it is quite probable that significant changes in mangrove species distribution have occurred in the late Quaternary, with local extinction of species taking place in some islands and some species' re-establishment in the Holocene as favorable habitats became available once again.

ENVIRONMENTAL SETTING AND MANGROVE SWAMP DEVELOPMENT

Broad global environmental settings within which mangrove swamps develop have been described by Thom (1982, 1984). These represent settings within which particular combinations of geomorphological processes are dominant, which affect the ecological constraints on, and population dynamics of, mangrove species (Table 2). It is argued in this paper that setting also influences potential for flux of organic carbon and probably trophic structure of the mangrove ecosystem.

An environmental setting has three essential components: i) "background" geophysical: the geographical character of the setting, sea-level/tectonic history, and climatic and tidal factors, ii) geomorphic: the general character of sedimentation and dominant processes, and iii) biologic: "microtopography" and plant response. In the global context, a major group of settings are the five terrigenous settings, refined from models of delta and drowned valley development (Thom 1982). The three carbonate settings do not represent large areas of mangrove growth. However, in this study of islands in the Pacific only larger "high" islands have significant river systems draining them, and terrigenous sediment inputs are generally small compared to most river deltas. In the Pacific, carbonate settings form an important element.

Four environmental settings can be recognized in the Pacific, and their relation to those of Thom (1982, 1984) is shown in Table 2. Some mangrove swamps occur in a combination of settings. The first setting is the deltaic/estuarine terrigenous setting, setting I. Most of the Pacific under consideration experiences a microtidal regime (tidal range of < 1 m) so tide-dominated settings are unimportant.

Where wave energy is high, reefs tend to flourish and mangroves are protected, so wave-dominated settings are rare; consequently composite settings are also rare. Thus settings II, III and IV are restricted or absent in the Pacific. The second setting is the embayment/harbor/lagoon setting. This corresponds to the drowned bedrock valley setting, setting V. The third setting is the reef flat setting and it corresponds to the carbonate settings, principally setting VII, but also setting VIII. The fourth setting is the inland mangrove and mangrove depression setting. This is characteristic of small "low" islands in the Pacific, and, not being extensive in a global context, has no equivalent in the classification of Thom.

Sediment inputs are not large on any of the Pacific islands; consequently the geomorphological development of mangrove swamps has been largely controlled by one factor, sea-level history. While a general pattern of sea-level change for the late Quaternary has been determined from radiometrically-dated raised reefs on the Huon Peninsula, New Guinea (Chappell 1983), no universal pattern of late Holocene sea-level change can be applied to the Pacific islands. Individual sea-level curves relative to specific islands or island groups indicate that islands have experienced different sea-level histories as a result of tectonic movements, lithospheric flexure, hydro-isostatic adjustments, or other deformations of the earth's crust (Bloom 1970, 1980, Adey 1978, Pirazzoli and Montaggioni 1985). Nevertheless, it is shown below that patterns of Holocene development have been reasonably similar within any one setting, even on islands experiencing different late Holocene sea-level histories.

Deltaic and Estuarine Mangrove Swamps

Deltaic and estuarine mangrove swamps are only extensive on "high" islands of the Pacific on which river systems are well developed. Nowhere do they reach the degree of complexity or development of mangrove swamps of parts of New Guinea, where mangroves reach 300 km up the Fly River. However, active erosion of geologically young volcanic rocks on islands in the Pacific can

provide a deltaic habitat ideal for rapid mangrove establishment.

There are extensive mangrove swamps around Viti Levu and Vanua Levu, Fiji, where they are particularly associated with the deltas of the Rewa, Ba, Labasa, and other rivers. The broad zonation consists of a seaward fringe of *Rhizophora stylosa*; *R. x selala*, or occasionally *R. samoensis*, is found along the river margins, and a mixed forest of *Bruguiera gymnorhiza*, *Xylocarpus granatum* Koen, and *Lumnitzera littorea* (with *R. samoensis* and *Excoecaria agallocha* in the Ba delta) grows on the higher ground landward (Richmond and Ackermann 1975, Hassall 1980). These swamps have developed in their present form since the last glacial, with the transgression of sea level to its present level. In the Rewa delta, a radiocarbon date on mangrove peat of 5500 ± 110 years B.P. from beneath estuarine mud at a depth of 4.5 m below sea level implies that 5500 years ago, sea level was considerably below that of the present (Bloom 1980). Sugimura et al. (1984) record the following dates on shell material from beneath mangrove swamps: 4400 ± 200 years B.P. 1.6 m below mean sea level at Lombau, 1630 ± 250 years B.P. 1.6 m above sea level at Lombau, and 2640 ± 140 years B.P. 2.4 m below mean sea level at Kalokolevu, southern Viti Levu. These suggest continued decelerating transgression until 1500–2000 years ago and then minor sea level fall.

In New Caledonia, mangroves of the Dumbea River have been studied in detail by Baltzer (1969), who recorded a patterning based primarily on elevation and resultant tidal inundation; the lowest areas are occupied by *Rhizophora* sp. (evidently not *R. mucronata* as recorded by Baltzer, as this is reported absent by Tomlinson 1978), and *Bruguiera* sp.; the higher areas support *Avicennia officinalis* L. and, in more remote sites, *Lumnitzera racemosa* Willd. Relative sea-level history differs from that in Fiji and radiocarbon dates have been reported for mangrove remains 5.15 m and 3.35 m below present of 7300 ± 170 and 6800 ± 165 years B.P., respectively, close to the present mangrove substrate of 5750 ± 150 and 5600 ± 150 years B.P. (Baltzer 1970). Sea level appears to have remained fairly

stable with respect to the west coast of New Caledonia for the last 6000 years.

In Micronesia mangroves are also extensive in and around the estuaries of Palau and Ponape and the broad zonation described by Fosberg (1947) from the Garamiscan River, Babeldaob, Palau appears to be widespread in the area (Hosokawa, Tagawa and Chapman 1977). This consists of a seaward zone dominated by *Sonneratia alba* [recorded initially as *Sonneratia caseolaris* (L.) Engl. and revised by Fosberg (1960), though not by Hosokawa, Tagawa and Chapman (1977)], an intermediate zone of *Rhizophora mucronata*, and a landward zone of *Bruguiera gymnorrhiza*, *Nypa fruticans* Wurmb. and other species.

The deltaic/estuarine setting has the greatest spatial variability of mangrove habitats in response to microtopography and landforms. Most obviously restricted to the deltaic environment are those habitats associated with fluvial watercourses, which may extend some distance upstream, in which species such as *Nypa fruticans* or *Rhizophora x selala* are dominant. The deltaic environment is a relatively dynamic setting in which rapid deposition of terrigenous sediments can lead to microtopographic changes which influence mangrove species dynamics (Thom 1967). These are also sites of active coastal progradation, with mangrove colonization of seaward shoals, and with replacement of mangroves to landward by freshwater vegetation types, as in the Rewa delta (Bloom 1980).

Mangroves of Embayments, Harbors and Lagoons

Mangroves can be extensive in sheltered embayments, lagoons or harbors, which are often areas of fine-grained sediment accumulation. Mangrove swamps are found in the lagoon at Truk and in Lela Harbor, Kusaie. In New Zealand, the most extensive stands of *Avicennia marina* var. *resinifera* are fringing the harbors of Northland (Küchler 1972). Although there is only one species of mangrove, it nevertheless forms taller stands along the edge of fluvial watercourses or tidal creeks than the stunted shrubs characteristic of the mudflats to landward.

Mangrove swamps, dominated by species of *Rhizophora*, are well developed in the lagoons of Tongatapu, Vava'u, and in the totally enclosed lagoon of Nomuka, Tonga. Similar swamps composed of a seaward zone of *Rhizophora* spp. and occasional fringing *Avicennia*, and a landward thicket of *Ceriops tagal* occur in the Port Stanley embayment, Malekula, Vanuatu (Marshall and Medway 1976).

Little work has been done on patterns of sedimentation, microtopographic habitats, or Holocene history of mangroves of embayments in the Pacific. Detailed work on geomorphological processes and landform units in mangrove swamps of the embayments of ria shorelines in northern and northwestern Australia has demonstrated patterning of mangrove vegetation communities in response to alluvial and colluvial sediment inputs, or to the location of sand and shingle ridges (Semeniuk 1985). A similar patterning of mangrove vegetation in response to landform units and sediment inputs could be developed for mangrove swamps of embayments on Pacific islands. Diversity of habitats is less than in the deltaic/estuarine setting, but because sediment inputs are less, landforms are less dynamic; consequently mangrove communities are more stable. Mangroves in embayments have developed to their present extent since sea level has stabilized close to its present level. During the late Quaternary there rarely would have been such lengthy periods of sea-level stability allowing similar mangrove swamp development, nor would favorable topographic settings have been as widespread when sea level was lower.

Mangrove Development on Reef Flats

In many islands of the Pacific, mangroves have spread over recently developed reef flats. Though reef flats are extensive around both "low" islands and "high" islands of the Pacific, they generally support more extensive mangrove on the "high" islands, where they grow in the relative shelter of a fringing reef, as for instance on reef flats of Lakeba, Lau Islands (Garnock-Jones, 1978). Often mangrove forests are more extensive on the least exposed leeward shores, as in Palau and Ponape (Hosokawa, Tagawa and Chapman 1977).

Mangroves established on reef flats can grow on sandy or muddy substrates, or directly over an almost bare reef-flat surface. There may be a sand or shingle barrier affording protection to the mangroves, as on "low-wooded" islands of the Great Barrier Reef (Thom 1975, 1984, Stoddart 1980a). In some cases, a shingle barrier may totally impound a mangrove swamp, forming inland mangrove swamps as on Funafuti, Tuvalu. It is evident that for mangroves to develop over a bare reef flat surface, it is necessary for the reef-flat itself to reach a particular stage of evolution. As corals are rarely found growing above a level between mean low water springs and mean low water neaps, and mangroves do not establish much below mean sea level, mangroves are best developed where the reef flat is emergent. In such a case mangroves are often associated with fields of fossil microatolls. This relationship has been demonstrated on the Great Barrier Reef, where emergent microatolls were described ranging in age from 6310 ± 90 to 2370 ± 70 years B.P. (Scoffin and Stoddart 1978). Microatolls found with mangroves developing around them ranged in age from 5850 ± 170 to 4870 ± 70 years B.P. and Stoddart (1980a) proposed that this represented a period of cessation of vertical reef growth, providing a substrate suitable for gradual, opportunistic colonization by mangroves. The age structure of microatolls on the Great Barrier Reef has been examined in more detail by Chappell et al. (1983), again demonstrating the association of the seawardmost mangroves with microatolls in the range 5925 ± 115 to 4420 ± 105 years B.P.

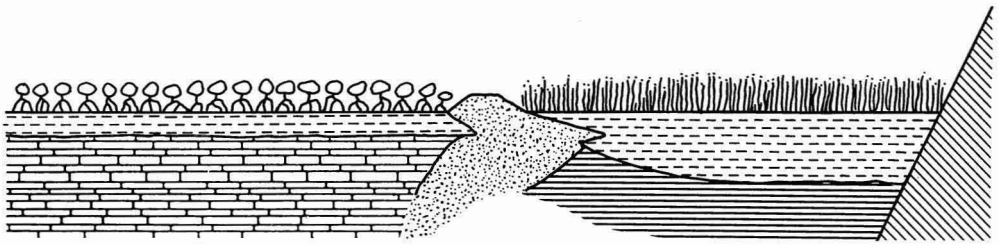
In the Pacific a similar pattern of expansion of mangrove swamps, following cessation of vertical reef-flat growth and emergence of microatolls, is likely. Emergent fossil *Helipora* have been recorded in the mangrove swamp of *Rhizophora* sp. at Funafuti, Tuvalu (David and Sweet 1904). On the north coast of Tongatapu, Tonga, mangroves, principally *Rhizophora* spp., are closely associated with fields of emergent microatolls. Individual trees are often localized behind individual fossil coral heads which give them some shelter from currents or waves. A radiometric age of

4490 ± 60 years B.P. has been determined from one microatoll associated with mangroves (Woodroffe 1983).

A feature of mangroves on reef flats is that much of the sediment is autochthonous, with a high organic content, sometimes even a mangrove-derived peat. In the eastern Caroline Islands progradation of mangroves over a horizontal reef-flat surface has been accompanied by deposition of approximately 1 m of woody mangrove peat (Figure 2). Mangrove peat also occurs at greater depths. Samples from between 6.2 and 4.5 m below present mangrove level from Truk and Ponape, where mangrove swamps are associated with an estuary, have been radiometrically dated at between 6500 ± 190 and 5550 ± 270 years B.P. (Bloom 1970). Bloom has interpreted a rate of submergence of these islands of approximately 1.9 m/1000 years from 6500 to 4100 years B.P. A date of 4090 ± 150 years B.P. on a sample of mangrove peat, 1.7 m below present, is taken to mark the end of this period of relatively rapid submergence, and a slower rate of submergence is proposed for the last 4000 years, though radiocarbon dates during this time are unreliable and ambiguous (Bloom 1970). A similar stratigraphy is recorded from Lakeba (Figure 2) where mangroves are underlain by a fibrous peat and a fine-grained mud (McLean 1979). A radiocarbon date of 4470 ± 155 years B.P. on a loose coral sample underlying the swamp deposits indicates that in Lakeba also expansion of mangroves over the reef flat has occurred in the last 4000 years. On the south coast of Upolu Island, Western Samoa, samples of peaty mangrove mud from 5.8–6.1 m and 5.2–5.5 m below present mangrove sediments have been radiometrically dated to 4845 ± 95 and 4655 ± 95 years B.P. respectively, and samples from 3.6–4.3 m and 2.7–3.0 m below present have been dated to 3060 ± 95 and 1595 ± 85 years B.P. respectively (Bloom 1980).

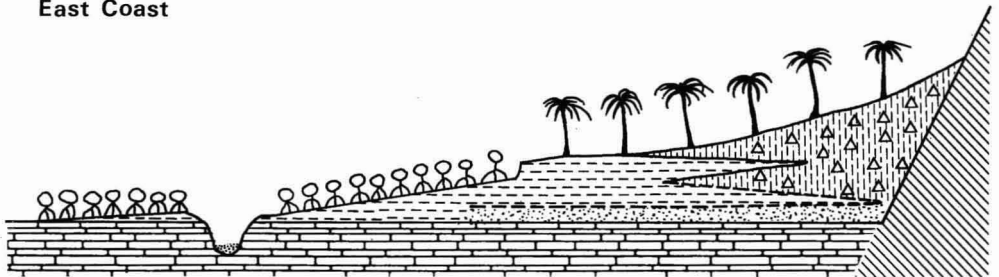
It is apparent that there is considerable variation throughout the Pacific in the individual histories of reef flat and mangrove swamp development relating to differences in relative sea-level history. Sea level appears to have been different with respect to individual

TRUK (After Bloom, 1970)



LAKEBA (After McLean, 1979)

East Coast



Southwest Coast

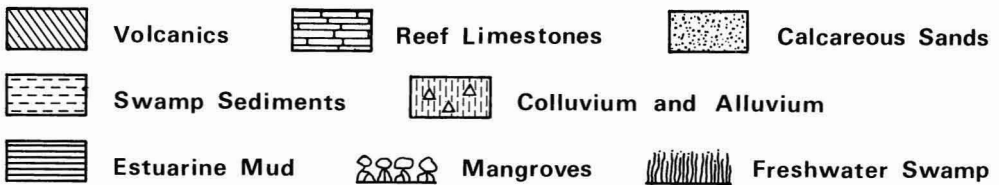
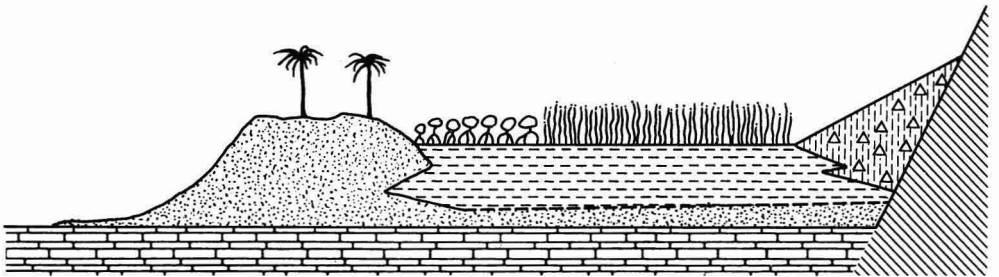


FIGURE 2. Cross section and stratigraphic relationships of mangrove swamps at Sapuk, northeast Moen, Truk, Caroline Islands (after Bloom, 1970), and eastern and southwestern coasts of Lakeba, Lau Islands, Fiji (after McLean, 1979).

islands or island groups 4000 years ago, ranging from Western Samoa, where it may have been more than 5 m below present, to islands of Micronesia, where it may have been 1.7 m below present, to Tonga, where it was evidently above present as it was in parts of the Great Barrier Reef. It will require much more work to determine how sea level has varied relative to individual islands, or island groups in the Pacific, nevertheless it can be demonstrated that under a series of different sea-level histories, vertical reef growth has ceased in the mid-Holocene, and mangrove forests have extended over reef flats during the late Holocene. Sedimentation rates within these mangroves are low; there may be some colluvial and alluvial input (Figure 2), but sediments are partly autochthonous. The mangrove swamps are consequently relatively stable, with species patterning largely determined by configuration of the reef and reef flat.

Inland Mangroves and Mangrove Depressions

On small islands and atolls in the Pacific mangroves are frequently found growing inland. *Bruguiera gymnorrhiza* has been reported in totally enclosed sink-holes in the limestone of Palau, and on atolls of the Marshall Islands there are 'mangrove depressions' in which *Bruguiera* and occasionally *Lumnitzera littorea* grow, often with *Acrostichum aureum* (Fosberg 1975). These depressions are usually rock-bottomed, but may have organic-rich muddy or sandy sediments in them. Some may be connected to the sea by a subterranean connection. On a smaller scale, though, they are reminiscent of inland mangroves of Barbuda, Little Cayman, and Inagua in the West Indies (Stoddart, Bryan and Gibbs 1980, Stoddart 1980b, Lugo 1981).

Inland mangrove also occurs on islands of Tuvalu, and is particularly extensive on the reef-top islands, Niutao and Nanumanga. Figure 3 illustrates distribution of two species of mangrove, *Rhizophora stylosa* and *Lumnitzera littorea*, and of the shrub *Pemphis acidula* which is often associated with mangrove, on three of the islands of Tuvalu. The islands are in different stages of development over the initial reef platform; Nui is an atoll

with extensive but shallow lagoon and mangroves cover less than 0.5% of the land area. On Vaitupu, land fills a larger proportion of the smaller reef platform and there is a greater area of mangrove around the almost landlocked lagoons with mangroves covering 1.2% of the land area. On the smallest reef platform, Nanumanga, land fills almost the entire platform and the completely landlocked lagoon is surrounded by an extensive woodland of *Rhizophora*, covering 9.2% of the land area. There appears to be a relationship between lagoon morphology, degree of lagoon restriction, and mangrove development, each in turn a function of the stage of late Holocene reef-top island formation in much the same way as they are a function of reef-flat development in the mangroves of reef flats. Occurrence of mangrove is related to development of island topography which at this stage has not been dated. Nevertheless development of this type of mangrove requires a stable sea level, and there would appear to have been few opportunities for similar inland mangrove to have developed when Quaternary sea levels have been rapidly fluctuating. There is virtually no habitat variability in these mangroves, and little evidence of successional change. There may be some solution of limestone by acidic waters from the mangroves, but the dynamics of this setting respond to late Holocene change of reef-top island environments.

PRODUCTIVITY AND ENVIRONMENTAL SETTING

The most significant aspect of mangrove primary productivity, except where timber is harvested as it is, for instance, in Babeldaob and Ponape, Micronesia, is the production of plant detritus, and the detrital food webs that this supports (Odum and Heald, 1972). Total litter-fall beneath mangroves, although not equivalent to total productivity, is an indication of the rate of production of detritus. Estimates are available from a wide range of mangrove forests, and are useful in comparing primary production in different forests, providing that collection and drying techniques are similar.

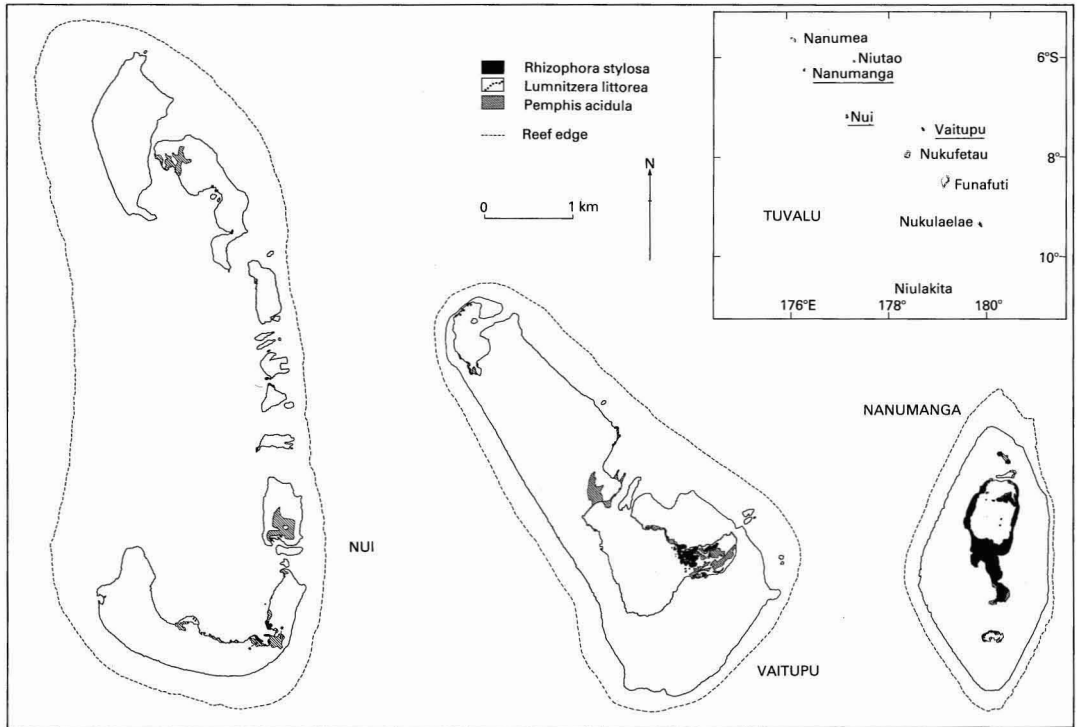


FIGURE 3. The distribution of mangroves and *Pemphis acidula* on Nui, Vaitupu and Nanumanga, Tuvalu (based on aerial photographic interpretation and ground survey).

The most comprehensive studies of litter-fall beneath several species of mangrove are from Florida (26°N) and Queensland, Australia (18°S), and the majority of sites in these locations indicates a total dry weight of litter-fall of around 7–8 t/ha/yr (Lugo and Snedaker 1974, Pool, Lugo, and Snedaker 1975, Duke, Bunt, and Williams 1981, Bunt 1982, Clough and Attiwill 1982). Recently, studies of lower latitude, structurally and floristically more diverse mangrove forests in the Indo-West Pacific region have indicated that litter-fall rates may be higher than 10 t/ha/yr and can reach 14–15 t/ha/yr (Chai 1982, Sasekumar and Loi 1983, Ong, Gong, and Wong 1985, Leach and Burgin, 1985). Similarly, application of a rapid survey measure of productivity based on light transmission through the canopy has indicated that mangroves in New Guinea are as productive as the more productive sites in Australia (Boto, Bunt, and Wellington 1984).

A decrease of productivity with increasing latitude is indicated by estimates of litter-fall beneath *Avicennia marina* (Forsk.) Vierh. in Australia. Average rates have been estimated as 8.0 t/ha/yr at 18°S (Duke, Bunt and Williams 1981), 5.8 t/ha/yr at 34°S (Goulter and Allaway 1979) and 2.0 t/ha/yr at 38°S (Clough and Attiwill 1975). An average rate of 7.1 t/ha/yr beneath *A. marina* at 30°S in South Africa (Steinke and Charles 1984) appears broadly consistent with this trend.

However, generalizations about litter production at particular latitudes conceal considerable spatial variation between habitats in mangrove swamps at any one latitude. Lugo and Snedaker (1974) have shown the importance of geomorphological setting of mangrove forests in relation to spatial variations in productivity, demonstrating that, in the West Indian region, riverine mangroves are more productive than fringe mangroves, which are more productive than overwash, and lastly

basin mangroves. In studies of monospecific stands of *Avicennia* at 37°S in New Zealand, Woodroffe (1985b) has estimated that the average rate of litter-fall over an entire mangrove stand is 2.7 t/ha/yr, broadly accordant with the latitudinal trend described above, but that locally, on creek banks, litter-fall may be as high as 8.1 t/ha/yr (Woodroffe 1982). Thus local variations in litter-fall can be expected within a mangrove habitat in response to environmental factors such as salinity, soil chemistry, or frequency of tidal inundation often reflected by mangrove height and biomass. There may be further regional trends as a result of variation in tidal amplitude or climate.

Very few data on mangrove productivity are available from islands in the Pacific. Average litter-fall of 7.8 t/ha/yr has been recorded beneath *Rhizophora stylosa* on Vaitupu, Tuvalu (Woodroffe and Moss 1984). The mangrove stand on Vaitupu is an example of inland mangrove (Figure 3), though not entirely cut off from the open sea; it is less than 6 m tall and covers less than 6 ha. These results indicate that detrital productivity per unit area of restricted inland mangrove on "low" islands or atolls can be within the range observed for extensive, more luxuriant mangrove forests elsewhere.

There is clearly a need to study mangrove swamps in each environmental setting, and to examine spatial variability in productivity within each setting. The deltaic/estuarine mangrove swamps show the greatest habitat diversity, and perhaps therefore the greatest spatial variability in detrital production. They also receive greater inputs of freshwater containing nutrients and in areas of riverine mangrove they may support litter-fall in excess of 10 t/ha/yr. Mangrove swamps associated with deltas on low-latitude volcanic islands experiencing high precipitation, as, for example, in the Solomon Islands or Fiji, probably contain stands of mangroves most productive per unit area.

Mangroves of embayments also show a mosaic of habitats whose complexity is a response to inputs of sediments and freshwater runoff. Local riverine habitats or tidal creeks receiving increased nutrients are areas of

enhanced productivity; elsewhere species patterning and productivity may be largely responses to tidal inundation and salinity gradients. Mangroves on reef flats show similar patterns to those of embayments, except that in few cases will stream discharge or sedimentation be as concentrated or pronounced as in embayments, and species patterns are more often determined by underlying substrate factors. Finally, inland mangroves rarely receive much runoff or tidal exchange and therefore have the least habitat diversity. These will be the least productive of detritus, though as the data from Vaitupu show, litter production can be at least comparable, per unit area, with many mangrove swamps in Florida and Queensland.

The environmental setting of mangrove swamps is important not only in determining spatial variability in rate of detrital production in wetlands through habitat variability, but also in relation to biological functioning of wetlands. It is hypothesized that flux of organic carbon from mangrove swamps differs between settings in much the same way as patterns of sediment movement and sedimentation.

Although coastal wetlands are considered to be linked to the functioning of inshore ecosystems, there is still controversy as to whether there is a net export of organic carbon and nutrients, or whether there may be net import (Nixon 1980). Data supporting a net export of organic carbon have been published from a mangrove estuary and basin mangrove in southwest Florida (Heald 1969, Twilley 1985), from mangrove swamps on a "high" island off the Queensland coast (Boto and Bunt 1981, Boto 1982), and from a mangrove basin in New Zealand (Woodroffe 1985c). However, these sites represent a varied set of geomorphological settings from very different regions, and it would be premature to extrapolate the magnitude of export to other mangrove forests.

A relationship between coastal morphometry and biological functioning has been demonstrated by Mann (1975), who has shown that tidal and hydrological factors being constant, the form of an embayment controls the exchange of water and of organic carbon. This

relationship has been taken further by Odum, Fisher, and Pickral (1979) who hypothesize that in addition to geomorphology of a wetland drainage basin, relative magnitudes of tidal range and freshwater input determine the potential for organic carbon export from a wetland. On this basis some generalizations can be made about the four environmental settings of mangrove swamps in the Pacific (Figure 4), which encompass a far wider range of geomorphological situations than addressed by Mann (1975) or Odum, Fisher, and Pickral (1979).

Tidal regime is undoubtedly an important control on organic carbon flux from mangrove swamps. Where tidal range is large, tidal flows may completely dominate estuarine hydrodynamics. Increased tidal amplitude appears to account for export of a greater proportion of mangrove net primary production (Twilley 1985). However, as most of the Pacific experiences a microtidal regime, tidal characteristics are not important as a control on biological functioning of mangroves in the Pacific.

Thus the major factors determining flux from Pacific island mangrove swamps are geomorphological and hydrological, and have much in common with the factors responsible for sediment movement and sedimentation, of which the record of Holocene development is an indicator (Figure 4).

Deltaic/estuarine mangrove swamps are developed at the mouths of major rivers and, in microtidal areas, hydrology of the river dominates sediment movement and exchange of waters with the open sea. Characteristics of river flow will depend on the geologic and topographic nature of the drainage basin and regional climate. Seaward progradation attests to a residual seaward flux of sediment. Much of the mangrove swamp associated with delta distributaries or an estuary will be effectively flushed, and detritus will be exported. Flushing efficiency may vary throughout the wetland; some areas may be distant from active flushing and subject only to infrequent inundation. In this case their importance in terms of export of particulate organic carbon may be less. For instance interdistributary basins in Tabasco, Mexico, are underlain by

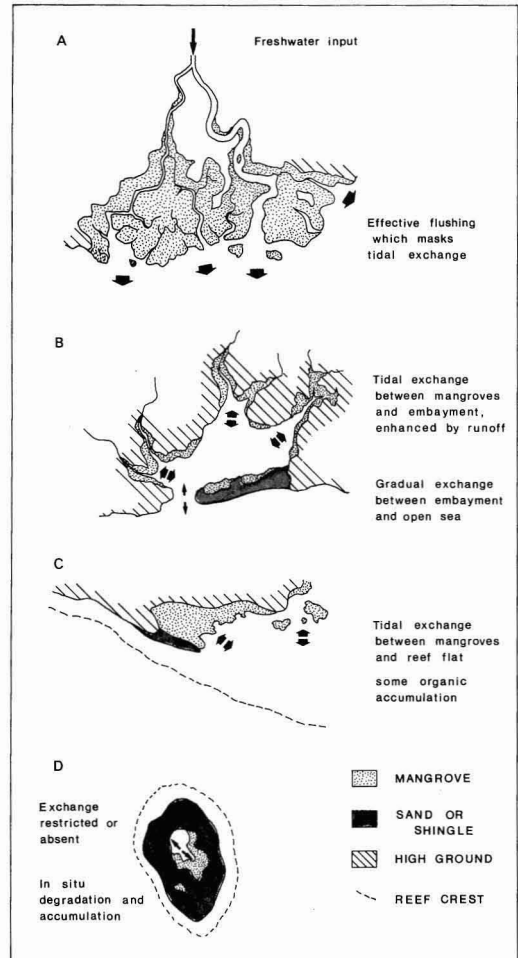


FIGURE 4. The four environmental settings: typical topographic characteristics and potential organic carbon fluxes. A Deltaic/estuarine mangroves. B Mangroves of embayments/harbors/lagoons. C Mangroves of reef flats. D Inland mangroves and mangrove depressions.

more peaty substrates than other habitats, indicating some organic carbon accumulation (Thom 1967), and basin mangroves of backswamp areas of southwest Florida are only seasonally inundated (Twilley 1985). In estuarine/deltaic settings, organic carbon produced in coastal wetlands is added to that already carried by the river and much is transported out to sea. Much of the processing and consumption by subsequent trophic levels occurs out in the open sea, and it has been recognized in the Pacific that productive in-

shore fisheries are associated with large river deltas (Macnae 1974, Baines 1981).

Mangroves of embayments, lagoons, and harbors are less dominated by hydrological factors. Sedimentation patterns are dominated by marine processes with localized alluvial and colluvial input. Flushing of mangrove swamps is largely tidal, with freshwater runoff only locally important, resulting in enrichment of the embayment with detritus. Exchange of organic carbon with open sea water will depend on water residence time in the embayment. In particularly enclosed embayments organic carbon accumulates and is consumed by higher trophic levels within the embayment itself.

Mangroves of reef flats generally have low rates of inorganic sediment accumulation and receive little freshwater runoff or sediment, excepting reef-derived carbonate sediments. On "high" islands some situations will occur where runoff is experienced and where there are alluvial and colluvial sediment inputs. These situations are similar to mangroves of embayments. Where the substrate is mangrove-derived peat or peaty mud some organic carbon is accumulating in the swamp. The principal flushing is tidal, but frequency of inundation and velocity of flow may not be effective in removing all detrital production. Little research has been done to examine the linkages between functioning of the mangrove swamp and the reef itself in this setting.

Inland mangrove or mangrove depressions represent a situation where there is very restricted, or no, exchange of waters, and organic carbon flux is minimal. Detritivores, especially crabs, feed within the swamp. Where there are sediments these are highly organic and indicate organic accumulation.

Environmental setting, through geomorphological and hydrological factors, influences the potential for organic carbon export and biological functioning of the system (Figure 4). Deltaic/estuarine mangroves are potentially the most effectively flushed, followed by mangroves of embayments and those of reef flats, while inland mangroves may be scarcely flushed at all.

Related to organic carbon flux is the location of breakdown and consumption of mangrove detritus or its epiflora and epifauna. In

deltaic/estuarine mangrove swamps, detritus contributes to the inshore food web and commercially viable fisheries. The extent to which higher trophic levels of the food web are contained within the embayment or inshore is a function of water residence time and diffusive exchange. In the case of mangrove swamps of reef flats, most of the processing of detritus occurs in the mangroves or over the reef flat. In inland mangroves most of the detritus must be broken down *in situ*.

It should be possible to test the model of flux proposed in Figure 4 for each environmental setting. It is likely to follow that the structure of the food web in and adjacent to the mangrove swamps will differ between environmental settings. A wider trophic diversity is predicted in and seaward of deltaic/estuarine mangrove swamps where there will be pelagic detritivores as well as those of the swamp substrate and tidal creeks.

This does not mean that mangrove ecosystems are less important on reef flats or inland on "low" islands. Deltaic/estuarine mangrove swamps may export more organic carbon to the sea and make a contribution to inshore fish and prawn catches. However, mangroves in other environmental settings are significant producers of detritus and support organisms which are important subsistence items as well as fuel, construction materials, dyes, and drugs (Saenger, Hegerl and Davie 1983) for local inhabitants. Mangrove swamps of reef flats are generally important as nurseries for mullet (*Mugilidae*) and baitfish (*Clupeidae* and others), and, together with inland mangroves, are a source of crabs (for instance *Scylla serrata* and *Sesarma* spp.).

Nor does the fact that inland mangroves are often of very limited extent on Pacific islands make them less significant ecosystems. Indeed the importance of small stands of mangroves on "low" islands may be out of all proportion to their areal extent, because they may provide a source of food or materials for local people which otherwise would not be available.

CONCLUSION

The distribution of mangroves in the Pacific shows a marked attenuation in species num-

ber, often with a decrease in stature, from west to east, with mangroves largely absent from Polynesia. On those islands where they occur, mangroves have extended rapidly in late Holocene times and must have been considerably more restricted, if not locally extinct, during periods of rapid sea-level change in the Quaternary.

The four environmental settings within which mangroves are found in the Pacific are, i) deltaic/estuarine mangroves, ii) mangroves of embayments/harbors/lagoons, iii) mangroves of reef flats, and iv) inland mangroves and mangrove depressions. Patterns of present sedimentation and late Holocene history differ between settings but are relatively similar within settings. This is despite the fact that relative sea-level history can vary from one island or island group to another, and that sea-level history has been a major constraint on lateral extension of mangrove swamps in the late Holocene.

Environmental settings can be ranked in the order: deltaic/estuarine mangroves > mangroves of embayments/harbors/lagoons > mangroves of reef flats > inland mangroves in respect to a number of factors. These factors include landform and mangrove habitat diversity, rates of sedimentation, rates of landform change and mangrove community dynamics, opportunities for freshwater nutrient input and consequent enhanced productivity, potential for organic carbon flux, and perhaps also trophic diversity.

In a global context mangroves are most extensive in terrigenous settings, and are best developed in deltaic or estuarine areas. Perhaps as a result there has been a tendency to emphasize the export of organic carbon from mangroves, in line with theories of "outwelling" from salt marshes. Undoubtedly some mangrove detritus does move from mangrove swamps out into the open sea, but much more research is needed to quantify this. However, in the Pacific, where mangroves are not extensive, and where they often occur in other environmental settings, it is not always appropriate to extrapolate patterns of organic carbon export which are associated predominantly with terrigenous settings. Some mangroves develop in environments which are more restricted, with less water exchange,

and in which there may be organic matter accumulation in the substrate. Preliminary evidence indicates that restricted inland mangrove stands, and even local stands close to the latitudinal limit of mangroves, can be as important producers of detritus, per unit area, as more luxuriant mangrove forests elsewhere. This production may contribute to in-shore fisheries, in deltaic/estuarine mangrove swamps, but it is important for the valuable indigenous fauna in all settings.

The structure and functioning of mangrove ecosystems needs to be examined for each of the four environmental settings in the Pacific. It may be inappropriate to apply management strategies developed for mangrove forests in one environmental setting to those of another. In particular, mangrove stands of limited extent on small "low" islands need to be examined. Because these are small they are vulnerable to destruction, yet they may support resources which local inhabitants cannot find in alternative environments on these islands.

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