THE ECOLOGY OF MANGROVE VEGETATION IN BINTUNI BAY, IRIAN JAYA, INDONESIA

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Rudhi Pribadi

Department of Biological and Molecular Sciences
UNIVERSITY OF STIRLING, SCOTLAND
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DEDICATION

I dedicate this thesis to my parents, brother and sisters.

DECLARATION

I hereby declare that this thesis has been composed by myself and except where otherwise stated the work contained herein is my own.

Rudhi Pribadi

V SMALL LITTERFALL AND LEAF LITTER DECOMPOSITION

VI LEAF HERBIVORY

VII SEED PREDATION

7.5.3 Dominance

VIII REGENERATION AFTER FELLING

References

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ABSTRACT

The ecology of mangrove forests on *Potential Acid Sulphate soils* at Bintuni Bay (132° 55' - 134° 02' E and 2° 02' - 2° 97' S), Irian Jaya, Indonesia was studied. The annual rainfall is 3000 mm and there is mixed semi-diurnal tide of 1 - 5.6 m amplitude. The water has a varying salinity of 0 - 27 ‰.

Forest structure was studied in plots of 10 m x 10 m along three transects across Sikoroti Island and in three 50 m x 50 m plots in mixed *Rhizophora* - *Bruguiera* forest. All trees > 10 cm trunk diameter were enumerated, measured and identified. Of the nine tree species, *Rhizophora apiculata* was the most dominant, followed by *Bruguiera gymnorrhiza* and *Ceriops decandra*. There was good regeneration seven years after clear-felling in plots on Amutu Besar and Amutu Kecil Islands.

Small litterfall production, measured using ten 1 m x 1 m litter traps in each of the three 50 m x 50 m plots, was 11.09 t ha^{-1} y^{-1}, and greatest during the wet season (December, 1.29 t ha^{-1}) and least during the dry season (July, 0.61 t ha^{-1}). The annual litterfall mineral element accession was (kg ha^{-1} y^{-1}): N 240.4, P 6.1, K 43.2, Na 136.2, Ca 204.4 and Mg 48.7. Leaf decomposition of five species was studied in litterbags on the forest floor under trees of the same species. *Sonneratia alba* decomposed quickly with a half-life of 24 days, and *Bruguiera parviflora* was the slowest with a half-life of 124 days. Decomposition rates of all species followed a single exponential decay model.

Leaf herbivory of young stands of *Rhizophora apiculata* and *Bruguiera gymnorrhiza* was significantly different among sites, species, plant height and leaf-age. Seed predation on six species was studied in three different sites. Twenty propagules of each species were secured by string in each of six 10 m x 10 m sub-plots within each of five 10 m x 60 m plots. On average 62.1 % of the seeds were dead after 36 d. Predation was higher in the lower intertidal zone, and *Avicennia alba* and *Bruguiera parviflora* were the most predated.

The results suggested that the Bintuni Bay mangroves can be sustainably managed but the best silvicultural system needs to be determined.

I INTRODUCTION

1.1 Mangrove ecosystems

The term "mangrove" may be used in two senses. First it describes the constituent plants of tropical intertidal forest communities of which the major plant components belong to only nine genera from five families, with minor components from 11 genera each from a different family (Tomlinson 1994). In a second sense, the term refers to the complex of tree-dominated plant communities fringing sheltered shores. Such mangrove ecosystems exist in tropical areas on all continents and frequently extend into subtropical areas. The most luxuriant and diverse mangrove forests occur in south-east Asia (Waisel 1972).

Mangroves have long attracted the attention of scientists because of their habitat (silt-rich, saline, coastal waters), and the curious structures of many of their species (flying buttresses, stilt roots, pneumatophores, viviparous reproduction) (Whitmore 1984). The ecosystems are highly productive with a high litter production (Snedaker & Brown 1981, Proctor 1984) and are believed to enhance near-shore primary and secondary production (Macnae 1974; Mann 1982). The mangrove intertidal habitats are the major ecosystems along sheltered subtropical and tropical coasts and are reported to have a total area of 43.7 million ha (Rodin *et al.* 1975).

Odum (1969) described mangroves as interface or open systems because of their flow-through pathways for transporting matter. These pathways are driven by physical (tides, terrestrial runoff, and rainfall) and biological (litter production, decomposition, mineral uptake and faunal activities) factors that control the rate of matter import, export and storage (Pool *et al.* 1975). The result of these flows and transformations is the import of inorganic matter from terrestrial ecosystems and the export of both particulate and dissolved organic matter to adjacent marine ecosystems.

1.2 The biological functions

Two important functional roles of mangroves have become the subject of considerable research and debate; namely, to what extent do they export nutrients and detritus to the coastal waters and how important are they as nursery areas for fish and crustaceans of commercial importance (Chong *et al.* 1990)?

Litterfall occurs throughout the year, and through the feeding activities of microbial decomposers and the larger detritivore animals the litter is processed into fine particles of organic detritus (Odum & Heald 1975). This organic detritus forms a significant fraction of the available food particles in mangrove-lined estuaries (Mann 1972; Odum & Heald 1975). The organic particles that become colonized by bacteria, fungi, and other micro-organisms are a main food source for a range of detritus-consuming omnivorous organisms (Odum & Heald 1975), including prawns, crabs, and a number of fishes. This food web, with the principal flow of energy along the route : mangrove leaf detritus –> bacteria and fungi –> detritus consumers –> lower carnivores –> higher carnivores, is characteristic of shallow muddy estuaries with extensive plant communities such as mangroves, seagrasses, or microalgae.

Mangroves provide important feeding and nursery areas for many fish species, especially mullets (*Mugyl sp.*) (Knox & Miyabara 1984). Their most important function for fisheries however is their role as nursery areas. The freshwater prawn *Macrobrachium spp.*, with more than 100 species in tropical areas, is dependent on the brackish-water environment for the completion of its life cycle. Pregnant females migrate from freshwater rivers and lakes to the mangrove swamps along the coasts, where the eggs hatch into free-swimming larvae. After completion of the pelagic larval stage, the larvae metamorphose to a benthic stage and crawl back upstream to freshwater. The marine species, on the other hand, spawn in near-shore waters, and the newly hatched larvae are transported to the mangroves along the coasts, where they stay until they reach the juvenile stage and migrate offshore (Knox & Miyabara 1984).

Attempts have been made to determine the relationship between mangrove areas and offshore shrimp production. Martosubroto & Naamin (1977) suggested that there is a significant linear relationship between the two, and that any reduction in mangrove area will cause a reduction in shrimp production. A regression analysis of annual prawn production with mangrove area and latitude, using a world-wide data set (Turner 1977), showed that in Indonesia one could expect a production of about 100 kg of prawns / ha / year of mangrove. Nair (1977) has attempted to quantify the economic tradeoffs between mangrove forestry and offshore prawn fisheries in Sabah.

In Australia, Staples *et al.* (1985) found a high positive correlation between the length of the mangrove-lined section of rivers and the mean annual commercial catch (1973 to 1982) of the banana prawn (*Penaeus merguiensis* de Man) in different areas of the Gulf of Carpentaria. Adults of the commercially important penaeid prawns usually spawn at sea and after a short larval life (2 - 3 weeks), the post larval stage settles in the near inshore areas and estuaries (Dall *et al.* 1990). Many species spend their juvenile phase in or associated with vegetation such as mangroves or seagrass beds. In an analysis combining many penaeid species from several countries, Turner (1977) demonstrated a positive correlation between the offshore yield of prawns and the amount of mangrove present in the nursery area.

1.3 Previous research

Most research on the ecology of mangroves has been done near their latitudinal limits such as in Australia and Florida (USA). These areas are characterized by low-diversity systems in contrast to the high-diversity systems of tropical Asia. In Florida, for instance, there are only six mangrove tree species and considerable areas consist of single-species stands (Lugo & Snedaker 1974), whereas in Indonesia up to 37 tree species may be present (Kartawinata *et al.* 1979).

Using CD-ROM facilities from ASFA (Aquatic Sciences and Fisheries Abstracts), LSC (Life Sciences Collection), and GEOBASE (Elsevier Science Ltd.) which were backed up by more than 6 000 journals, books, conference proceedings, monographs and reports, more than 4 000 new titles on mangrove research between 1978 and 1996 were found. Even though most are from Australia (710 titles) and America (865), there is progress from some Asian countries such as India (579), Malaysia (215), Thailand (164), Philippines (163), Indonesia (138), China (132) and Japan (115).

1.4 Mangrove utilization in Indonesia

For centuries Indonesians have traditionally utilized mangroves, mostly for firewood (almost all mangrove woody plants), charcoal (*Bruguiera* and *Rhizophora*), tannin (*Bruguiera* and *Rhizophora*), medicine (*Acanthus* and *Sonneratia*), timber (*Xylocarpus, Bruguiera, Rhizophora* and *Ceriops*) and even boats (*Heritiera*) (Soegiarto 1984).

The Riau Archipelago Province (Sumatra) has long been known as a centre for mangrove charcoal, and the Forestry Service there (unpublished ms) reported in 1984 that in Riau there were about 836 charcoal kilns with a total production of 22 207 t year^{-1}. The products are exported mostly to Singapore and Hong Kong.

The large-scale commercial exploitation of mangroves in Indonesia has begun relatively recently with the production of charcoal, logs, poles and chip-wood for paper pulp. In early 1982 when the total mangrove area in Indonesia was about 4.25 million ha, mangrove areas that had been surveyed for logging amounted to 674 200 ha of which 401 000 ha were already exploited (Darsidi 1984). In the same year, for instance, 163 000 ha of the mangrove forests in Irian Jaya were already on lease (Darsidi 1984) and no less than 10 private corporations were ready to get a share in the remaining 205 000 ha of the allocated 368 000 ha (Direktorat Bina Program Kehutanan 1981).

The mangrove wood chip industry is quite new in Indonesia. The first chip mill was established in Tarakan, East Kalimantan and produced around 70 000 m^3 / year of chips (Burbridge & Koesoebiono 1980). In 1984 the Bina Lestari Timber Company completed the construction of a chipmill in Riau with a maximum capacity of about 176 000 m^3 / year (Soegiarto & Polunin 1981), and in 1988 another chipmill industry was already operating in Bintuni Bay in Irian Jaya with a production capacity of about 300 000 m^3 / year (Erftemeijer *et al.* 1989).

During the past decades, the demand for mangrove resources has been steadily increasing, not only for the products but also for the land itself. Of these two demands, the latter is potentially more destructive, since the end result is a completely different environment such as human settlements, industrial sites, agricultural lands and brackish-water fish ponds (Soemodihardjo & Soerianegara 1989).

The most extensive form of mangrove land conversion is undoubtedly the "tambak" or brackish-water fish ponds. There is no doubt that fish are a very important source of animal protein for the people of tropical Asia. Thus any attempts to improve nutrition and to cope with projected population increases must involve substantial increases in fish production. Among the South-east Asian Nations, Indonesia has the second largest total catch, both for marine and freshwater fishes. The greatest potential for expansion of fish production in Indonesia would appear to lie in brackish-water culture and the harvesting of natural marine living resources. Both of these have their greatest impact in the coastal zone (Knox & Miyabara 1984).

There were 155 081 ha of tambak in Indonesia in 1980, mainly in Java, Sulawesi and Sumatra (Soewito 1982). In the Fourth Five-Year-Development Programme of 1984 -1989, where the effort to increase foreign exchange earning from fishery sectors was encouraged, the government sponsored the opening of thousands of hectares of mangrove and their conversion to brackish-water fishponds, particularly for the culture of prawns. It was to be carried out mostly outside Java (Soemodihardjo & Soerianegara 1989).

1.5 The aims of this study

Bintuni Bay has some of the most extensive, best developed mangrove in South-east Asia. Presently a number of commercial development projects are carried out in the Bay area including fisheries, forestry, oil and gas exploitation. In spite of their importance the Bintuni Bay mangroves have been little studied and there is a need for basic ecological information on them.

The main purpose of this study were to describe mangrove vegetation and some of the ecological processes within it in an accessible part of the Bay. Specifically, the thesis aims were:

1. to describe the physical environment of the mangrove;
2. to describe the mangrove floristically, including the structure and composition of the vegetation, and its regeneration;
3. to determine the small litterfall production, quantify its nutrients, and to estimate its rate of decomposition;
4. to estimate the leaf herbivory and seed predation in the commoner tree species;
5. to use the data to provide information on how the Bintuni Bay mangroves might be managed and conserved.

II STUDY AREA AND STUDY SITES

2.1 Introduction

Indonesia has a coast line of about 81 000 km and about 13 000 islands (Soegiarto 1979). The islands show much diversity of coastal features, related partly to contrasts in the geology and geomorphology of the hinterland and the bordering sea floors, and partly to variations in adjacent marine environments. A substantial proportion of the coast has mangroves, from several meters to several kilometers wide (Soemodihardjo & Soerianegara 1989).

2.1.1 Climate

Large differences in climate occur within Indonesia but the larger proportion of the Indonesian coastal regions has a humid tropical climate with seasonal winds and precipitation, a high annual rainfall, and a high air temperature (Sandy 1976; Bird 1982). In terms of Köppen's classification (Köppen 1923), most of the coastal regions are in Category A: tropical rainy, a hot climate with no cool season, with the average temperature of each month over 18 °C.

According to Marr (1976) the parts of Indonesia which are north of the equator are affected by a dry monsoon which extends from October to April with northeasterly winds strongest in December and January. The wet monsoon extends from May to September with southwesterly winds strongest in July and August. The surface layers of the sea cool during the northeast monsoon, when heat loss through evaporation exceeds heat gain from radiation. The parts which are south of the equator are influenced by winds which tend to be northwesterly or westerly from October to April and southeasterly from May to September. The heat gain of the sea's surface layers by radiation almost always exceeds heat loss by evaporation and heat transfer is affected only by horizontal transport.

2.1.2 Soil

Research on mangrove soils in Indonesia has been limited to a few localities, including Rambut Island (Kartawinata & Waluyo 1977), Ujung Karawang (Sukardjo 1982), Cilacap (Soerianegara 1971) and South Sumatra (Matondang 1979). Wiranegara & Hardjowigeno (1984) reported that the mangrove soils of the Berau River estuary and Tibi Island (East Kalimantan) had a high content of clay and organic carbon, were poor in nutrients, and in the order Entisol, sub-order Aquent (Soil Survey Staff / USDA 1987).

2.1.3 Tidal pattern

Wyrtki (1961) placed the tides in Indonesian waters in four categories (Fig.2.1 and 2.2):

1. Semi-diurnal. Daily, two high waters and two low waters almost equally high, e.g the Malacca Straits north west of Bagan Siapi-api,
2. Mixed, prevailing semi-diurnal. Daily, two high waters and two low waters, but different in height and high water time, e.g. East Indonesian Seas,
3. Mixed, prevailing diurnal. Temporarily only one high water and one low water daily, but temporarily also two high waters and two low waters, which differ much in height and high water time, eg. The Java Sea,

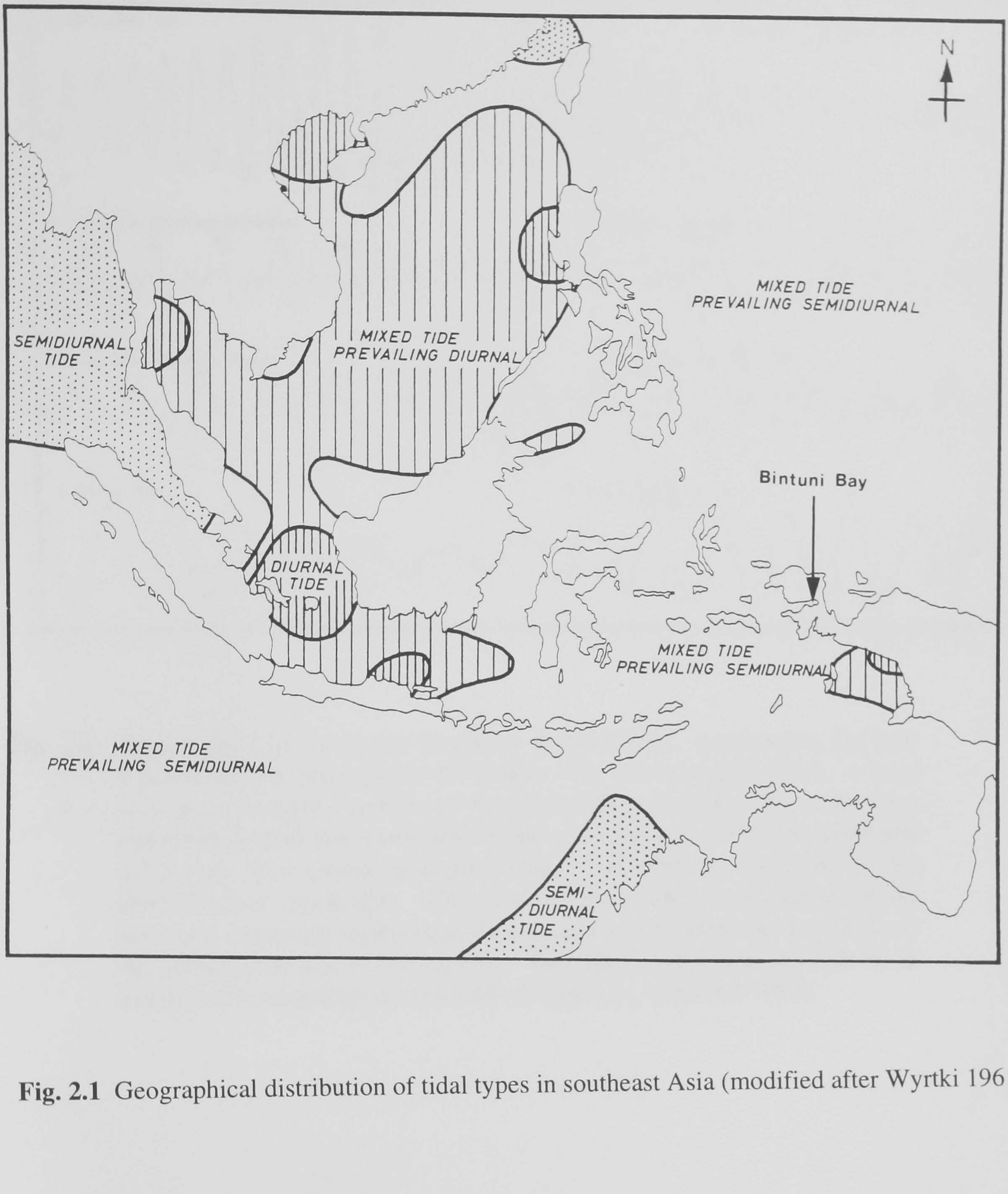


Fig. 2.1 Geographical distribution of tidal types in southeast Asia (modified after Wyrtki 1961).

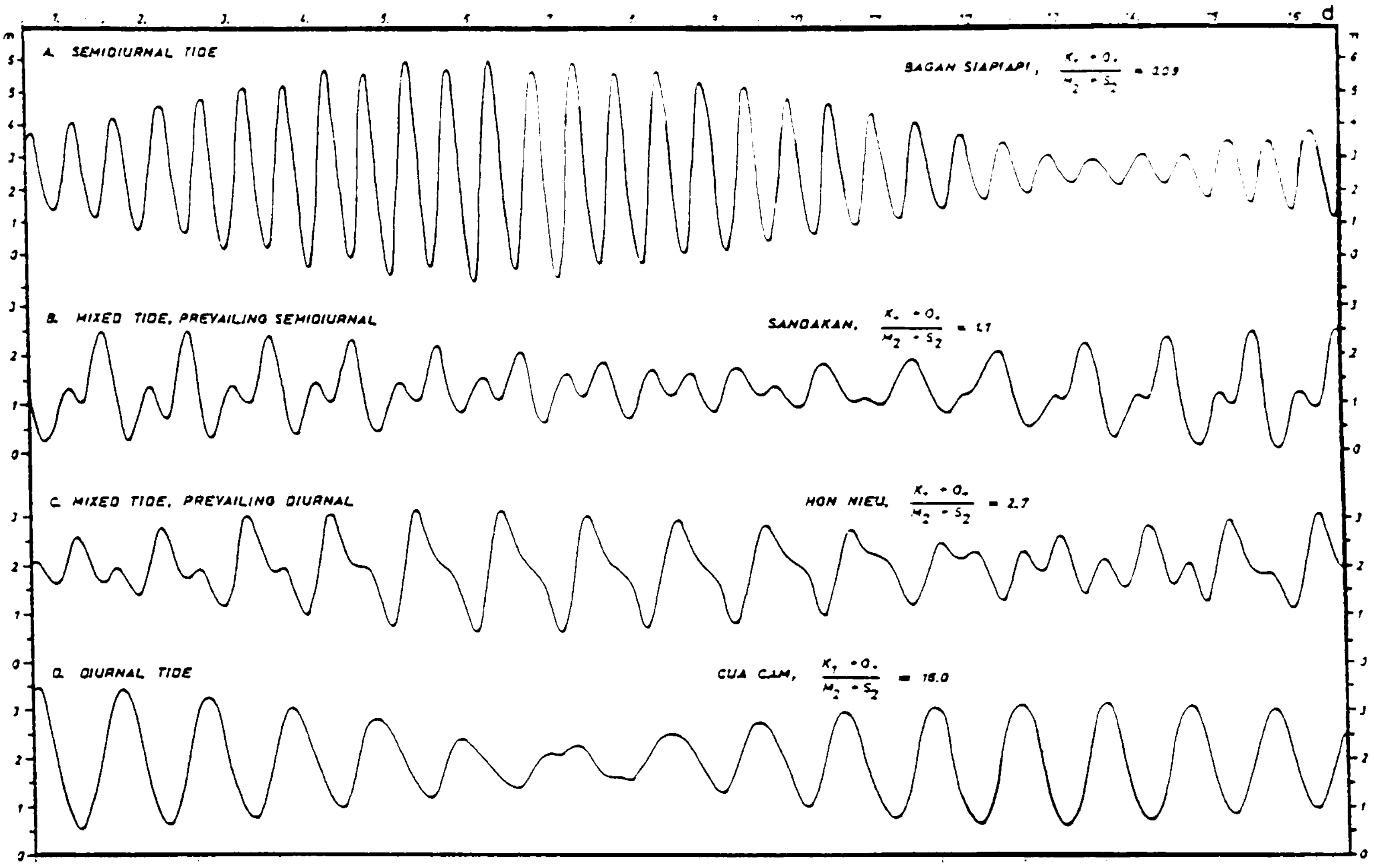


Fig. 2.2 Typical tidal curves in the Southeast Asian Waters, representing the four types of tides during a period of 16 days. The proved expression $K_1 + O_1 / M_2 +$ S2 is used, being the quotient of the sums of the amplitudes of the two most important diurnal and semidiurnal tides. $K_1 + O_1$ is the sum of the amplitude of the two most important diurnal tides, indicating the amplitude of the diurnal tide at spring tide, while $M_2 + S_2$ is the sum of the amplitude of the two most important semidiurnal tides which is indicating the amplitude of the semidiurnal tide at spring tide. The name before the quotient is an example of a coastal town with each of tidal type. (Dietrich 1944).

4. Diurnal. Only one high and one low water daily, e.g. Karimata and Bangka Straits.

The tidal range varies from place to place, depending on external factors such as depth of water, size of basin, and coastal configuration (Birowo & Uktolseya 1982). Hence, the inundation pattern of mangroves depends on the tidal pattern, the high tide level and topography. This has been studied by Watson (1928), de Haan (1931), Walter & Steiner (1936), Chapman (1936), Chapman & Ronaldson (1958), MacNae (1968) and Baltzer (1969).

Watson (1928), in his review of the Malay Peninsula's mangroves, first put forward the concept of Inundation Classes. De Haan (1931), based on his work in the Cilacap mangrove area (south coast of central Java), subsequently modified Watson's classes by including the impact of the fresh water. Chapman (1976) reviewed the inundation classifications and united them them with his own study of Jamaican mangroves (Chapman 1944) (Table 2.1):

Table 2.1 Comparison of mangrove tidal inundation classes in Old World and New World tropics (after Chapman (1976).

Watson (1928)	de Haan (1931)	Dominant in Old World	Chapman (1944)	Dominant in New World
	A. Brackish to saline. Salinity at flood tide 10 - 30 ‰.			
1. Land flooded at all high tides	A1. Areas flooded 1-2 times daily, minimum 20 days per month.	*Sonneratia alba* *Sonneratia apetala* *Avicenia marina*	530 - >700 submersions per annum.	*Rhizophora mangle*
2. Flooded by medium high tides	A2. Areas flooded 10 - 19 days per month	*Rhizophora*		
3. Flooded by normal high tides		*Bruguiera*	400 - 530 submersions per annum	*Avicennia germinans*
	A3. Flooded 9 days per month	Landward fringed *Xylocarpus granatum*		
4.Flooded by spring tides only	A4. Flooded only a few days per month	*Lumnitzera littorea* *Bruguiera sexangula*	150 - 250 submersions per annum	*Laguncularia* *Salina*
5. Flooded by storm high tides only		Halophytes or salt flats	4 - 100 submersions per annum	*Salina* or *Laguncularia -Conocarpus*
	B. Fresh to brackish water. Salinity 0 - 10 ‰			
	B1.More or less under tidal influence	*Nypa*		
	B2.Areas seasonally flooded			

2.1.4 Flora and fauna

Qualitative descriptions of the structure and composition of mangrove forest have been published for Indonesia by Kartawinata *et al.* (1979), Mustafa *et al.* (1979), Sukardjo & Kartawinata (1979), Soemodihardjo *et al.* (1980), Direktorat Bina Program Kehutanan (1981), Sunaryo (1982), Hardjosuwarno *et al.* (1982), Hardjosuwarno (1984), and Darnaedi & Budiman (1984). Altogether 91 vascular plant species have been recorded from Indonesian mangroves: 37 species of trees, five of shrubs, nine species of herbs, nine of lianas, 29 epiphytes and two parasites (Kartawinata *et al.* 1979).

Physiognomically, mangrove forests are uniform and sometimes regarded as monotonous (van Steenis 1958). They usually consist of only one stratum with the mature forest composed of only a few species. Mangroves can grow on a variety of substrata such as mud, sand, reef flat and even on relatively solid rock. They are best developed on calm and protected muddy coastal plains where plenty of fresh water is supplied from surrounding rivers . In such places, e.g. the south and east coast of Sumatra and Kalimantan, mangrove trees grow up to 50 cm diameter, have straight trunks, and reach 50 m in height. On reef flats, sand or rock, the mangroves are stunted and often with twisted stems (Sukardjo & Kartawinata 1979).

The mangrove fauna consist of terrestrial and marine components. Examples of the terrestrial components are: bats (*Pteropus vampyrus*), monitor lizards (*Varanus salvator*), wild pigs (*Sus scrofa*), crab-eating monkeys (*Macaca fascicularis* Raffles) and proboscis monkeys (*Nassalis larvatus* Wurmb), and various birds and insects. The marine faunal component tends to be dominated by gastropods and brachyurans (Kartawinata *et al.* 1979). In Bintuni Bay, Erftemeijer (1989) found several endemic animals including 18 species of fishes, 12 birds, three reptiles, at least two mammals and several invertebrates. Although most of these species are endemic to New Guinea mainland or to the New Guinea - North Australia region, some of them are found exclusively in the Bay area such as some rainbowfishes (*Melanotaenia*) and the Vogelkop tree kangaroo (*Dendrolagus urisinus*). There also some species that are internationally considered vulnerable, threatened or near-threatened: the New Guinea freshwater crocodile (*Crocodylus novaeguinae*), estuarine crocodile (*Crocodylus porosus*), blue crowned pigeon (*Goura cristata*), and great-billed heron (*Ardea sumatrana*).

2.2 Study area : Bintuni Bay

2.2.1 Topography

Bintuni Bay is a sheltered bay in the south of the Bird's Head Peninsula in the western part of Irian Jaya, Indonesia (Fig. 2.3). It is located between 132° 55' and 134° 02' E and 2° 02' and 2° 97' S. The Bay is bordered by extensive mangroves (Fig. 2.4) of which the total area is estimated, from the Regional Physical Planning Programme for Transmigration maps (RePPProT 1986), from the interpretation of satellite and aerial photographs, and from the vegetation map of Stellingwerf (1957), to be about 260 000 ha (Erftemeijer 1989). Numerous rivers flow into the bay and the mangroves are heavily intersected by rivers, channels and creeks, some of which are over 4 km wide and up to 21 m deep (Erftemeijer 1989).

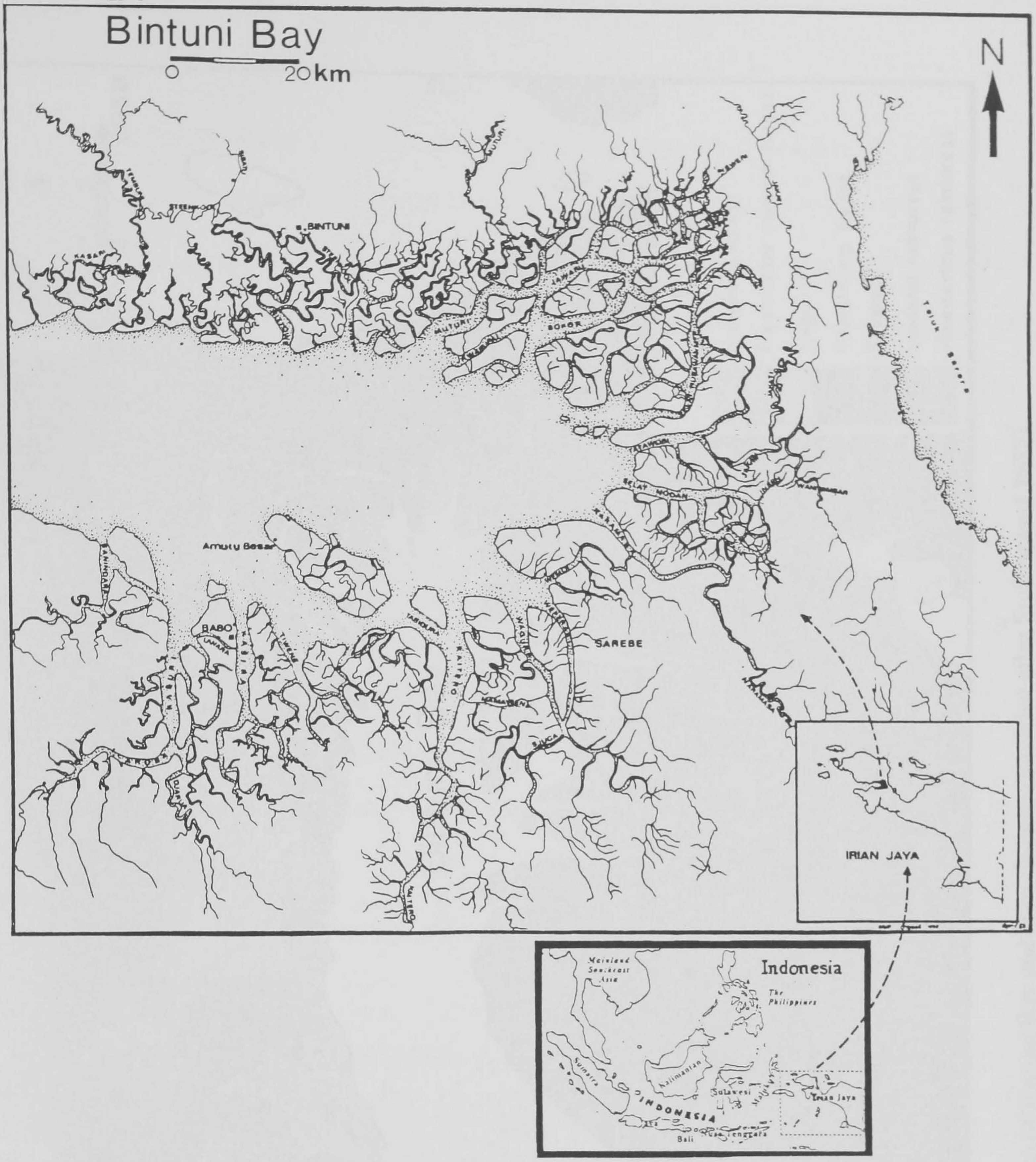


Fig. 2.3 Map showing the location of Bintuni Bay, Irian Jaya, Indonesia. The Bay is surrounded by a dendritic network of rivers and has many islets which are occupied by mangroves (modified after Petocz 1984)

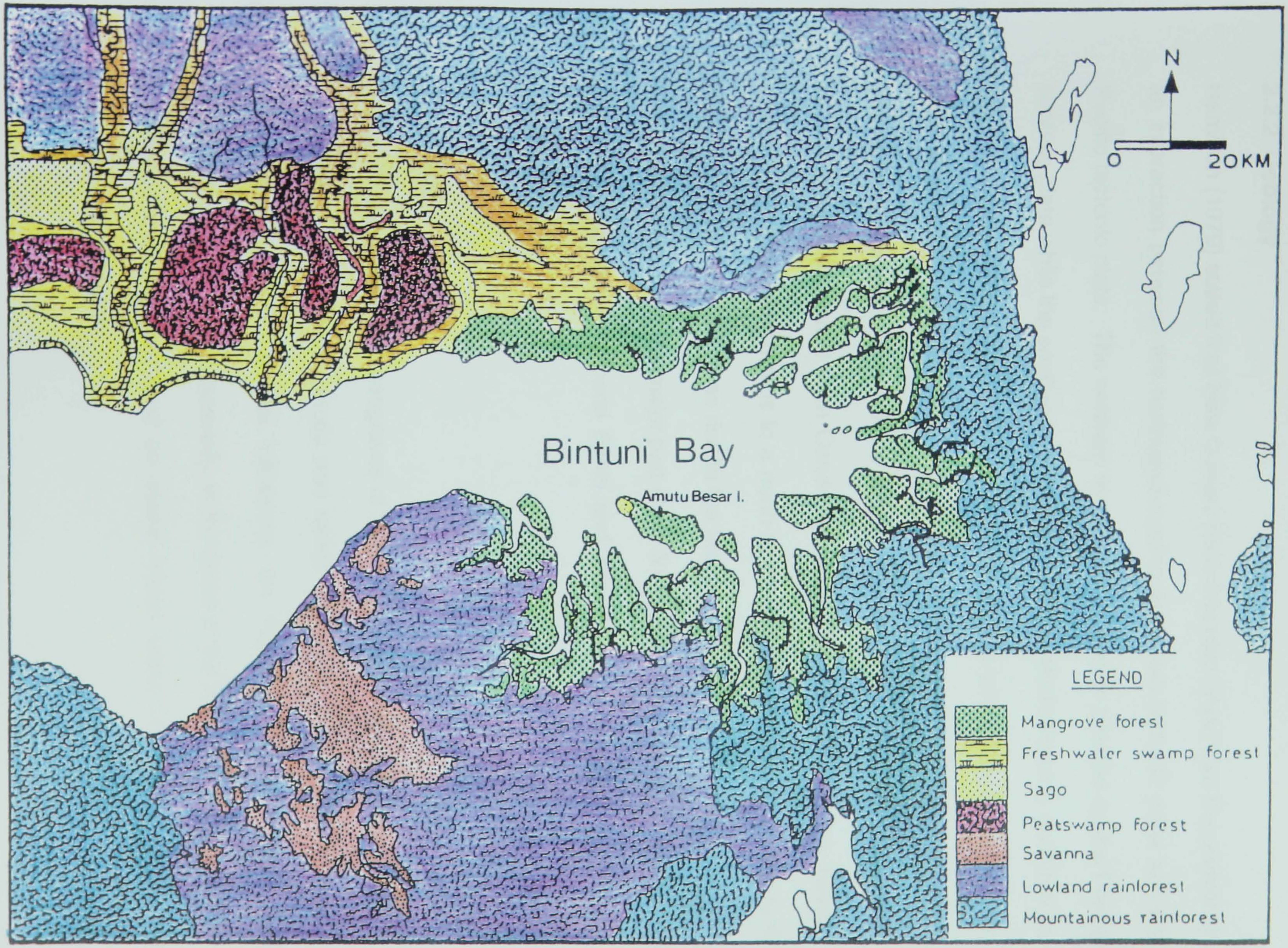


Fig. 2.4 The vegetation map of Bintuni Bay and surroundings (modified after Stellingwerf 1957).

2.2.2 Geology

Hamilton (1979) stated that New Guinea (including Irian Jaya) was the product of an interaction between the northward-moving Australian tectonic plate and the Pacific tectonic plate. The northern fringe of Irian Jaya is situated on the Pacific tectonic plate while the southern half and much of the Bird's Head is underlain by the Australian tectonic plate which is estimated to slip under the Pacific tectonic plate at about 12.6 cm per year. The Ransiki and Sorong Fault Zones separate the Australian tectonic plate of the Bird's Head from the Pacific tectonic plate. Bintuni Bay is separated from Cendrawasih (or Geelvink) Bay by the Jakati - Jamur Fault zone, which runs in a north-south direction through the isthmus of the Bird's Head where it gives rise to the Masikeri Mountains. The southern part of the Bird's Head and the major part of the Bomberai Peninsula are separated in the South Vogelkop-Bomberai Basin and The Bintuni Basin by the Lenggoru Folded Belt (Fig. 2.5).

2.2.3 Soil

The soils underneath the mangroves of Bintuni Bay and parts of the swamps are classified as saline peats, muds and sands (Fig. 2.6). Their origin is mainly marine but significant alluvial influences are found in the floodplains and estuaries of larger rivers, especially at the head of the Bay. Saline peats have developed over sand or mud on stable island areas of the mangrove belt (Haantjens *et al.* 1967).

The bare tidal flats along the north coast of the bay are mainly sandy, whereas fine materials are concentrated in the east at the head of the Bay, where

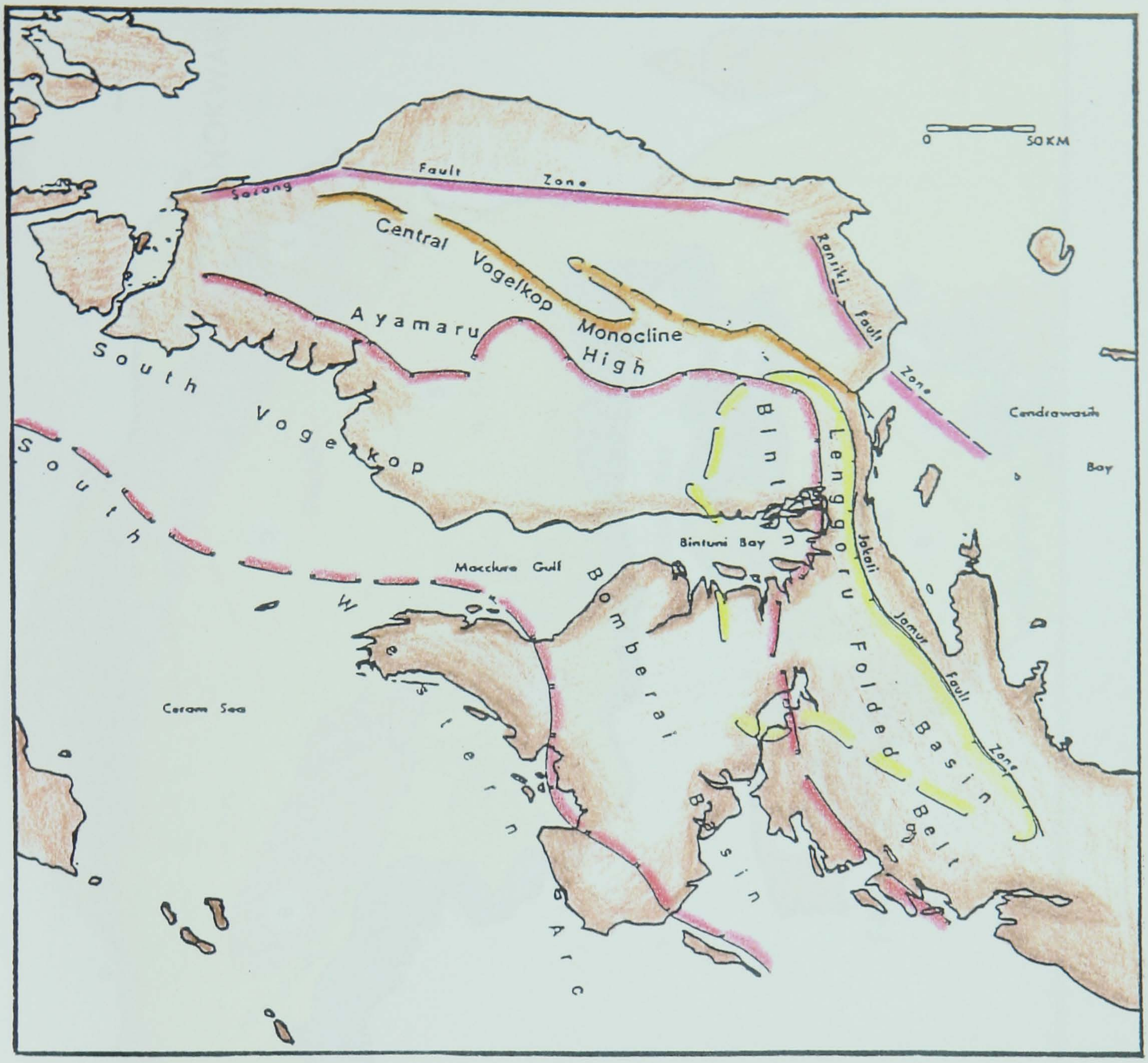


Fig. 2.5 Geological sketch map of the Bird's Head Region of Irian Jaya (modified after Audretsch *et al.* 1966).

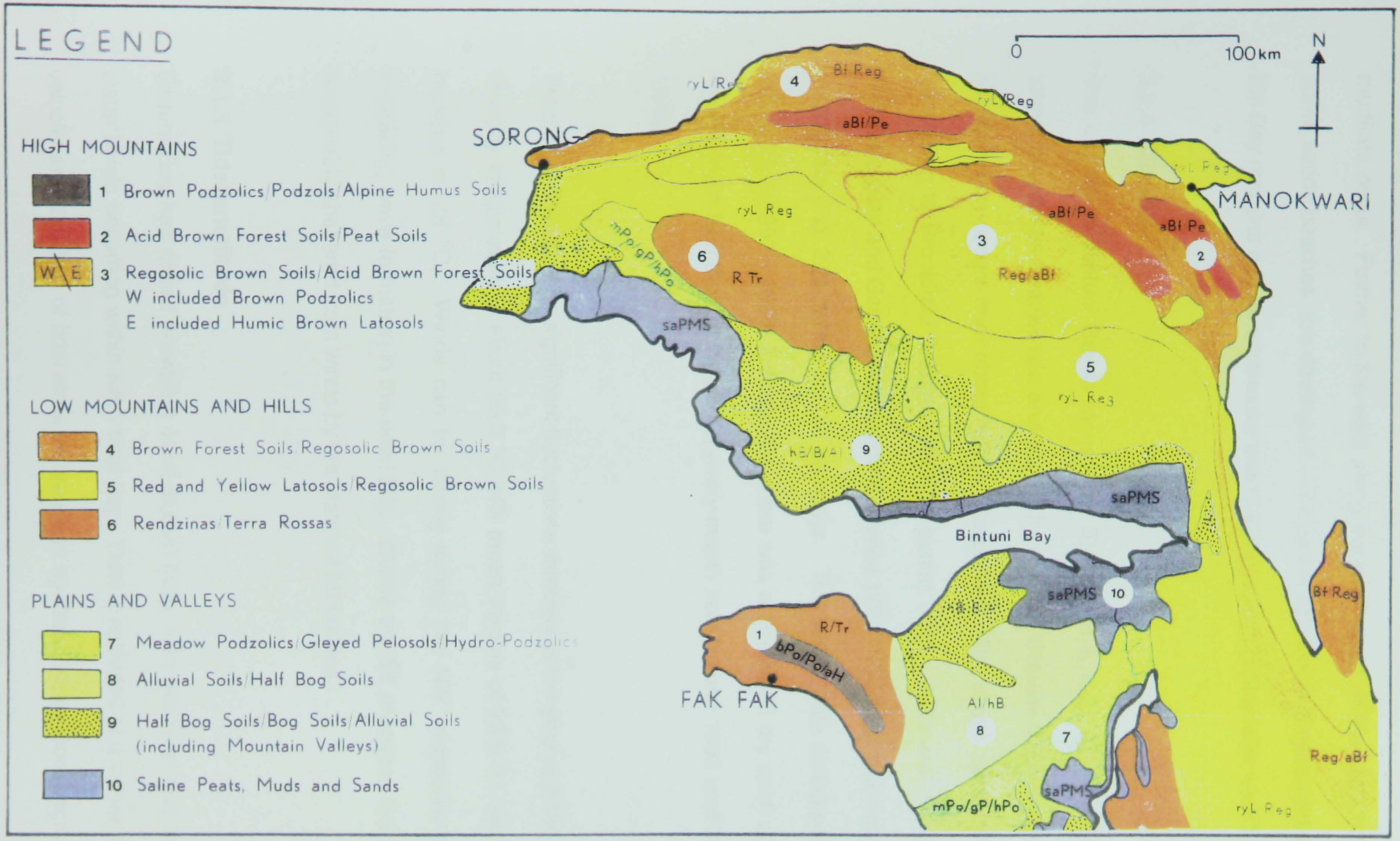


Fig. 2.6 The distribution of major soil groups of western Irian Jaya (modified after Haantjens *et al.* 1967)

mudflats occur. Further to the west along the north coast of the MacCluer Gulf some sandy beaches are developed. The recent alluvium is widespread around the Bay margins and penetrates far inland along valleys (Erftemeijer *et al.*1989).

2.2.4 Climate

The climate of Bintuni Bay is monsoonal (Brookfield & Hart 1966). The NW monsoon causes heavier rain and occurs from about October to March and the SE monsoon occurs from about April to September. The mean annual rainfall (according to Brookfield & Hart (1966) for period 1925 - 1961 and Indonesian Meteorological and Geophysical Office for period 1981 - 1994), ranges from 2500 - 3500 mm (Fig. 2.7) falling on 136 rain days. The rainfall data during period of this study (1993 - 1994) indicate that there was a prolonged dry spell with the rainfall much less than the mean for every month from 1 June 1993 until 31 May 1994.

Temperatures show no significant fluctuations throughout the year and the mean monthly temperature is about 26.8 °C with mean minima of 25.9 °C and mean maxima of 28 °C. Winds can be strong during the NW monsoon, greatly increasing wave formation in the open Bay. During the SE monsoon the Bay is reasonably sheltered from winds by the Masikeri Mountains.

2.2.5 Tidal amplitude

Bintuni Bay has mixed prevailing semi-diurnal tides, with two high and two low water levels occurring within each tidal day. Tidal amplitudes and values for the velocity and direction of tidal streams are given by Dinas Hidro-Oseanografi TNI-

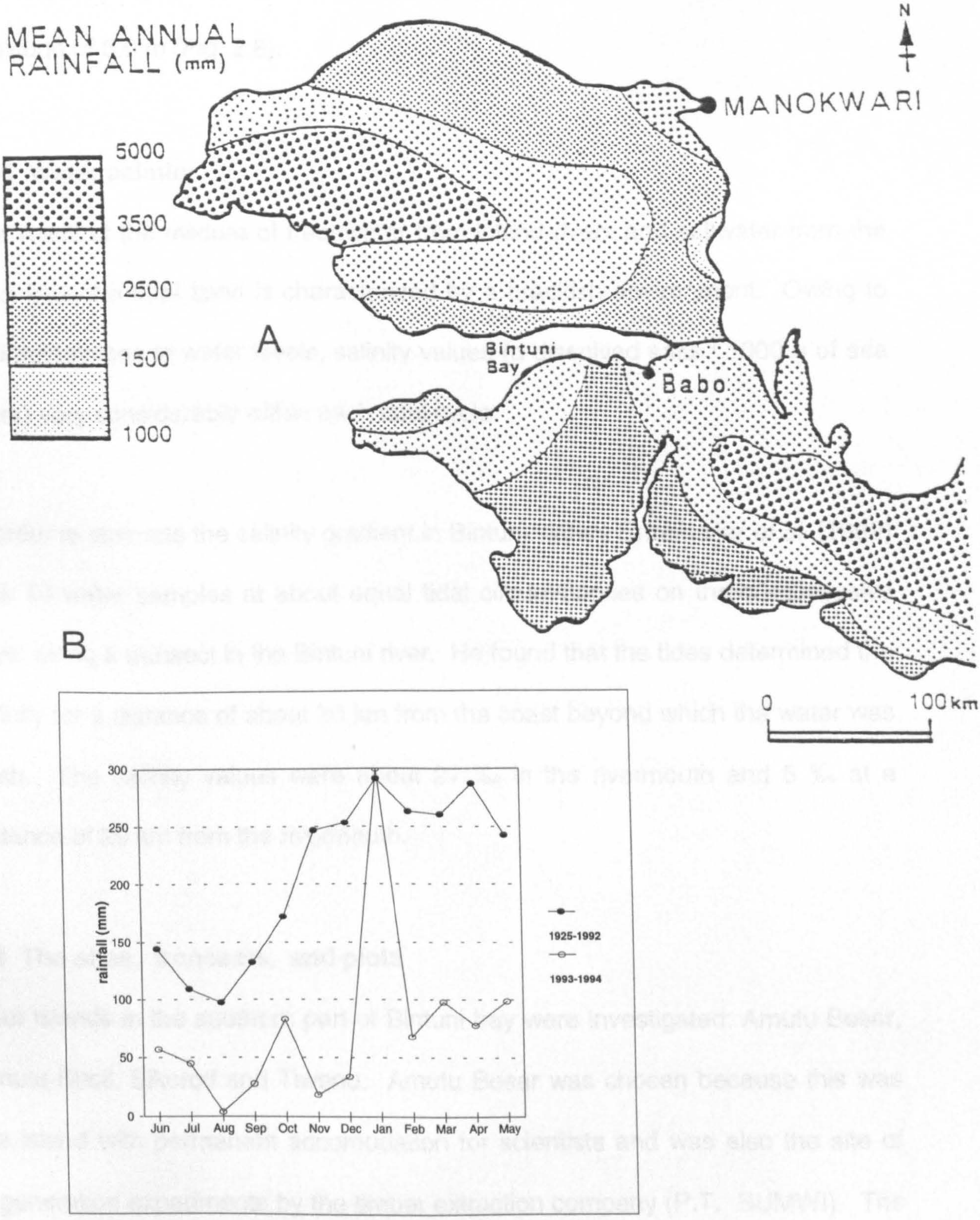


Fig. 2.7 Mean annual rainfall distributions in western Irian Jaya (A) and mean monthly rainfall distributions (combining values for 1921 - 1961 and 1981 - 1992) and mean monthly rainfall from 1 June 1993 to 31 May 1994 at Babo (B).

AL (Dinas Hidro - Oseanografi 1993, 1994). At the rivermouth of Sungai Wasian (Fig. 2.3), the bay has a minimum tidal amplitude of 1.0 m and a maximum tidal amplitude of 5.6 m (Fig. 2.8).

2.2.6 Water salinity

As a result of the mixture of freshwater from inland rivers and saltwater from the open Bay, the tidal zone is characterized by a brackish environment. Owing to tidal fluctuations in water levels, salinity values (g dissolved salts / 1000 g of sea water) vary considerably within each tidal cycle.

In order to estimate the salinity gradient in Bintuni waters Erftemeijer *et al.* (1989) took 10 water samples at about equal tidal circumstances on three successive days along a transect in the Bintuni river. He found that the tides determined the salinity for a distance of about 30 km from the coast beyond which the water was fresh. The salinity values were about 27 ‰ in the rivermouth and 5 ‰ at a distance of 29 km from the rivermouth.

2.3 The sites, transects, and plots

Four islands in the southern part of Bintuni bay were investigated: Amutu Besar, Amutu Kecil, Sikoroti and Tiwene. Amutu Besar was chosen because this was the island with permanent accomodation for scientists and was also the site of regeneration experiments by the timber extraction company (P.T. BUMWI). The other islands were chosen because they were readily accessible by the available boats. Amutu Kecil had substantial areas of logged forest while Sikoroti and

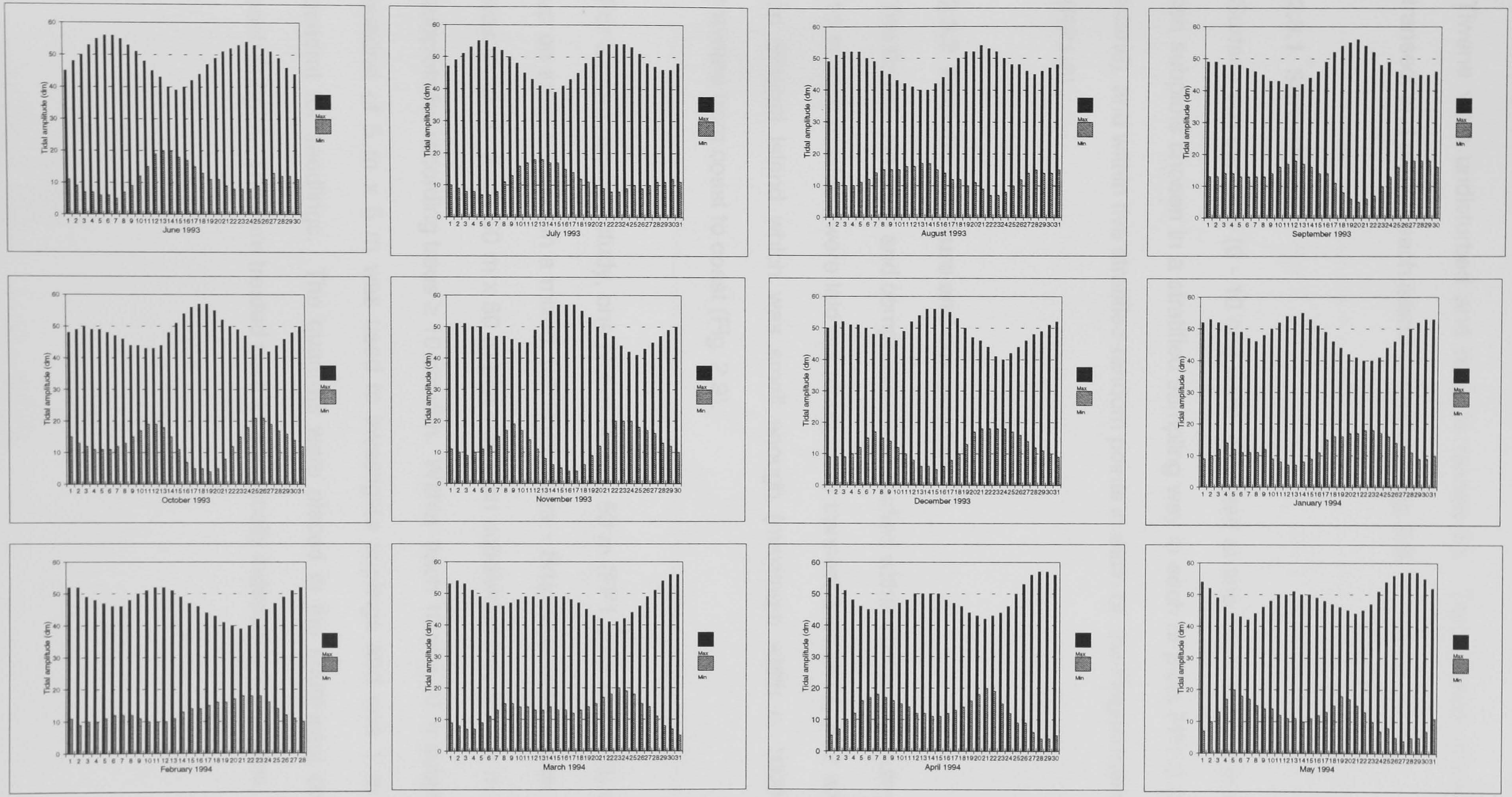


Fig. 2.8 The daily maximum and minimum of tidal amplitude at the mouth of Wasian River, Bintuni Bay, from June 1993 - May 1994 (Dinas Hidro-Oseanografi 1993, 1994).

Tiwene were undisturbed and likely to remain so. The location of each site, transect and plot on each island is shown in Fig. 2.9.

2.3.1 Surface soil

Surface soil samples (0 - 10 cm) were collected at one random point in each of ten subplots chosen in a stratified sampling way in each of plots FP1-3 (Sikoroti island), and within five stratified-random points in each of the Regeneration Plots (RP1-6).

2.3.2 Floristic structure and composition

The floristic structure and composition was studied within contiguous sub-plots of 10 m x 10 m which were laid out along three transect lines (FT1, FT2 and FT3) on Sikoroti Island which was small enough (maximum width c. 1000 m) to traverse from coast to coast (Fig. 2.9).

For a more detailed study, one plot of 50 m x 50 m (FP1, FP2 and FP3) was set up on each transect in a mixed, tall *Rhizophora - Bruguiera* zone where litterfall was studied. Each 50 m x 50 m plot was then subdivided into 25 10 m x 10 m subplots for recording trees ≥ 10 cm dbh. Within each 10 m x 10 m subplot, one quadrat of 5 m x 5 m was used to investigate saplings and one 1 m x 1 m quadrat for seedlings. The quadrats were placed in the south-east corner of each subplot. They are treated here as statistically independent samples.

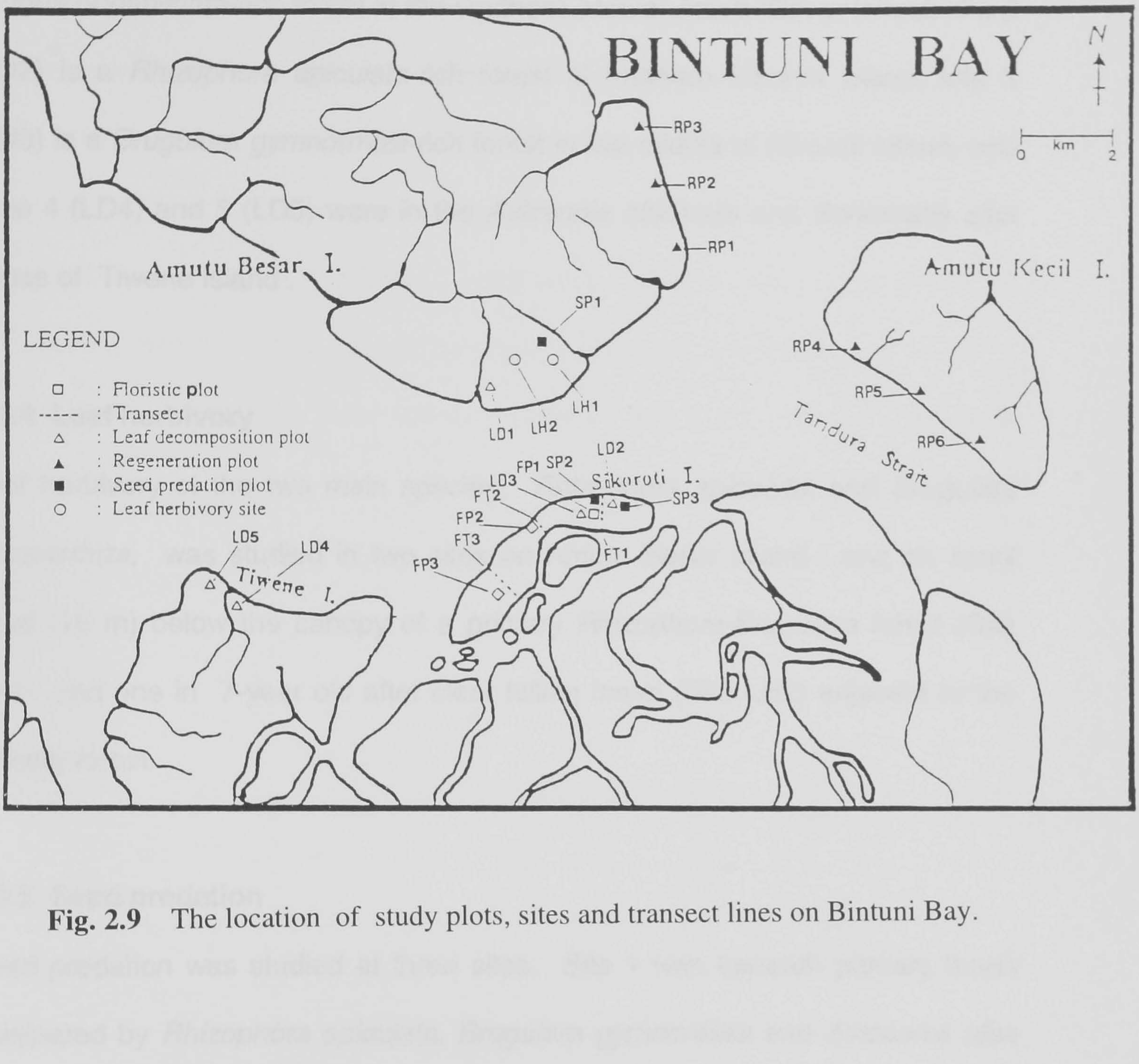


Fig. 2.9 The location of study plots, sites and transect lines on Bintuni Bay.

2.3.3 Leaf decomposition

Leaf decomposition was investigated at five different sites : site 1 (LD1) is a *Bruguiera parviflora*-rich forest in the southern area of Amutu Besar Island; site 2 (LD2) is a *Rhizophora apiculata*-rich forest of northern Sikoroti Island; site 3 (LD3) is a *Bruguiera gymnorrhiza*-rich forest in the middle of Sikoroti Island; and sites 4 (LD4) and 5 (LD5) were in the *Avicennia officinalis* and *Sonneratia alba* zones of Tiwene Island .

2.3.4 Leaf herbivory

Leaf herbivory of the two main species, *Rhizophora apiculata.* and *Bruguiera gymnorrhiza*, was studied in two sites on Amutu Besar Island : one on small trees (<5 m) below the canopy of a primary *Rhizophora-Bruguiera* forest (Site LH1 , and one in 7-year old after clear felling forest (Site LH2) adjacent to the primary forest.

2.3.5 Seed predation

Seed predation was studied at three sites. Site 1 was beneath primary forest dominated by *Rhizophora apiculata*, *Bruguiera gymnorrhiza* and *Avicennia alba* in the southern area of Amutu Besar Island (SP1). Site 2 was located in the *Avicennia-Sonneratia* zone in the northern part of Sikoroti Island (SP2), and Site 3 (SP3) was in the transitional zone dominated by young *Rhizophora*, *Bruguiera* and *Ceriops* on the same island. In every site there were five 10 m x 60 m plots which were each subdivided into six 10 m x 10 m subplots.

2.3.6 Regeneration after felling

Six further 50 m x 50 m plots were randomly set up in each of two forest sites which were clear felled seven years ago. These plots will later be referred to as the Regeneration Plots (RP1-6). Site 1 (RP1-3) is on the north-east coast of Amutu Besar Island, and site 2 (RP4-6) is on the south-west coast of Amutu Kecil Island (Fig. 2.9) facing the small strait of Taridura. These sites were chosen because of their different treatments. Within site 1, seedlings of *Rhizophora apiculata* were planted by logging company workers in a 2 m x 2 m array one year after the clear felling, whereas site 2 was left to regenerate naturally.

III SURFACE-SOIL PROPERTIES

3.1 Introduction

The mangrove soil is determined by a range of processes. Some of these, such as sea-level change or soil erosion, may effect the mangroves directly but more often they change certain characteristics of the sediment which in turn render it more or less suitable for the mangroves (Hutchings & Saenger 1987). Thom (1982) indicated that there are two major types of intertidal landforms : those which contain a veneer of transported or trapped sediment over a consolidated parent material, and those which are the result of sedimentary accretion, producing prograding shorelines.

There are two types of mangrove sediments (Chapman 1975): (1) allochthonous, brought into the swamp from either landward or seaward, and (2) autochthonous, deposited *in situ* and including mangrove-derived peats, where allochthonous sediment supply is low.

Understanding mangrove-soil relationships is complicated because of the ability of most mangrove species to grow on a variety of substrates, and to alter their substrate through peat formation or by changing the patterns of sedimentation (Kuenzler 1974).

In addition to the composition and texture of the soil, nutrient availability in mangrove soil is an important consideration. Although the total concentrations of nutrients in a particular mangrove soil will reflect the chemistry of its parent material and of the surounding waters, the availability of nutrients will depend largely on the type of soil and its microbial characteristics (Hutchings & Saenger 1987).

3.2 Methods

Ten soil samples were collected in a stratified random way from each of the Floristic Plots (FP1-3) and the Regeneration Plots (RP1-6), using a cylindric soil sampler (8 cm diameter, 10 cm depth). Samples were air dried, ground using a pestle and mortar, and sieved through a 2-mm mesh and sent to Stirling University for analysis.

The pH was measured using a Corning-Eel Model 7 pH meter in both a 1:2 soil : deionised water, and a 1:2 soil : 0.01 M $CaCl_2$ solution. The mixtures were shaken for 2 h and allowed to stand for 1 h before measurement. Electrical Conductivity (EC) was measured using a conductivity meter in a soil sample saturation extract (Rowell 1994). Loss-on-ignition (LOI) was determined in a muffle furnace at 550 °C for 2 h.

Total nitrogen and phosphorus were extracted from 1.5-g subsamples of soil which were digested in a sulphuric acid/hydrogen peroxide mix with a selenium catalyst (Allen 1989). Nitrogen and phosphorus were then determined by colorimetry, using a Kontron Uvikon 860 spectrophotometer, following an indophenol-blue method (Rowland 1983) for nitrogen and a stannous chloride - molybdenum blue method (Allen 1989) for phosphorus.

Exchangeable cations were measured by leaching 5-g subsamples of soil with ten successive additions of 10 ml of 1 M ammonium acetate solution which was adjusted to mean soil pH_{H_2O}. Leachates were then analysed by a Varian AA-575 S atomic absorption spectrophotometer using a nitrous oxide - acetylene flame for calcium and magnesium and an air - acetylene flame for sodium and potassium.

With regard to Rowell (1994), total acidity and exchangeable aluminium were determined in 10-g subsamples of soil leached with ten successive additions of 10 ml 1 M potassium chloride solution. From each extract 10 ml were titrated with 2.5 mM sodium hydroxide solution using the indicator phenolphthalein. The result of this titration corresponded to total acidity. After adding 10 ml of 1 M potassium fluoride to the titrated solution, a subsequent titration with 5 mM hydrochloric acid determined the exchangeable aluminium. The difference between the two was equal to exchangeable hydrogen. Cation exchange capacity (CEC) was then calculated from the sum of the total exchangeable cations plus total acidity.

Sulphate-sulphur was determined using the turbidimetric method of Butters & Chenery (1959). Soil subsamples were prepared for this turbidimetric method by a calcium phosphate extraction (Probert 1976). Two g of subsample were diluted into 10 ml of 0.01 M calcium phosphate. After shaking overnight, the solutions were filtered and the background colour removed using 0.2 g washed charcoal.

A further set (five each from FP1-3) of soil samples were collected on 7 October 1996. They were placed fresh in sealed containers and sent to SEAMEO - BIOTROP soil laboratory, Bogor, where they were analysed for pH.

3.3 Data analysis

A one-way analysis of variance was applied to assess the differences of the result of soil chemical analysis among the three Floristic Plots (FP1 - 3). For the Regeneration Plots (RP1 - 6) the results were compared using a two-way nested balanced analysis of variance, considering plot as a random factor and site as a fixed factor (Zar 1996). Pearson product-moment correlation coefficients (Zar 1996) were calculated to determine the possibility of a linear relationship between some of the soil properties. All data were log-transformed in order to correct the heteroscedasticity, nonnormality and nonadditivity of the data, prior to the statistical analysis.

3.3 Results

Tables 3.1 and 3.2 show the mean values of surface soil chemical properties of the floristic plots (FP1-3) and regeneration plots (RP1-6). The analysis of variance showed that among FP1-3, most of the compared variables had significantly different values except EC (electrical conductivity), Na^+, ESP (exchangeable sodium percentage), and H^+. The two sites of the regeneration study had significantly different values.

Table 3.1 The mean values (with standard deviation) of soil chemical properties (n = 10) from surface soil (0 - 10 cm) of three floristic plots (FP1-3) of Sikoroti Island, Bintuni Bay. Means within a row followed by same letter are not significantly different (One-way ANOVA, p≤0.05; comparisons by Tukey-test). Ranges are given in parenthesis.

	Plot		
	FP1	**FP2**	**FP3**
pH $_{(H_2O)}$	**2.6 ± 0.1** a	**2.7 ± 0.2** a	**3.6 ± 1.1** b
	(2.4 - 2.9)	(2.5 - 3.0)	(2.6 - 5.3)
pH $_{(CaCl_2)}$	**2.7 ± 0.2** a	**2.6 ± 0.1** a	**3.6 ± 1.1** b
	(2.4 - 3.2)	(2.3 - 2.8)	(2.5 - 5.6)
LOI (%)	**45.0 ± 3.3** a	**34.4 ± 4.1** b	**29.2 ± 6.8** b
	(39.7 - 51.1)	(27.0 - 42.1)	(17.2 - 3.7)
EC (dS m^{-1})	**5.7 ± 0.9** a	**5.3 ± 0.6** a	**5.0 ± 0.6** a
	(3.4 - 6.4)	(4.3 - 6.2)	(4.1 - 5.8)
Total N (%)	**1.095 ± 0.1** a	**0.855 ± 0.1** b	**0.881± 0.1** b
	(0.916 - 1.247)	(0.751 - 1.048)	(0.689 - 0.987)
Total P (%)	**0.048 ± 0.0004** a	**0.042 ± 0.0005** a	**0.060 ± 0.0011** b
	(0.040 - 0.053)	(0.031 - 0.046)	(0.048 - 0.083)
K^+ (meq 100 g^{-1})	**2.86 ± 0.6** a	**1.49 ± 0.6** b	**2.08 ± 0.7** b
	(2.00 - 4.26)	(0.87 - 2.77)	(1.08 - 3.02)
Na^+ (meq 100 g^{-1})	**147.7 ± 15.8** a	**106.5 ± 19.2** a	**132.7 ± 76.9** a
	(109.9 - 170.1)	(68.0 - 130.8)	(54.9 - 347.7)
ESP (%)	**57.17 ± 1.9** a	**58.60 ± 2.2** a	**63.19 ± 9.1** a
	(52.99 - 59.95)	(62.14 - 54.69)	(52.55 - 88.91)
Ca^{2+} (meq 100 g^{-1})	**16.01 ± 1.9** a	**11.34 ± 1.9** b	**11.08 ± 2.2** b
	(13.87 - 19.37)	(7.85 - 13.26)	(7.55 - 13.55)
Mg^{2+} (meq 100 g^{-1})	**70.81 ± 6.3** a	**41.63 ± 9.2** b	**42.59 ± 12.8** b
	(58.25 - 79.05)	(25.72 - 52.27)	(23.24 - 62.69)
Al^{3+} (meq 100 g^{-1})	**13.42 ± 1.4** a	**13.71 ± 1.7** a	**7.38 ± 5.9** b
	(10.90 - 16.20)	(11.00 - 16.80)	(0.00 - 16.70)
H^+ (meq 100 g^{-1})	**7.10 ± 2.4** a	**6.90 ± 3.5** a	**6.60 ± 6.7** a
	(1.15 - 9.50)	(2.15 - 12.95)	(0.30 - 18.60)
CEC (meq 100 g^{-1})	**257.9 ± 22.4** a	**181.6 ± 30.9** b	**202.4 ± 79.3** b
	(207.4 - 291.3)	(121.6 - 218.6)	(89.0 - 391.1)
Base saturation (%)	**92.0 ± 1.6** a b	**88.5 ± 2.5** a	**93.2 ± 4.9** b
	(89.4 - 95.1)	(84.1 - 92.4)	(87.2 - 99.9)
SO_4-S (%)	**1.34 ± 0.2** a	**1.13 ± 0.1** a b	**0.93 ± 0.4** b
	(1.06 - 1.65)	(0.86 - 1.28)	(0.15 - 1.31)

Table 3.2 The mean values (with standard deviation) of soil chemical properties (n = 5) from surface soils (0 - 10 cm) of six Regeneration Plots (RP1 - RP6) on Amutu Besar Island (Site 1) and Amutu Kecil Island (Site 2) in Bintuni Bay. Means within a row followed by the same letters are not significantly different (Nested ANOVA, $p \leq 0.05$; multiple comparisons by Tukey-test). Ranges are given in parentheses.

	Site 1			Site 2		
	RP1	**RP2**	**RP3**	**RP4**	**RP5**	**RP6**
pH$_{(H_2O)}$	**2.8 ± 0.2** a (2.5 - 3.1)	**2.8 ± 0.2** a (2.5 - 3.1)	**3.3 ± 0.5** a (2.7 - 4.2)	**3.5 ± 0.1** a (3.3 - 3.7)	**4.3 ± 0.8** ab (3.0 - 5.5)	**4.6 ± 0.3** b (4.1 - 5.1)
pH$_{(CaCl_2)}$	**3.2 ± 0.3** a (2.7 - 3.7)	**3.0 ± 0.1** a (2.8 - 3.2)	**3.6 ± 0.5** a (3.1 - 4.5)	**3.7 ± 0.1** a (3.5 - 3.9)	**4.4 ± 0.8** ab (3.2 - 5.5)	**4.6 ± 0.1** b (4.4 - 4.8)
LOI (%)	**41.8 ± 0.1** a (41.7 - 42.0)	**46.6 ± 0.1** a (46.4 - 46.8)	**55.0 ± 6.7** b (45.9 - 65.6)	**22.7 ± 0.1** a (22.5 - 22.9)	**24.9 ± 4.9** a (17.6 - 32.6)	**22.3 ± 0.1** a (22.2 - 22.4)
EC (dS m^{-1})	**5.0 ± 0.1** a (4.8 - 5.2)	**4.8 ± 0.1** a b (4.7 - 4.9)	**4.6 ± 0.2** b (4.3 - 4.9)	**4.3 ± 0.4** a (3.7 - 4.9)	**3.7 ± 0.4** a (3.3 - 4.2)	**3.6 ± 0.3** a (3.1 - 4.1)
Total N (%)	**0.90 ± 0.02** a (0.87 - 0.93)	**0.89 ± 0.0** a (0.89 - 0.90)	**0.91 ± 0.2** a (0.55 - 1.10)	**0.72 ± 0.04** a (0.66 - 0.78)	**0.60 ± 0.1** a (0.44 - 0.77)	**1.01 ± 0.01** b (1.00 - 1.02)
Total P (%)	**0.037 ± 0.0002** a (0.034 - 0.040)	**0.043 ± 0.0002** b (0.040 - 0.045)	**0.038 ± 0.0004** a b (0.030 - 0.043)	**0.053 ± 0.0002** a (0.050 - 0.056)	**0.062 ± 0.0009** b (0.048 - .0.075)	**0.080 ± 0.0001** b (0.078 - 0.082)
K^+ (meq 100 g^{-1})	**1.13 ± 0.03** a (1.09 - 1.17)	**1.31 ± 0.1** a (1.19 - 1.43)	**2.58 ± 0.6** b (1.90 - 3.49)	**1.90 ± 0.03** a (1.85 - 1.95)	**1.77 ± 0.2** a (1.43 - 2.10)	**2.61 ± 0.1** b (2.41 - 2.81)
Na^+ (meq 100 g^{-1})	**197.9 ± 5.4** a (190.0 - 205.8)	**98.1 ± 1.1** b (96.0 - 99.0)	**152.9 ± 38.2** c (109.0 - 220.8)	**162.0 ± 1.4** a (160.1 - 164.1)	**66.6 ± 18.5** b (37.5 - 95.8)	**50.5 ± 0.3** b (50.0 - 51.1)
ESP (%)	**67.58 ± 0.7** a (66.67 - 68.39)	**49.27 ± 0.4** b (48.48 - 49.71)	**57.58 ± 5.8** c (50.68 - 67.66)	**80.28 ± 0.2** a (79.93 - 80.44)	**56.83 ± 3.1** b (51.01 - 59.96)	**56.80 0.2** b (57.06 - 56.62)
Ca^{2+} (meq 100 g^{-1})	**15.26 ± 0.03** a (15.22 - 15.30)	**15.96 ± 0.03** a (15.92 - 16.00)	**18.78 ± 1.8** b (15.67 - 21.39)	**8.53 ± 0.1** a (8.40 - 8.65)	**10.70 ± 1.2** b (8.35 - 11.84)	**8.63 ± 0.1** a (8.45 - 8.75)
Mg^{2+} (meq 100 g^{-1})	**54.05 ± 0.05** a (53.99 - 54.10)	**59.87 ± 0.01** a b (59.85 - 59.89)	**72.73 ± 8.6** b (61.69 - 87.50)	**27.35 ± 0.1** a (27.15 - 27.55)	**29.74 ± 4.5** a (22.58 - 36.89)	**26.35 ± 0.2** a (26.1 - 26.56)
H^+ (meq 100 g^{-1})	**20.08 ± 1.4** a (18.00 - 22.00)	**19.49 ± 0.7** a (18.45 - 20.55)	**12.55 ± 6.4** a (1.50 - 20.85)	**2.12 ± 0.1** ab (1.95 - 2.35)	**5.88 ± 3.5** a (0.35 - 11.40)	**0.81 ± 0.1** b (0.74 - 0.95)
Al^{3+} (meq 100 g^{-1})	**4.40 ± 0.3** a (4.00 - 4.80)	**4.40 ± 0.3** a (4.00 - 4.80)	**2.58 ± 2.4** a (0.00 - 6.20)	**0.03 ± 0.04** a (0.00 - 0.10)	**1.20 ± 0.8** b (0.00 - 2.40)	**0.03 ± 0.04** a (0.00 - 0.10)
CEC (meq 100 g^{-1})	**292.8 ± 5.7** a (283.7 - 301.5)	**199.2 ± 0.7** b (198.0 - 200.0)	**262.1 ± 39.3** a (204.2 - 326.3)	**202.0 ± 1.3** a (200.3 - 204.0)	**115.9 ± 27.4** b (73.5 - 159.8)	**89.0 ± 0.4** b (88.3 - 89.5)
Base Saturation (%)	**91.6 ± 0.5** a b (90.8 - 92.3)	**88.0 ± 0.4** a (87.4 - 88.5)	**94.2 ± 3.3** b (89.1 - 99.4)	**98.9 ± 0.1** ac (98.8 - 99.0)	**94.5 ± 2.7** b (91.4 - 99.5)	**99.1 ± 0.1** c (98.9 - 99.1)
SO_4-S (%)	**1.23 ± 0.1** a (1.06 - 1.40)	**1.16 ± 0.1** a (1.00- 1.32)	**1.28 ± 0.2** a (0.97 - 1.49)	**0.59 ± 0.1** a (0.49 - 0.70)	**0.62 ± 0.3** a (0.17 - 1.08)	**0.39 ± 0.0** a (0.39 - 0.40)

Soil pHs in FP1 - 3 (mean pH H_2O 3.0, mean pH $CaCl_2$ 3.0) and in RP1 - 3 (mean pH H_2O 3.0, mean pH $CaCl_2$ 3.3) were very low, while RP4-6 were less acid (mean pH H_2O 4.1, mean pH $CaCl_2$ 4.2). There was no significant difference between the pH values measured in deionised water and calcium chloride probably because most of the samples were moderately saline. The pH of the additional samples collected on 7 October 1996 was higher (mean pH H_2O for FP1-3 was 4.9, mean pH $CaCl_2$ was 5.3).

The highest value of EC was 6.4 $dS.m^{-1}$ (FP1) and the lowest value was 3.1 $dS.m^{-1}$ (RP6). There was no significant difference among the values from the FPs, and values from RP4 - 6 were always lower than the values from RP1 - 3. Loss-on-ignition (LOI) had a wide range from 17.2 % to 65.6 %. Among the floristic plots, FP1 was significantly higher than FP2 and FP3, while among the regeneration plots, RP3 was significantly higher than RP1 and RP2.

Total nitrogen and phosphorus were also markedly different among plots of the floristic and regeneration study sites, except that plots RP1-3 did not show any differences in nitrogen concentrations among themselves.

Exchangeable cations were dominated by Na^+, followed by Mg^{2+}, Ca^{2+} and K^+. The Na^+ value was significantly different among the RP plots and ranged from 50.5 meq. 100 g^{-1} (RP6) to 198 meq. 100 g^{-1} (RP1). Exchangeable Al^{3+} was high in FP1-3 and was significantly different among the three plots. The highest value (16.8 meq.100 g^{-1}) was found in FP2 while in FP3 Al^{3+} was not detectable from some of the samples. Soil samples from RP4-6 had substantially lower values of Al^{3+} than the samples from RP1-3.

Soil sulphate-sulphur was high in all soil samples. The value was only slightly different among the floristic plots. In the regeneration plots even though there was no significantly different value among the plots within the site, the values from Amutu Kecil Island were always much lower than the values from Amutu Besar Island.

The correlation coefficients proved that there are close relationships between some of the soil properties (Table 3.3). The pH, SO_4-S, LOI and Al^{3+} of the samples from FP1-3 and RP4-6 were mostly significantly correlated. The pH was always negatively correlated with the rest, while SO_4-S was positively correlated with LOI and Al^{3+}. Conversely, in RP1-3, LOI was positively correlated with pH and negatively correlated with Al^{3+}.

3.5 Discussion

In general the soils are *Potential Acid Sulphate soils* (Soil Survey Staff 1975) which are commonly found in mangroves. These soils always have at least 0.75 % of their dry weight as sulphur in the form of sulphides and have less than 2.25% $CaCO_3$. In terms of soil salinity and sodicity most of the samples belong to the *saline sodic soils* (U.S. Salinity Laboratory Staff 1954), which are characterised by an EC of more than 4 $dS.m^{-1}$ and an ESP more than 15 %. Only plots RP5 and RP6 had EC values slightly lower than 4 $dS.m^{-1}$.

Table 3.3 Matrix of correlation coefficients among some soil properties of Bintuni Bay.

		pH	SO_4-S	Al^{3+}
FP1-3				
	SO_4-S	-0.82**		
	Al^{3+}	-0.96**	0.79**	
	LOI	-0.81**	0.82**	0.75**
RP1-3				
	SO_4-S	-0.17		
	Al^{3+}	-0.77**	0.26	
	LOI	0.78**	0.22	-0.85**
RP4-6				
	SO_4-S	-0.77**		
	Al^{3+}	-0.22	0.70**	
	LOI	-0.59*	0.90**	0.79**

Note : * $P \leq 0.05$, ** $P \leq 0.01$

In all the Bintuni Bay samples the pH value was less than or occasionally slightly higher than 4. The higher pH in the moist samples from FP1-3 agrees with previous workers who have air-dried soils before analysis (Aksornkoae *et al.* 1991, Hesse 1961 and Marius 1982) even though in a few cases (Naidoo & Raiman 1982, Higashi & Shinagawa 1985) (Table 3.4) there was only a little change of pH after drying.

The low pH is almost certainly caused by the production of sulphuric acid by the oxidation of reduced sulphur compounds. Dent (1986) explained that drainage or air-drying allows oxygen to enter the soil and pyrite is then oxidised, generating sulphuric acid. The reaction of pyrite with oxygen is a slow process, but pyrite is rapidly oxidised by iron III. Iron III is thereby reduced to iron II, but iron III is regenerated from iron II by the bacterium *Thiobacillus ferrooxidans.* This catalytic oxidation of pyrite can take place only at pH less than 4, because iron III is soluble only under these acid conditions. Possibly another group of sulphur-oxidising bacteria may be involved in the initial acidification of the system. The process was summarized by Breemen (1972) (Fig. 3.1).

Aluminium was found to be high, especially in the Floristic Plots, compared with the results of the samples from Thailand (Aksornkoae *et al.* 1991) and South Africa (Hesse 1961) which were analysed when fresh. The acidity of the soil samples was likely to have been responsible for the increased solubility of aluminium. Martin (1986) stated that Al^{3+} is insoluble at a pH value above about 4, but is increasingly soluble at lower pH values. Al^{3+} was always found

Table 3.4 Surface soil samples analysis from a range of mangrove forests.

	Asia				Africa			Australia
	Thailand	India	Japan	Indonesia	S.Africa	Sierra Leone	Senegal	Queensland
	1	2	3	4	5	6	7	8
Depth (cm)	0 - 15	0 - 15	0 - 10	0 - 50	0 - 25	0 - 20	0 - 20	0 - 5
pH $_{(H_2O)}$ (fresh)	7.0	7.5	7.7	7.6	6.2	6.6	6.9	6.2 to 7.0
pH $_{(H_2O)}$ (air-dried)	4.1		7.2		6.3	4.6	3.4	
LOI (%)	14.95			62.1	2.5			
C (%)		0.62	22.3	31.5		11.9	47.8	7.99
EC (dS m^{-1})		4.7	4.5		10			
Total N (%)		0.069	1.22	1.26		0.44	2	0.26
C / N		8.98	18.28	25		36	23.9	30.73
Total P (%)	0.0018					0.151		0.042
K$^+$ (meq 100g^{-1})	0.68	0.68	0.60	6.40	3			
Na$^+$ (meq 100g^{-1})	19.56	8.34	16.70	149.30	45			
ESP (%)	59.73				75			
Ca^{2+} (meq 100g^{-1})	4.00	10.81	4.10	68.80	5			
Mg^{2+} (meq 100g^{-1})	8.50	8.02	4.20	69.50	7			
Al^{3+} (meq 100g^{-1})	0.98				0.28			
CEC (meq 100g^{-1})	21.75			292.4	60			
SO$_4$-S (%)	0.063		1.84		2	0.42	3.1	

Note :
1. Aksornkoae *et al* (1991), Muang District, Ranong.
2. Sah *et al* (1985), Prentice Island, south-west Sunderbans.
3. Higashi & Shinagawa (1985), sandy soil (94%), Ishigaki, Okinawa .
4. Kartawinata & Waluyo (1977), clayey-silt, Jakarta Bay.
5. Naidoo & Raiman (1982), sandy soil (60%), Durban , South Africa.
6. Hesse (1961), fibrous mud under *Rhizophora*, Freetown, Sierra Leone.
7. Marius (1982), clayey (70%), Casamance, Senegal.
8. Boto & Wellington (1984), well-sorted silt with clay (15 - 20%), Hinchinbrook Island, Queensland, Australia.

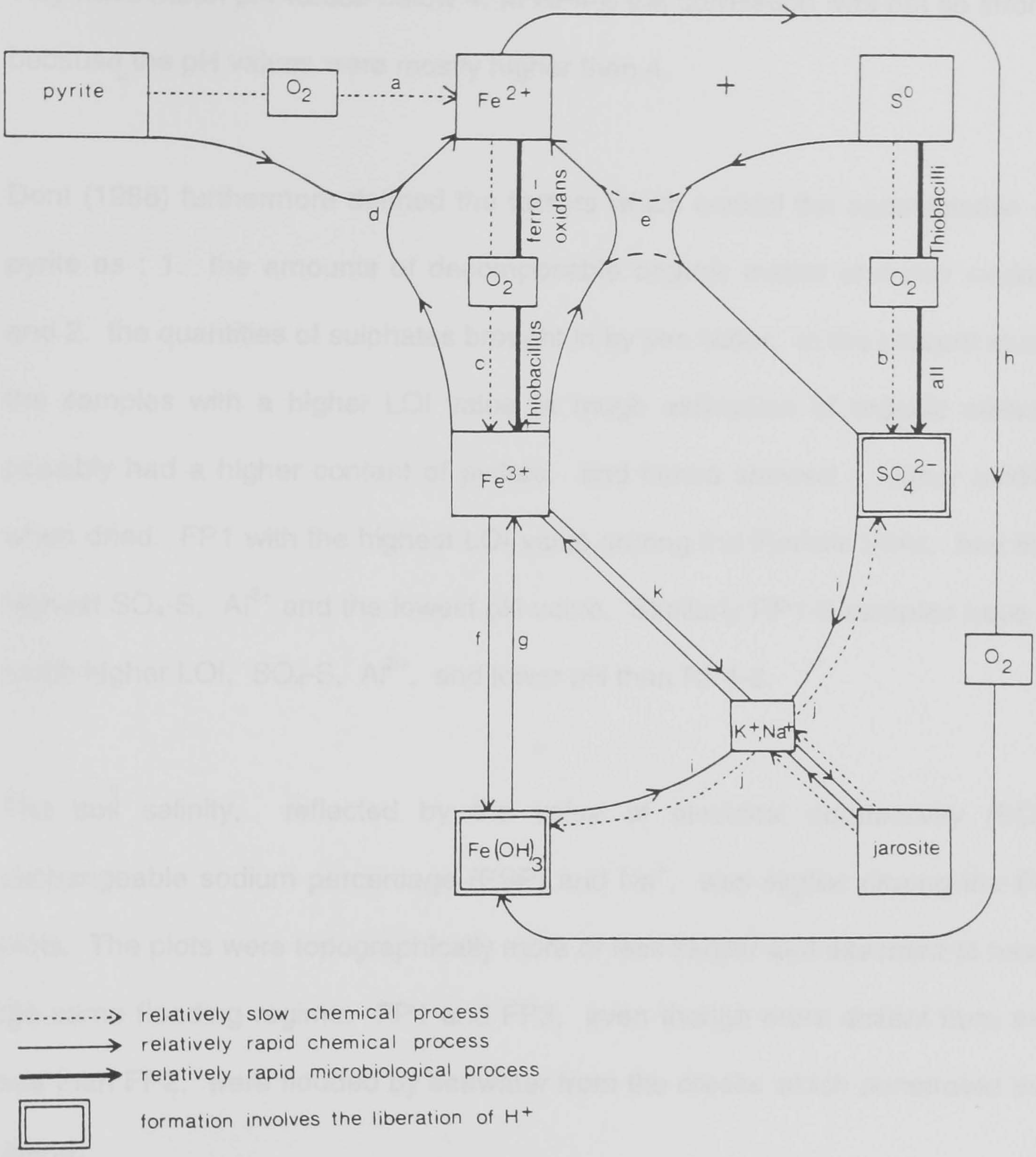


Fig. 3.1 Pyrite oxidation pathway (after Breemen 1972)

significantly negatively-correlated with pH in FP1-3 and RP1-3 (Table 3.3) since they have mean pH values below 4. In RP4-6 the correlation was not so strong because the pH values were mostly higher than 4.

Dent (1986) furthermore defined the factors which control the accumulation of pyrite as : 1. the amounts of decomposable organic matter and iron oxides, and 2. the quantities of sulphates brought in by sea water. In the present study the samples with a higher LOI value (a rough estimation of organic matter) possibly had a higher content of pyrites, and hence showed a higher acidity when dried. FP1 with the highest LOI value among the Floristic Plots, had the highest SO_4-S, Al^{3+} and the lowest pH value. Similarly RP1-3 samples have a much higher LOI, SO_4-S, Al^{3+}, and lower pH than RP4-6.

The soil salinity, reflected by the value of electrical conductivity (EC), exchangeable sodium percentage (ESP) and Na^+, was similar among the FP plots. The plots were topographically more or less similar and assumed to have the same flooding regime. FP1 and FP3, even though more distant from the sea than FP2, were flooded by seawater from the creeks which penetrated the island.

There were very few significant within-plot variations but most factors varied significantly among plots. In floristic plots, the most important between-plot differences are for pHH2O and pHCaCl2 which were both about one unit higher in FP3 than in the other two plots, and exchangeable potassium which was nearly twice as high in FP1 as in FP2 and FP3. However, the soil properties did not vary in a patterned way across the plots and this was expected because the plots were chosen to have homogenous vegetation.

IV FOREST STRUCTURE AND COMPOSITION

4.1 Introduction

A distinctive character of mangrove forest is its low species richness (Tomlinson 1994). However, since the architecture of the forests is influenced by the magnitudes and periodicities of tides, nutrients, and stresses such as hurricanes, drought and salt accumulation, and because the action of these factors varies widely over geographic regions, mangrove stands exhibit wide regional and local variations in structural characteristics. High structural variation is associated with high species richness. Where species diversity is high, structural variation is greater (Cintron & Novelli 1984).

Tomlinson (1994) recognised three elements of mangrove vascular plant species: (a) major, (b) minor and (c) mangrove associates. Major elements are recognised have all or most of the following features:

1. Fidelity to the mangrove environment and not extending into other terrestrial communities.
2. A major role in the mangrove structure and the ability to form a pure stand.
3. Morphological specialisation such as aerial roots and vivipary of the embryo.
4. Some physiological mechanism for salt tolerance. They frequently visibly excrete salt.

5. Taxonomic separation from their relatives at least at the generic level and often at the subfamily or family level.

The minor element species are not conspicuous but occupy peripheral habitats and only rarely form pure communities. Their taxonomic isolation is mostly at the generic level. The mangrove associates are never inhabitants of strict mangrove communities and occur only in transitional vegetation.

Zonation, often into monospecific stands, is typical in mangroves. This phenomenon is sometimes used to explain a succession process since the zonation in space is often accepted as matching a zonation in time (Lugo 1980).

4.2 Methods

Within each 10 m x 10 m subplot of FP1-3 and FT1-3, all trees with dbh (diameter breast height at 1.3 m) ≥ 10 cm were tagged, measured (diameter and height), and identified to species.

Since mangrove trees have a unique shape and growth form which sometimes creates difficulties in deciding where to measure the diameter, a recommendation by Cintron & Novelli (1984) was applied:

1. When a stem forks below breast height, or sprouts from a single base close to the ground (1.3 m), each branch (dbh ≥ 10 cm) will be measured as a separate stem,

2. When the stem forks at breast height or slightly above, the diameter will be measured at breast height or just below the swelling caused by the fork,
3. When the stem has prop roots or a fluted lower trunk, the diameter will be measured at 30 cm above the highest protrusion,
4. When the stem has swellings, branches or abnormalities at the point of measurement, the diameter will be taken 30 cm above or below the irregularity where it stops affecting normal form.

The number of saplings (dbh 2 - < 10 cm) in each 10 m x 10 m subplot was recorded in one 5 m x 5 m quadrat, and the number of seedlings (stem diameter < 2 cm, just above the tip of the hypocotyl) in one 1 m x 1 m quadrat. The quadrats were placed in the south-east corner of each subplot. They are treated here as statistically independent samples.

The physiognomy of the sites was represented by a series of profile diagrams, each with a size of 10 m x 40 m. Each tree and sapling species present in these representative plots were plotted for their position and measured for dbh, height (bole and total height) and canopy width. The height of the highest spring tide was measured.

4.3 Data analysis

For each tree species in the 10 m x 10 m plots along the FT1-3 and in the FP1-3, the following were calculated according to Mueller-Dombois & Ellenberg (1974) :

Relative Density (RD) = 100 (ni/N) and Relative Dominance (RDo) = 100 (BAi/BA), where ni = the number of individuals of the species i, N = total number of individuals, BAi = basal area of the species i, and BA = total basal area.

The Cover Value Index (CVI), a measure of the relative importance of a species within the community of each site (Curtis, 1959), was calculated by summing the percentage of relative density and relative dominance.

Complexity Index (CI) (Holdridge *et al.* 1971), an expression of the diversity and abundance within forest communities, was calculated as one integrative measure that combines floral characteristics: number of species (S), density of individuals with DBH >10 cm (D), basal area (BA), and stand height (H). The index results in a quantitative description of the structural complexity of a vegetation community. The index was computed for a 0.1 ha basis as the product of S x D x BA x H x 10^{-3}.

The species diversity was measured using Simpson and Shannon-Wiener Indices (Brower & Zar 1977) :

$Ds = 1 - [\, ni\,(ni - 1) / N\,(N - 1)\,]$ $\quad$ $H' = \text{Log}\, N - 1/N \sum ni \log ni$

where

Ds = Simpson Index of Diversity

H' = Shannon Index of Diversity

ni = number of individuals of species i

N = total number of individuals

The evenness, a measure of the equitability of abundance of species, was derived using H':

$J' = H' / H'_{max}$, where

J' = the evenness

$H'_{max} = H' / \text{Ln no. of species}$

A one-way ANOVA and a correlation analysis were used to compare the mean diversity values among the study sites and species.

4.4 Results

4.4.1 Species composition

There were nine species of trees from six genera recorded from floristic plots (FP1-3) and floristic transects (FT1-3). However, there were at least another 21 species which appeared outside either the floristic plots or floristic transects (Appendix 1, Plate 4A, 6, 7, 8) but which did not occur in the samples.

The species density distribution of trees, saplings and seedlings in the floristic plots (FP1-3) and floristic transects (FT1-3) are compared in Figs. 4.1 and 4.2. In the trees category, *Rhizophora apiculata* BL. had by far the highest density in both floristic plots and floristic transects, followed by *Bruguiera gymnorrhiza* (L.) Lamk. and *Ceriops decandra* (Griff.) Ding Hou. The two last species often equalled or exceeded *Rhizophora apiculata* numbers in the sapling and seedling categories.

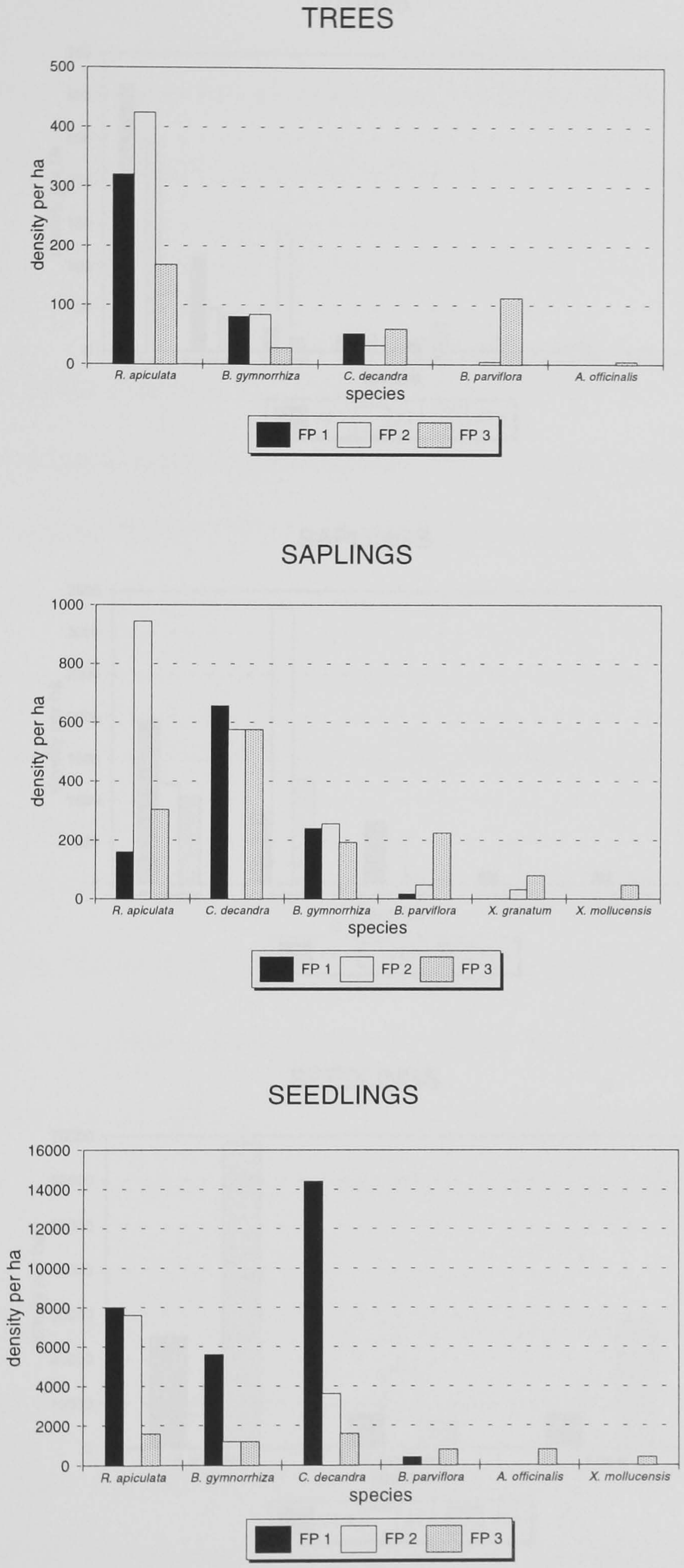


Fig. 4.1 Density distribution of all tree, sapling and seedling species in the floristic plots (FP1-3) on Sikoroti Island, Bintuni Bay.

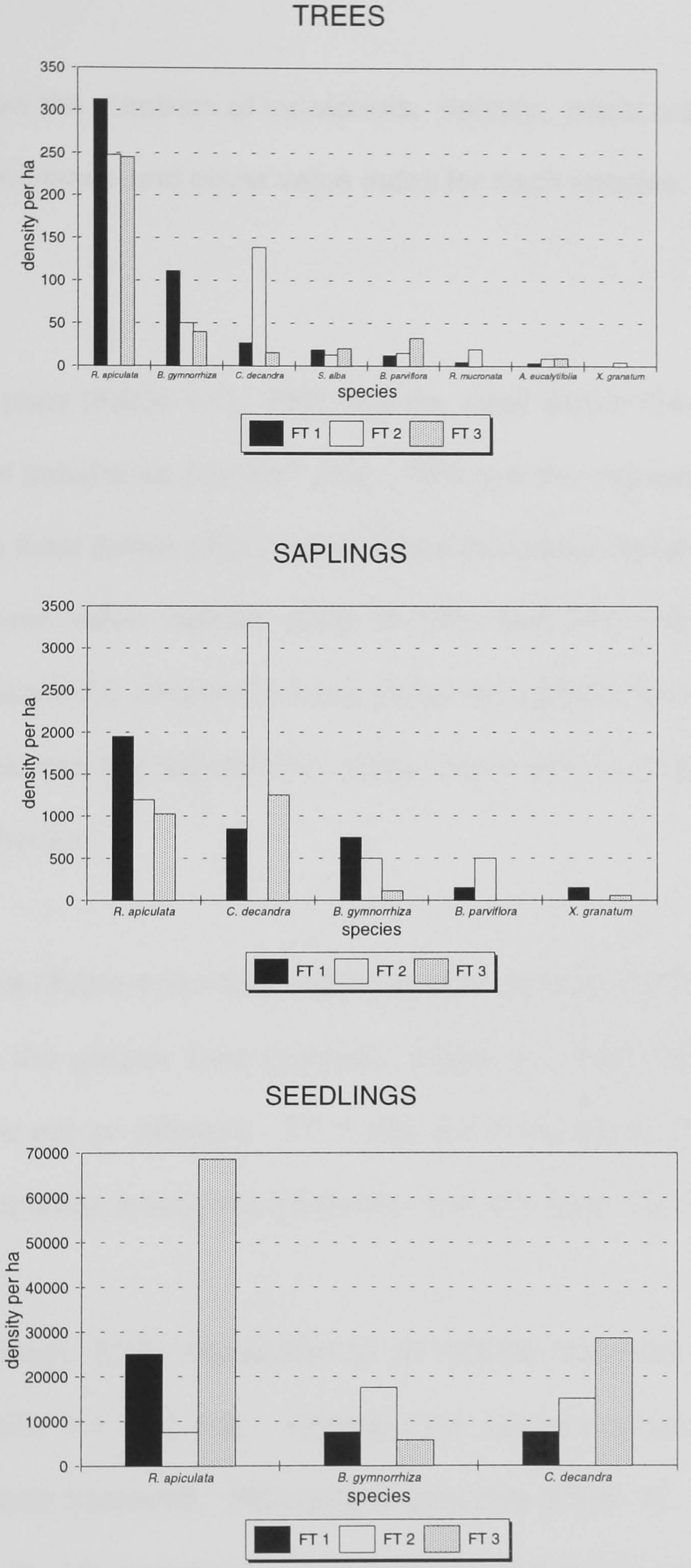


Fig. 4.2 Density distribution of all tree, sapling and seedling species in the floristic transects (FT1-3) on Sikoroti Island, Bintuni Bay.

Tables 4.1 - 4.6 show the numbers of individuals, density, basal area, relative density, relative dominance and cover value index for each species.

4.4.1.1 Trees

Among the floristic plots (Table 4.1), FP2 was the most dense (544 / ha) and had the highest total basal area (36.9 m^2 / ha). FP3 was the highest in species number (5), but the least dense (372 / ha) and had the lowest basal area (28.3 m^2 / ha). The cover value indices (CVI) of FP1 and FP2 had a similar distribution with *Rhizophora apiculata* having by far the highest value. In FP3, *Rhizophora apiculata* had the highest CVI value, but it did not greatly exceed those of the other species.

The floristic transects (Table 4.2) had a higher species number than the floristic plots which reflects the greater area sampled. However, their mean density and basal area were not so different. FT 2 was the most dense and had the highest number of species among the transects, but the least basal area.

The cover value indices (CVI) distribution in all floristic transects showed a similar pattern (Tables 4.1 and 4.2), although the species-composition was different among floristic transects. *Rhizophora apiculata* (Plate 1), had by far the highest value in all transects, followed by *Bruguiera gymnorrhiza, Sonneratia alba* J. Smith or *Ceriops decandra* (Plate 2) and less abundant species. *Sonneratia alba* had a high CVI in FT1 and FT3 because of a few

Table 4.1 Species of trees (trunk diameter ≥ 10cm) occurring in the 50 m x 50 m floristic plots in Sikoroti Island, with density (D), total basal area per ha (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI).

Species	D (ha^{-1})	BA (m2)	RD (%)	RDo (%)	CVI (%)
FP 1					
Rhizophora apiculata	320	26.0	70.8	80.3	151.1
Bruguiera gymnorrhiza	80	5.7	17.7	17.6	35.3
Ceriops decandra	52	0.7	11.5	2.1	13.6
FP 2					
Rhizophora apiculata	424	32.2	77.9	87.3	165.7
Bruguiera gymnorrhiza	84	4.0	15.4	10.8	26.2
Ceriops decandra	32	0.6	5.9	1.7	7.6
Bruguiera parviflora	4	0.1	0.7	0.3	1.0
FP 3					
Rhizophora apiculata	168	15.2	45.2	54.0	99.2
Bruguiera parviflora	112	5.8	30.1	20.6	50.7
Ceriops decandra	60	3.0	16.1	10.5	26.7
Bruguiera gymnorrhiza	28	3.4	7.5	11.9	19.4
Avicennia alba	4	0.9	1.1	3.0	4.1

Table 4.2 Species of trees (trunk diameter ≥ 10 cm) occurring in the floristic transects across Sikoroti Island, with density (D), basal area per ha (BA), relative density (RD), relative dominance (RDo) and cover value index (CVI).

Species	D (ha^{-1})	BA (m2)	RD (%)	Rdo (%)	CVI (%)
FT1					
Rhizophora apiculata	312.2	27.5	63.9	75.3	139.1
Bruguiera gymnorrhiza	111.1	5.4	22.7	14.9	37.7
Sonneratia alba	18.9	2.3	3.8	6.3	10.2
Ceriops decandra	26.7	0.6	5.5	1.7	7.2
Bruguiera parviflora	12.2	0.2	2.5	0.6	3.1
Rhizophora mucronata	4.4	0.3	0.9	0.9	1.8
Avicennia eucalyptifolia	3.3	0.1	0.7	0.4	1.1
FT2					
Rhizophora apiculata	247.8	17.6	49.8	65.2	114.9
Ceriops decandra	139.1	4.8	28.0	17.8	45.7
Bruguiera gymnorrhiza	50.0	2.2	10.0	8.1	18.1
Rhizophora mucronata	19.6	0.4	3.9	1.6	5.5
Avicennia eucalyptifolia	8.7	0.9	1.8	3.3	5.1
Bruguiera parviflora	15.2	0.5	3.1	1.9	5.0
Sonneratia alba	13.0	0.6	2.6	0.9	3.6
Xylocarpus granatum	4.4	0.3	0.9	1.2	2.1
FT3					
Rhizophora apiculata	244.9	16.1	67.6	56.8	124.4
Sonneratia alba	20.4	7.2	5.6	25.5	31.1
Bruguiera gymnorrhiza	39.8	3.1	11.0	10.9	21.8
Bruguiera parviflora	32.7	1.2	9.0	4.4	13.4
Ceriops decandra	15.3	0.5	4.2	1.7	5.9
Avicennia eucalyptifolia	9.2	0.2	2.5	0.8	3.4

Plate 1 *Rhizophora apiculata*: **A** young stand, **B** mature stand, mixed with *Bruguiera gymnorrhiza*.

Plate 2 Mangrove vivipary hypocotyles: **A** *Bruguiera gymnorrhiza* , **B** *Ceriops decandra*.

large trees. Other species had a more consistent relationship between density and basal area.

FP2 had the highest complexity index (22.5) among the floristic plots (Table 4.9), followed by FP3 (17.0) and FP1 (14.1). In the floristic transects the indices were ranked: FT1 (32.7) > FT2 (27.4) > FT3 (15.0).

Tables 4.7 and 4.8 show the values of Simpson and Shannon-Wiener's diversity indices among the floristic plots and floristic transects. FP3 was the most diverse. Among the transects FT3 was the least diverse. For trees, FT2 was the most diverse (Ds = 2.97, H' = 1.37) and the highest in evenness (J' = 1.52). FT1 was the most diverse and the highest in evenness in the sapling category and FT2 for the seedlings.

4.4.1.2 Saplings and seedlings

Sapling density was much higher than tree density (Tables 4.3 and 4.4). The species composition was similar to that of the trees, except for the absence of *Avicennia* and *Sonneratia* and presence of two new species of *Xylocarpus*. *Rhizophora apiculata* was still dominant, but in some places it was replaced by *Ceriops decandra*.

Among the floristic plots, FP1 had the highest seedling density and FP3 the least (Tables 4.5 and 4.6). FT3 was very dense compared with FT1 and FT2. *Rhizophora apiculata, Bruguiera gymnorrhiza* and *Ceriops decandra* were

Table 4.3 Species of saplings (stem diameter ≥ 2 cm <10 cm) occurring in 25 subplots of 5 m x 5 m within the 50 m x 50 m floristic plots on Sikoroti Island, with density (D), relative density (RD), relative dominance (RDo) and cover value index (CVI).

Species	**D** (**ha^{-1}**)	**RD** (%)	**RDo** (%)	**CVI** (%)
FP 1				
Ceriops decandra	656	61.2	63.8	124.4
Bruguiera gymnorrhiza	240	22.4	26.3	48.7
Rhizophora apiculata	160	14.9	10.1	25.0
Bruguiera parviflora	16	1.5	0.5	2.0
FP 2				
Rhizophora apiculata	944	50.9	45.2	96.1
Ceriops decandra	576	31.0	30.0	61.1
Bruguiera gymnorrhiza	256	13.8	22.7	36.5
Bruguiera parviflora	48	2.6	1.5	4.1
Xylocarpus granatum	32	1.7	0.5	2.3
FP 3				
Ceriops decandra	576	40.5	31.6	72.0
Rhizophora apiculata	304	21.4	22.0	43.4
Bruguiera gymnorrhiza	192	13.5	22.4	35.9
Bruguiera parviflora	224	15.7	16.1	31.9
Xylocarpus mekongensis	48	3.4	5.4	8.7
Xylocarpus granatum	80	5.6	2.5	8.1

Table 4.4 Species of saplings (stem diameter ≥ 2 cm <10 cm) occurring in the floristic transects across Sikoroti Island, with density (D), relative density (RD), relative frequency (RF) and cover value index (CVI).

Species	**D** (**ha^{-1}**)	**RD** (%)	**RF** (%)	**CVI** (%)
FT1				
Rhizophora apiculata	1950	50.7	27.3	77.9
Ceriops decandra	850	22.1	27.3	49.4
Bruguiera gymnorrhiza	750	19.5	27.3	46.8
Xylocarpus granatum	150	3.9	13.6	17.5
Bruguiera parviflora	150	3.9	4.6	8.4
FT2				
Ceriops decandra	3300	60.0	36.4	96.4
Rhizophora apiculata	1200	21.8	27.3	49.1
Bruguiera gymnorrhiza	500	9.1	27.3	36.4
Bruguiera parviflora	500	9.1	9.1	18.2
FT3				
Rhizophora apiculata	1029	41.9	40.0	81.9
Bruguiera gymnorrhiza	114	4.7	20.0	24.7
Ceriops decandra	1257	51.2	30.0	81.2
Xylocarpus granatum	57	2.3	10.0	12.3

Table 4.5 Species of seedlings occurring in 25 quadrats of 1 m x 1 m within the 50 m x 50 m floristic plots on Sikoroti Island, with density (D), relative density (RD), relative frequency (RF) and cover value index (CVI).

Species	D (ha^{-1})	RD (%)	RF (%)	CVI (%)
FP 1				
Ceriops decandra	14400	50.7	38.9	89.6
Rhizophora apiculata	8000	28.2	33.3	61.5
Bruguiera gymnorrhiza	5600	19.7	25.0	44.7
Bruguiera parviflora	400	1.4	2.8	4.2
FP 2				
Rhizophora apiculata	7600	61.3	55.0	116.3
Ceriops decandra	3600	29.0	30.0	59.0
Bruguiera gymnorrhiza	1200	9.7	15.0	24.7
FP 3				
Rhizophora apiculata	1600	25.0	33.3	58.3
Bruguiera gymnorrhiza	1200	18.8	25.0	43.8
Ceriops decandra	1600	25.0	8.3	33.3
Avicennia alba	800	12.5	16.7	29.2
Bruguiera parviflora	800	12.5	8.3	20.8
Xylocarpus mekongensis	400	6.3	8.3	14.6

Table 4.6 Species of seedlings occurring in the floristic transects across Siko-roti Island, with density (D), relative density (RD), relative frequency (RF) and cover value index (CVI).

Species	D (ha^{-1})	RD (%)	RF (%)	CVI (%)
FT1				
Rhizophora apiculata	25000	62.5	63.6	126.1
Bruguiera gymnorrhiza	7500	18.8	18.2	36.9
Ceriops decandra	7500	18.8	18.2	36.9
FT2				
Rhizophora apiculata	7500	18.8	42.9	61.6
Bruguiera gymnorrhiza	17500	43.8	28.6	72.3
Ceriops decandra	15000	37.5	28.6	66.1
FT3				
Rhizophora apiculata	68544	66.7	54.6	121.2
Bruguiera gymnorrhiza	5712	5.6	27.3	32.8
Ceriops decandra	28560	27.8	18.2	46.0

Table 4.7 Diversity indices of Simpson (Ds) and Shannon-Wiener (H′), and the evenness (J′) of mangrove trees, saplings and seedlings in the floristic plots on Sikoroti Island, Bintuni Bay.

	Ds	H′	J′
Trees			
FP1	1.81	0.78	1.64
FP2	1.58	0.69	1.14
FP3	3.13	1.26	1.80
Saplings			
FP1	2.27	0.98	1.63
FP2	2.71	1.14	1.64
FP3	4.03	1.53	1.97
Seedlings			
FP1	2.73	1.08	1.80
FP2	2.21	0.89	1.47
FP3	7.06	1.70	2.18

Table 4.8 Diversity indices of Simpson (Ds) and Shannon-Wiener (H′), and the evenness (J′) of mangrove trees, saplings and seedlings in floristic transects on Sikoroti Island, Bintuni Bay.

	Ds	H′	J′
Trees			
FT1	2.16	1.08	1.27
FT2	2.97	1.37	1.52
FT3	2.08	1.11	1.43
Saplings			
FT1	2.96	1.25	1.79
FT2	2.42	1.07	1.79
FT3	2.35	0.94	1.56
Seedlings			
FT1	2.26	0.92	1.93
FT2	3.08	1.04	2.19
FT3	1.93	0.79	1.65

dominant amongst the seedlings. As for the saplings, there was no *Sonneratia,* but *Avicennia* seedlings occurred in FP3.

4.4.2 Forest structure

4.4.2.1 Zonation

Figs. 4.3 - 4.5 show a typical mangrove zonation on Sikoroti Island. The profile was drawn on the floristic transects (Fig. 2.9). *Sonneratia alba* and *Avicennia eucalyptifolia* (Zipp. ex Miq.) Moldenke occupied the first zone (Fig. 4.3A), and normally consist of even-sized plants. In mature forest *Sonneratia alba* trees had a dbh up to 125 cm and 40 m height (Plate 3). Young *Sonneratia* and *Avicennia* are normally found as pure stands elsewhere, and occupy newly created mud flats as a pioneer species. Both species have dense pneumatophores.

The second zone inland (Fig. 4.3B) was mostly dominated by younger *Rhizophora apiculata,* and sometimes by *Rhizopora mucronata* Lamk. and occasional *Ceriops sp.* This zone is followed by third zone (Fig. 4.4A), which is dominated by *Rhizophora apiculata* with occasional *Bruguiera gymnorrhiza* and *Ceriops decandra.*

The fourth zone (Fig. 4.4B) is mixed *Rhizophora* - *Bruguiera* forest which is taller than in the previous zone. *Rhizophora apiculata* and *Bruguiera gymnorrhiza* trees had a dbh up to 70.5 cm and reached up to 45 m height. *Ceriops* trees occupied the lower canopy and had a smaller dbh. This zone occupied most of the area of Sikoroti Island except the creeks (Fig. 4.5.A).

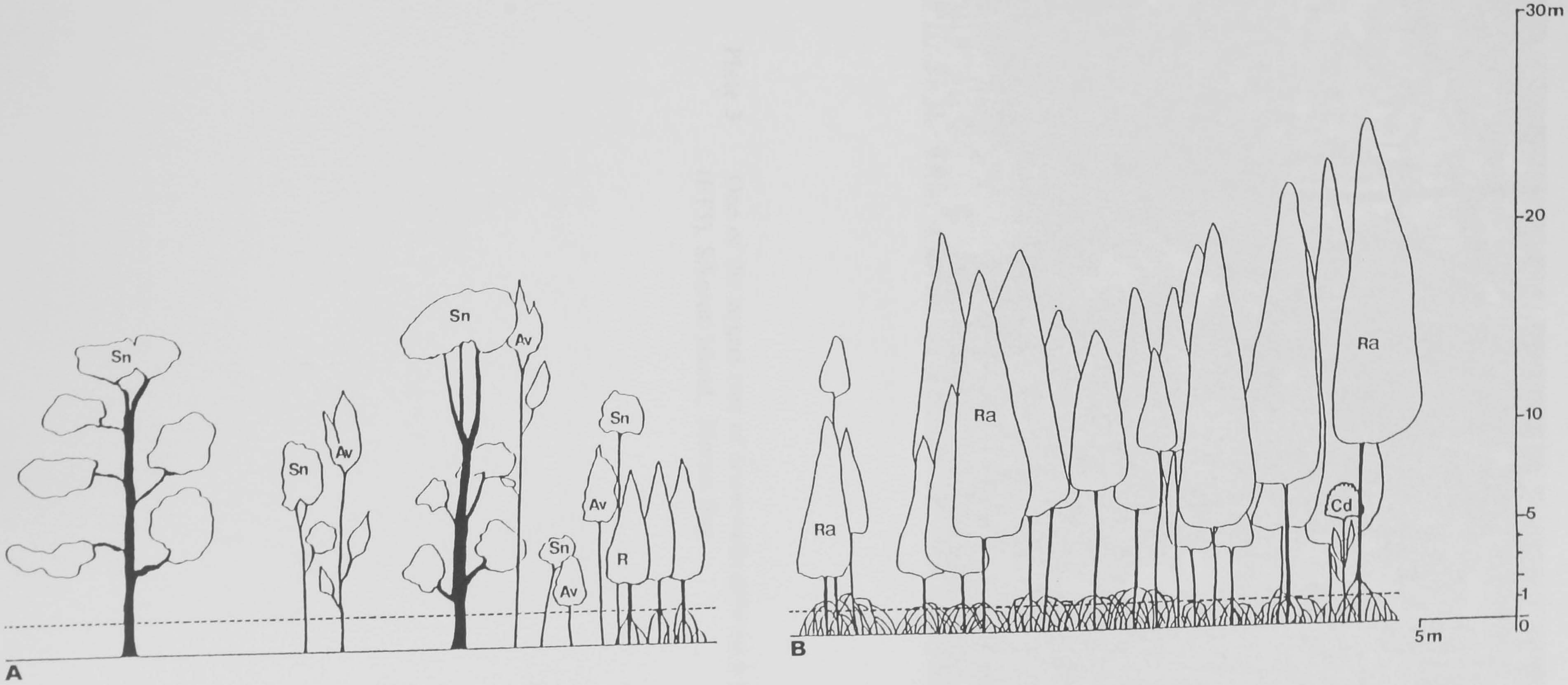


Fig. 4.3 Profile diagrams of a typical mangrove zonation of Sikoroti island. **A**. 0 - 30 m from the seashore, dominated by *Soneratia alba* (Sn), *Avicennia eucalyptifolia* (Av) and some smaller *Rhizophora apiculata* (Ra); **B**. 30 - 60 m, dominated by *Rhizophora apiculata*, with occasional small *Ceriops decandra* (Cd). ------ = the highest water level during the spring-tide.

Plate 3 One of the largest tree of *Sonneratia alba* on a floristic transect (FT3), Sikoroti Island, Bintuni Bay.

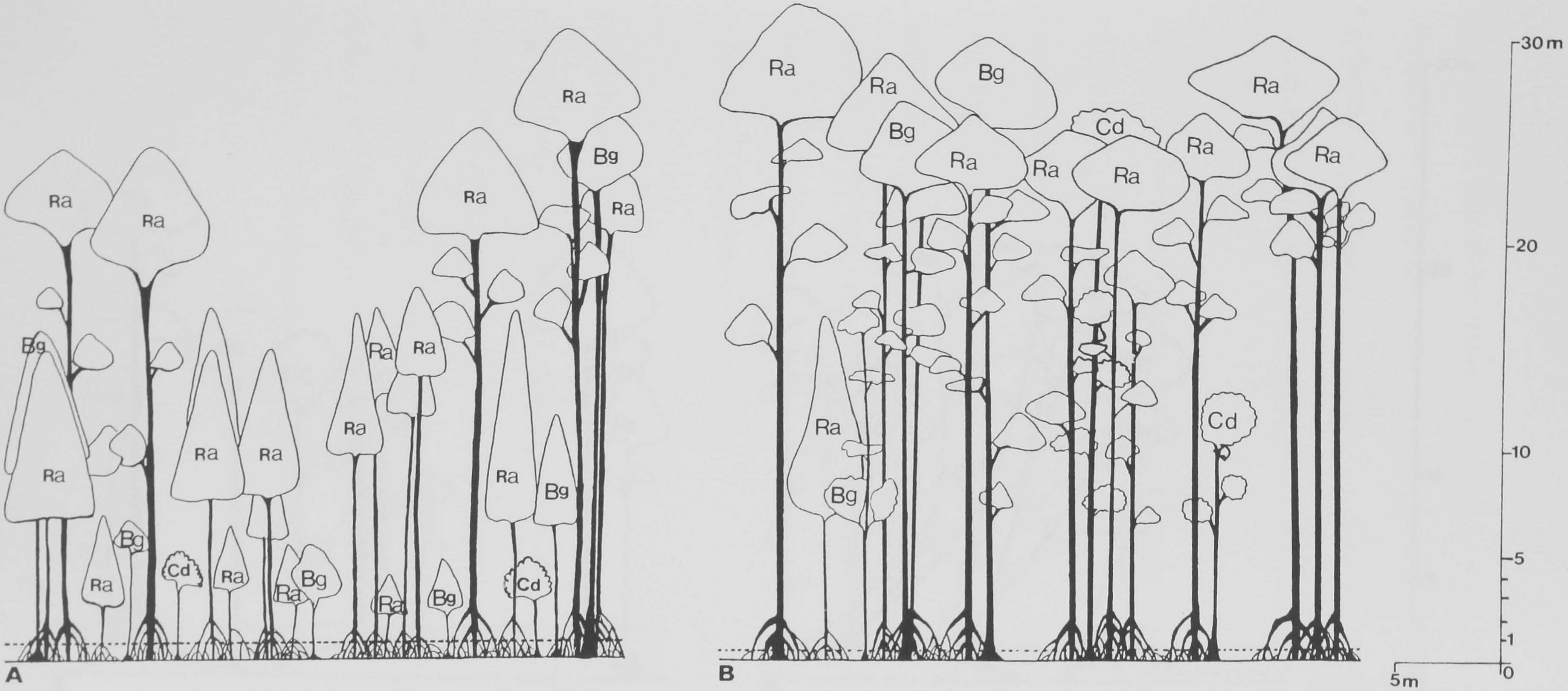


Fig. 4.4 Profile diagrams of a typical mangrove zonation of Sikoroti island, Bintuni Bay. **A**. 60 - 90 m from the seashore, transition from smaller to large *Rhizophora apiculata* (Ra), *Bruguiera gymnorrhiza* (Bg) and *Ceriops decandra* (Cd); **B**. >90 m from seashore, tall forest dominated by mature *Rhizophora apiculata* , *Bruguiera gymnorrhiza* and occasional *Ceriops decandra*. ------ = the highest water level during the spring-tide.

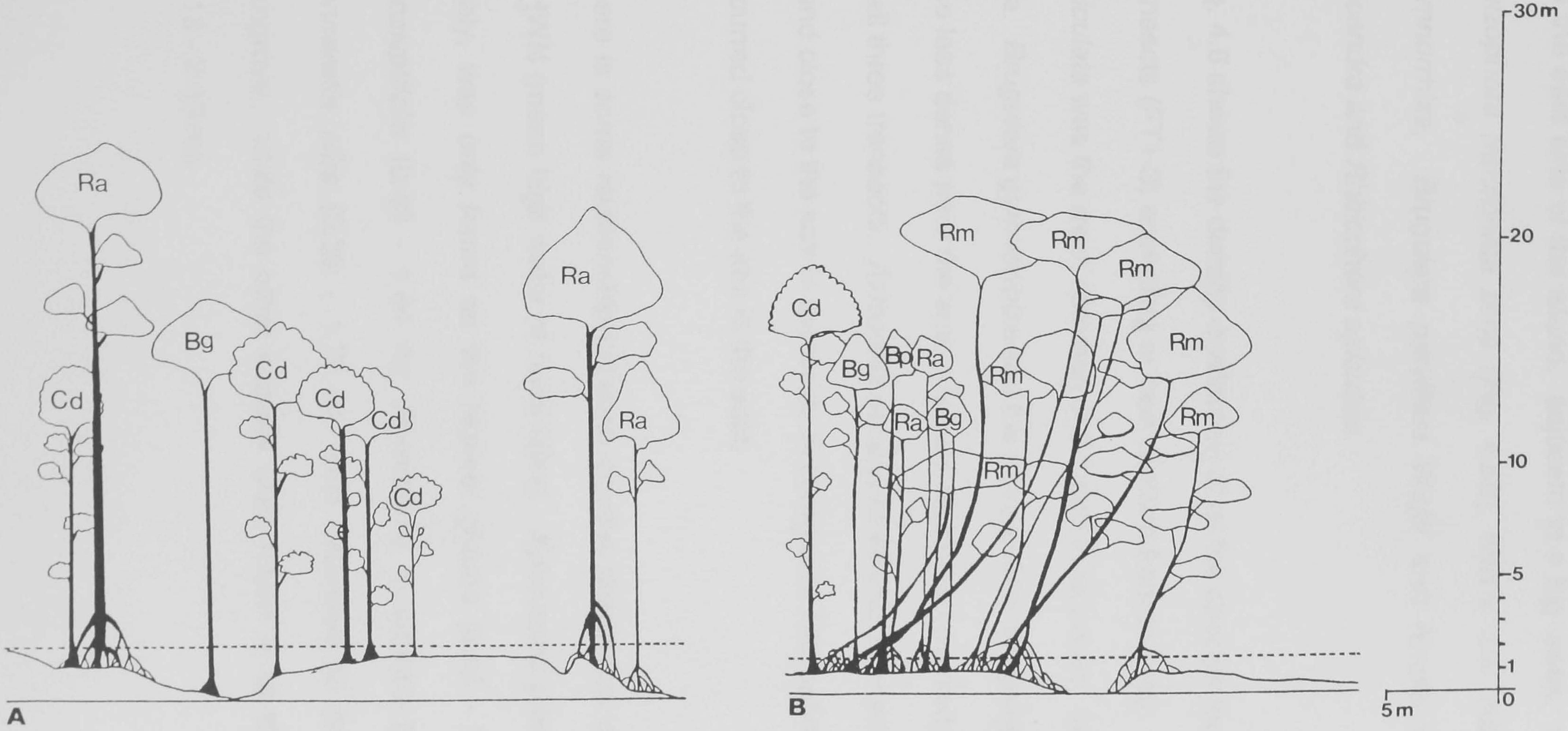


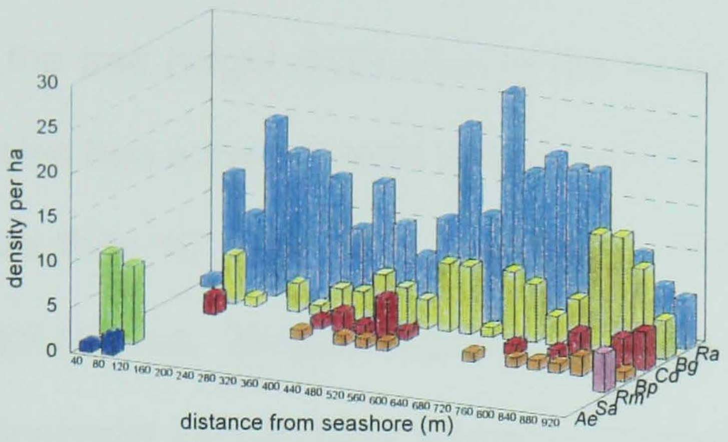
Fig. 4.5 Profile diagrams of typical mangrove zonation of Sikoroti island, Bintuni Bay. **A**. Middle island topography with creeks, dominated by *Rhizophora apiculata* (Ra), *Bruguiera gymnorrhiza* (Bg) and *Ceriops decandra* (Cd); **B**. The far edge of the island, adjacent to a bigger creek, characterized by leaning *Rhizophora mucronata* (Rm) and mixed *Rhizophora apiculata*, *Bruguiera gymnorrhiza*, *Bruguiera parviflora* (Bp) and *Ceriops decandra*. ------ = the highest water level during the spring-tide.

On the east side of the island, adjacent to a big creek, was the fifth zone, or *Rhizophora mucronata* zone (Fig. 4.5B), with a few individuals of *Bruguiera gymnorrhiza, Bruguiera parviflora* Wight and Arnold ex Griffith, *Ceriops decandra* and *Rhizophora apiculata.*

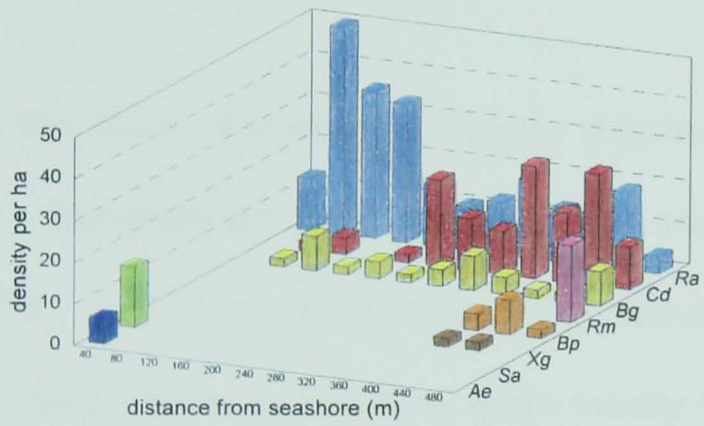
Fig. 4.6 shows the density distribution of all the species found in floristic transects (FT1-3) according to their position from the sea. *Rhizophora apiculata* was the most common and found in all zones, less densely near the sea. *Bruguiera gymnorrhiza* and the more patchy *Bruguiera parviflora* were also less dense near the sea. *Ceriops decandra* occurred in different patterns in all three transects. *Avicennia eucalyptifolia* and *Sonneratia alba* were only found close to the sea in the west, in contrast to *Rhizophora mucronata* which occurred close to the sea in the east.

There is some relationship between species distribution and height (m) above MHWN (mean high water of neap tides). *Xylocarpus granatum* which occured rarely, was only found on the highest ground (3.48 - 3.49 m). *Avicennia eucalyptifolia* (0.43 - 1.64 m), *Rhizophora mucronata* (0.13 - 0.43 m) and *Sonneratia alba* (0.35 - 1.78 m) were restricted to the lower part of the mangrove, while the other species were found at all the heights measured (0.13 - 3.49 m).

FT1



FT2



FT3

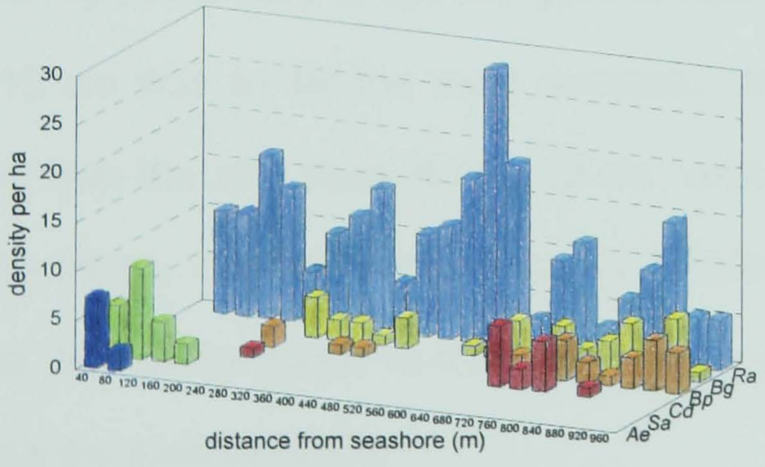


Fig. 4.6 Density distribution of each tree species on the floristic transects with distance from the sea. *Ae* = *Avicennia eucalyptifolia*, *Sa* = *Sonneratia alba*, *Rm* = *Rhizophora mucronata*, *Xg* = *Xylocarpus granatum*, *Bp* = *Bruguiera parviflora*, *Cd* = *Ceriops decandra*, *Bg* = *Bruguiera gymnorrhiza* and *Ra* = *Rhizophora apiculata*.

4.4.2.2 Tree height and diameter distribution

Fig. 4.7 shows the tree height distribution in the transects FT1-3. In general most of the species had a mean height in the range 10 - 19 m, and only a few had a height less than 10 m or more than 30 m. *Rhizophora apiculata* was found in all height classes, *Bruguiera gymnorrhiza* was commonest in the 10 - 19 m class. *Sonneratia alba* showed different patterns in all the transects, in contrast with *Avicennia eucalyptifolia* which appeared in the same class in all transects.

Fig. 4.8 shows the trunk diameter size-class distribution of all the trees in transects FT1-3. Generally the distributions in FT1 and FT2 were similar, and different from FT3. In FT1 and FT2 most of the species had trees in the 10 - 19 cm diameter class, while in FT3 they were mostly in the 20 - 29 cm class. *Bruguiera gymnorrhiza, Rhizophora apiculata* and *Sonneratia alba* were in all the diameter size classes, even though their distributions varied. In FT1 and FT2 *Rhizophora apiculata* and *Bruguiera gymnorrhiza* in the diameter size class of 10 - 19 cm was by far the most common. In FT3, however, the number of trees from the size class of 20 - 29 cm were higher than from the size class of 10 - 19 cm. *Sonneratia alba* shows a different trend in all sites. In FT1 trees in the 30 - 39 cm class, in FT2 the 10 - 19 cm class, in FT3 the > 60 cm class were the most common.

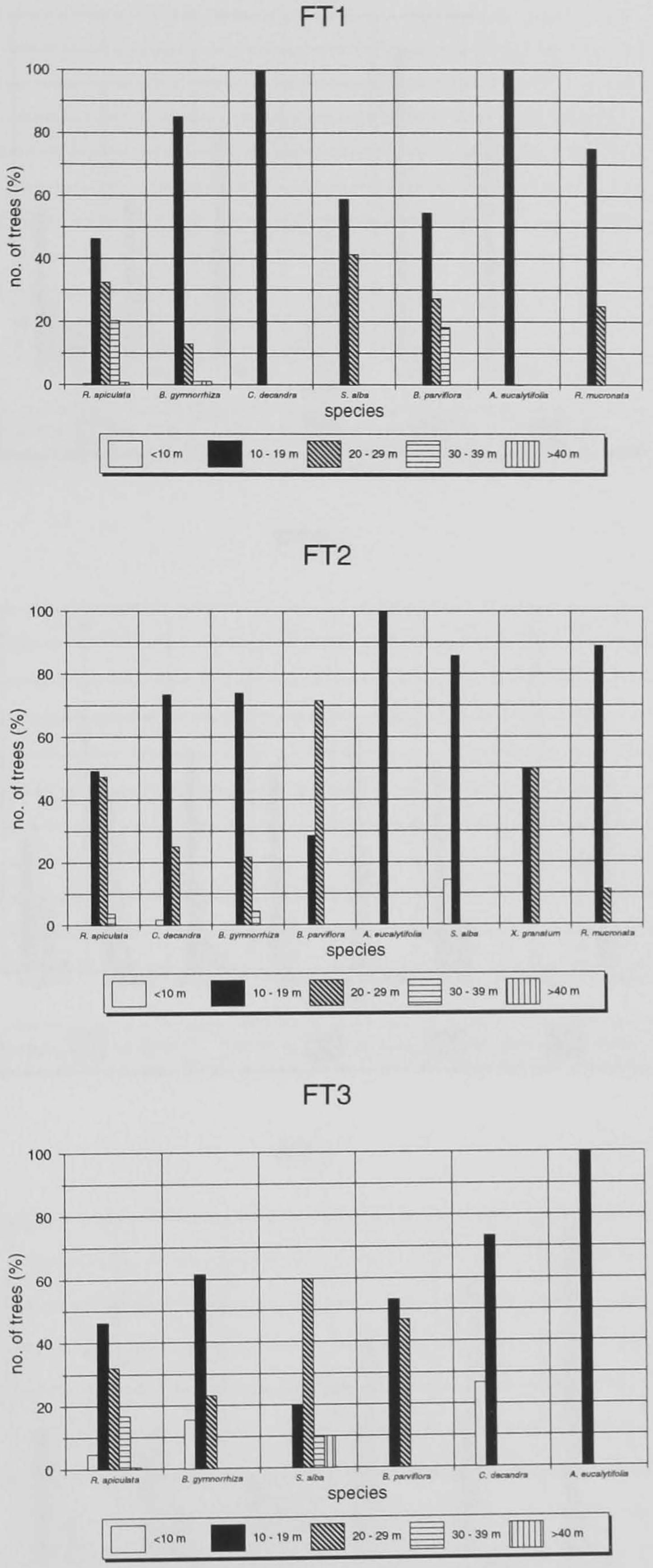


Fig. 4.7 Height size-class distribution of each tree species in the floristic transects of Sikoroti Island, Bintuni Bay.

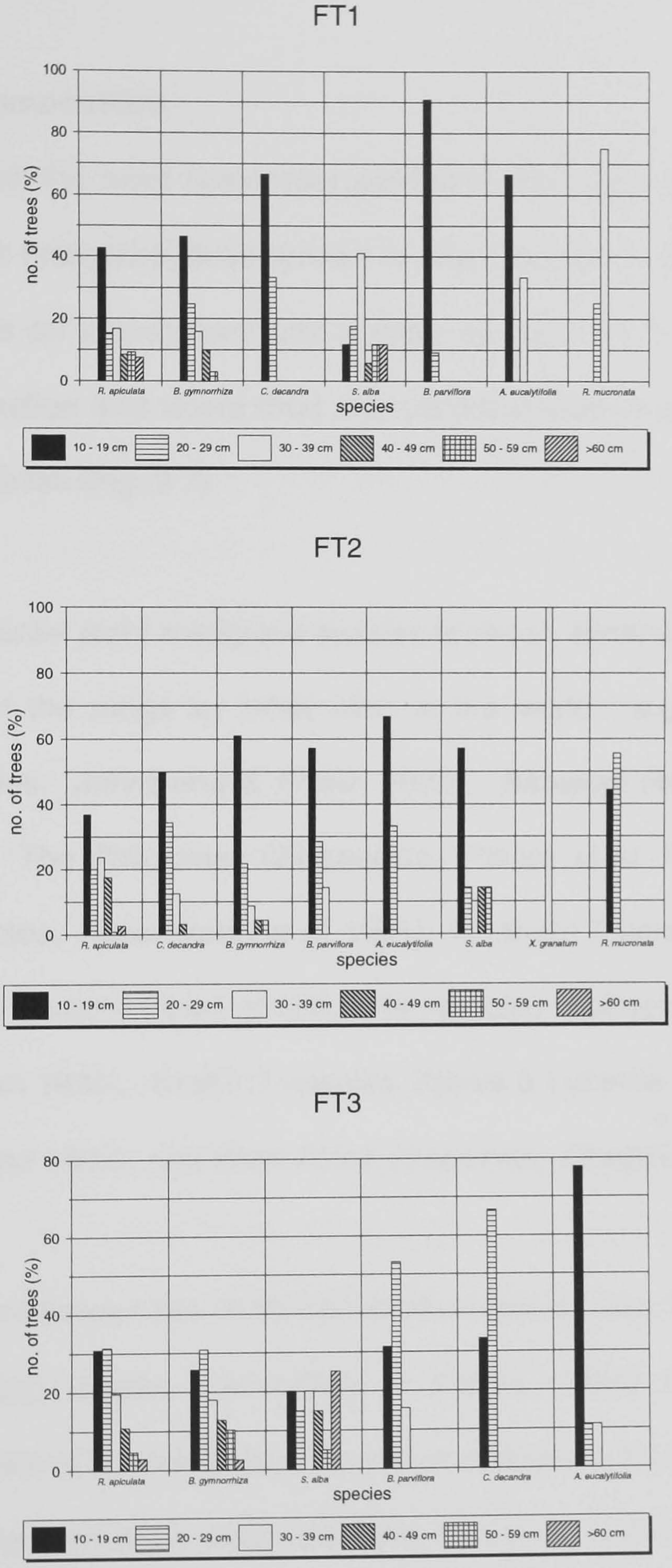


Fig. 4.8 Trunk-diameter size-class distribution of each tree species in the floristic transects of Sikoroti Island, Bintuni Bay.

4.5. Discussion

4.5.1 Species composition

Bintuni Bay has all the most favourable conditions discussed by Johnstone & Frodin (1982) for mangrove development in the Papuan Subregion: it is a deltaic area, it is an embayment and a deep estuary that is sheltered from excessive wave action and where mud and silt accumulation are taking place, and has a high rainfall (Fig. 2.7).

There are 30 vascular plant mangrove species found in Bintuni Bay which is at the higher end of the range for other sites in the world: e.g., Papua New Guinea (31 species, Johnstone & Frodin 1982), Sarawak (40 species, Chai 1975), Quezon, The Philippines (29 species, Fortes *et al.* 1989), Ranong, Thailand (24 species, Aksornkoae *et al.* 1991), Northern Australia (33 species, Wells 1983), the Eastern Coast of U.S.A. (4 species, Reimold 1977), Belize (5 species, Zisman 1990), Brazil (7 species, Kjerve & Lacerda 1993), Panama (11 species, D'Croz 1993), and West Africa (6 species, Chapman 1977a).

Bintuni Bay lies in between the north and south coasts of New Guinea and has species of the two coasts. According to Frodin (1985) the north coast mangroves are part of the wider Indo-Malesian mangrove formation, and the south coast mangroves have close affinities with north Australia. *Avicennia alba* is characteristic of the north coast, and *A. officinalis* L. and *A. eucalyptifolia* of the south coast, and all are common species in Bintuni Bay.

4.5.1.1 Trees

The number of tree species in the Floristic Transects (FT1-3) is higher than in the Floristic Plots (FP1-3) because of differences of their sizes and their positions in the forest zonation. The 0.25 ha Floristic Plots, were located only in one zone of vegetation whereas the Floristic Transects had areas ranging between 0.47 ha to 1 ha and stretched across all of the zones. The position factor is more important than sample size. FT2, for example, is the shortest transect but has more species than the other two transects, and the Floristic Plots which are all of the same size do not have a same number of species.

Tree density and basal area data (Tables 4.1 and 4.2) clearly show that *Rhizophora apiculata* is the main species in the study sites. It covers most of the mangrove area in Bintuni Bay, except for island edges fringed by the pioneers *Sonneratia spp.* or *Avicennia spp.*, or the creek banks which were usually occupied by *Rhizophora mucronata* (Figs. 4.3 and 4.4).

However, these data are difficult to compare with other mangrove areas because of differences in the plant size considered. In Florida, for example, Lugo & Snedaker (1974) considered all plants ≥ 2.5 cm dbh as trees and found the density was 5900 ha^{-1}. Chansang (1984) using the same size limit reported a density of 4997 ha^{-1} for Ko Yao Yai, Thailand. De Leon *et al.* (1993), reported a density of 493 ha^{-1} for trees ≥ 5 cm dbh in Carigara Bay, the Philippines. In Bintuni Bay for trees ≥ 10 cm dbh the mean density was 453 ha^{-1} (range 362 - 544 ha^{-1}). These values are higher than those for trees of the same size from Bungin River, South Sumatra (214 ha^{-1}, Sukarjo *et al.* 1984), and the Osa mangrove, Costa Rica (360 ha^{-1}, Holdridge *et al.* 1971).

Basal area comparisons suffer from the same problems as those of density. The average value of tree basal area in Bintuni Bay of 31.6 m^2 ha^{-1} (range 27.3 - 36.9 m^2 ha^{-1}), is much higher than the value in Bungin River, South Sumatra (average of 19.3 m^2 ha^{-1}, Sukarjo *et al.* 1984) or the Osa mangrove in Costa Rica (12.5 m^2 ha^{-1}, Holdridge *et al.* 1971). Considering all individuals greater than 2.5 cm dbh Pool *et al.* (1977) reported that the largest basal area, and probably the most structurally developed mangrove forests in the neotropics, occurred on the Atlantic coast of Costa Rica (96.4 m^2 ha^{-1}), or the Marismas Nacionales, near Teacapán, México (60.8 m^2 ha^{-1}).

Rhizophora apiculata is the main tree species in Bintuni Bay (Tables 4.1 and 4.2). This species is dominant throughout South East Asian mangroves e.g. Thailand (Poovachiranon & Chansang 1982; Chansang 1984; Aksornkoae *et al.* 1991), Malaysia (Chai 1975; Chan & Ujang 1982; Ong *et al.* 1982), Indonesia (Ogino & Chihara 1988), Philippines (Arroyo 1979; Fortes *et al.* 1989), Papua New Guinea (Paijmans & Rollet 1977; Chapman 1977b). Tomlinson (1994) reported *R. apiculata* as common or dominant in mangroves in the Malesian region as far west as Queensland and Papua New Guinea. In Bintuni Bay *Bruguiera gymnorrhiza* was usually ranked second but occasionally replaced by *Ceriops decandra* (FT2), *Bruguiera parviflora* (FP3), and *Sonneratia alba* (FT3).

Complexity index is an expression of the diversity and abundance within various types of forest communities, and performs an integrative measure that combines floral characteristics and forest structure components (Holdridge *et al.* 1971). The comparisons of the values of complexity index between mangroves in Bintuni Bay and some other mangrove areas are shown in Table 4.9. The values for Bintuni Bay, were slightly higher than for Bungin River, South Sumatra, but much higher than the average values for mangrove in Florida, Puerto Rico, and Costa Rica (except for the Moin riverine mangrove in that country, which has an extraordinarily high value).

A distinctive character of mangroves is their low diversity. Since there are only a few species in the Bintuni Bay samples, diversity indices were low and the similarity between any two compared samples was high. The evenness as a measure of the equitability of abundance of species, was also high. No attempt has been made to compare the diversity and eveness data with mangroves elsewhere since there is no sample size uniformity.

4.5.1.2 Saplings and seedling

Mangrove sapling and seedling composition in the study sites were mostly similar to the tree composition, except for the lack of *Avicennia* and *Sonneratia* species which do not usually grow under the mature canopy, but occur as pure, even-aged stands in newly-formed mud flats. There is no understory except their own seedlings and saplings either on the Floristic Plots or Floristic Transects. However, there are some herbs and shrubs found outside the plots and transects (Appendix 1, Plate 4A).

Tabel 4.9 The number of species, density (D), basal area (BA), stand height (H) and complexity index (IC) per 0.1 ha of several mangroves.

Location	No. of species	D	B A (m^2)	H (m)	IC
Florida [1]:					
Ten Thousand Islands	2	80	1.24	7.3	1.4
Rookery Bay	3	66	1.44	6.5	1.9
Puerto Rico :					
Vacia Talega [1]	3	98	1.71	13.0	6.5
Ceiba [1]	2	26	0.34	8.5	0.2
Mona Island [2]	2	179	2.97	15.0	15.9
México [1] :					
Roblitos	2	91	2.41	8.0	3.5
El Calón	2	61	0.83	9.0	0.9
Rio de las Cañas	3	103	5.61	16.0	27.7
Costa Rica [1] :					
Moin	4	118	9.53	16.0	72.0
Santa Rosa	2	80	2.22	10.0	3.6
Bungin River, S. Sumatra [3]					
Transect I	5	39.5	2.30	22.9	10.4
Transect II	9	44.4	1.40	11.1	6.2
Transect III	4	38.0	2.10	48.3	15.4
Bintuni Bay (this study)					
FP1	3	45.2	3.2	32.4	14.1
FP2	4	54.4	3.7	28.0	22.5
FP3	5	37.2	2.8	32.7	17.0
FT1	7	48.9	3.6	26.5	32.7
FT2	8	49.8	2.7	22.8	27.4
FT3	6	36.2	2.8	24.6	15.0

Note :

[1] Pool *et al.* (1977)

[2] Rogers & Cintrón (1974)

[3] Sukardjo et al. (1984).

Plate 4 **A** The mangrove "thistle" *Acanthus ilicifolius* , shoot with flowers and fruits. **B** *Xylocarpus granatum* , branch with fruit.

The sapling density (mean 1451 ha^{-1} in FP1-3 and 3936 ha^{-1} in FT1-3), was much lower than the corresponding seedling densities of 15 733 ha^{-1} and 60 939 ha^{-1}. Again there is a problem in comparisons because other workers have used different definitions of seedling and sapling. Sukarjo *et al.* (1984) used similar definitions to that for Bintuni Bay and comparisons were possible with the Bungin River, South Sumatra, which had many fewer saplings (930 ha^{-1}) but similar numbers of seedlings (35 486 ha^{-1}).

Rhizophora apiculata was the commonest seedling species, but as a sapling it was sometimes less common than *Ceriops decandra* or other species. Chai (1975) reported from Sarawak that *Rhizophora apiculata* regenerated well under a dense canopy in undisturbed forest, even though most of the plants died before they reached sapling size. Putz & Chan (1986) also found the same phenomenon in peninsular Malaysia and suggested that *Rhizophora apiculata* seedlings are not very shade tolerant and are gradually replaced by other faster growing but more shade tolerant species. They proposed that shade tolerance and dispersal characteristics should be included among the ecological factors influencing the distribution of tree species in mangroves.

It is not clear why *Ceriops* sometimes became dominant at the sapling stage. Chapman (1977b) found that *Ceriops* is a common understory shrub in most Indo-Malesian mangroves. Perhaps *Ceriops* is more shade tolerant, but it is not uncommon to find *Ceriops* seedlings in full sunlight in cleared areas (Chansang 1984).

4.5.2 Forest structure

4.5.2.1 Zonation

Mangroves often show a conspicious zonation of tree species, and sometimes there are mono-specific bands parallel to the shoreline (Snedaker 1982). Mangrove classification and concepts of zonation have been closely linked (Frodin 1985). Zonation patterns have been described for both palaeotropical mangroves (e.g. Watson 1928, Macnae 1969, Chai 1973, van Balgooy 1976, Chapman 1977b, Elsol & Saenger 1983) and neotropical mangroves (e.g., Bowman 1917, Davis 1940). West (1977) noticed that the zonal arrangement of New World mangroves appeared to be less pronounced than in the Old World, possibly because of the lesser number of mangrove species in the former.

In contrast Smith (1992) observed that not all researchers reported the classical view of mangrove zonation: e.g., Thom (1967) and Thom *et al.* (1975) described spatial patterns of occurrence, in Tanzania mangroves have been reported as both zoned (Chapman 1976) and unzoned (Macnae & Kalk 1962).

There have been many descriptions of likely causes for mangrove zonation, from plant succession due to land building (Davis 1940), response to geomorphological factors (Thom 1967, Woodroffe 1992), physiological adaptation to gradients across the intertidal zone (Macnae 1968), differential dispersal of propagules (Rabinowitz 1978a,b), differential predation on propagules across the intertidal zone (Smith 1987a,b,c), and interspecific competition (Clarke & Hannon 1971).

For Papua New Guinea, Johnstone & Frodin (1982) proposed six likely causes of zonation: 1. inundation and water depth, 2. wave action, 3. drainage (soil water and water table), 4. salinity regime, 5. substratum, and 6. biota and biotic interactions.

In Bintuni Bay there is a mangrove zonation as clearly shown in the Figs 4.3 - 4.5, though the causes are still unclear. The zonation in general is similar to that described from other Indo-Pacific regions (e.g. Watson 1928, Macnae 1969, Chai 1973), but there is a North Australian influence similar to that observed in Papua New Guinea (Johnstone & Frodin 1982).

The seaward side of Sikoroti Island was dominated by a mixture of mature *Sonneratia alba* and *Avicennia eucalyptifolia*, which formed a single zone (Plate 5). Watson (1928) and Richards (1964) regarded *Avicennia* and *Sonneratia* species as forming a single community, while Chapman (1975) considered them as forming two separate communities since the species had different soil requirements. He believed *Avicennia* to be associated with firmer, more sandy soils and *Sonneratia* with softer muds.

The second zone, is perhaps more appropriately termed “transitional” and is dominated by younger *Rhizophora apiculata* with occasional *R. mucronata* and *Ceriops*. The open area just behind the *Sonneratia* - *Avicennia* zone is the

Plate 5 **A** Typical condition of mangrove first zone in Bintuni Bay, dominated by *Sonneratia alba* (**Sn**) and *Avicennia eucalyptifolia* (**Av**).
B Close-up of the pneumatophores of the zone.

most likely suitable place for large numbers of seedlings of *Rhizophora apiculata*, which is less shade tolerant, to reach the sapling stage. Other than that, it occurs very locally in some open patches inside the mature forest.

In the next zone, the *Rhizophora* zone, *Rhizophora apiculata* saplings are still found but only occasionally. Instead, saplings of *Ceriops* and *Bruguiera gymnorrhiza*, believed to be more shade tolerant, are abundant.

The mixed, tall *Rhizophora* - *Bruguiera* zone is the largest and occupied most of the area of the island except for the first 100 m from the sea. In this closed - canopy zone, the number of saplings and seedlings, especially of *Rhizophora apiculata*, was reduced greatly. The forest floor was also largely free of undergrowth and herbs with the herb *Acrostichum sp.* and the shrub *Acanthus ilicifolius* L. (Plate 4) occurring very occasionally. This is perhaps because there were not many mud lobster (*Thalassina anomala*) mounds which, according to Chapman (1977b) and Paijmans & Rollet (1977), is the best place for their growth.

Chai (1975) showed that in Sarawak only very few low and small mounds occurred in *Rhizopora apiculata* forest. He felt that this is perhaps because of the frequent tidal inundation in the *Rhizophora apiculata* forest and the soft and friable nature of the soil which seemed to discourage the lobster. In contrast Paijmans & Rollet (1977) reported that in the Galley Reach area of Papua New Guinea, large mounds were absent in *Bruguiera parviflora* forest, but were very common in *Rhizophora* - *Bruguiera* forest.

Janzen (1985) hypothesized three possible reasons for the lack of a mangrove understory: 1. plants with low light resources cannot meet the metabolic demands of salt tolerance, 2. the herb, shrub and vine life forms are intrinsically incapable of growing in saline soils, 3. the characteristically small seeds of herbs, shrubs and vines do not generate sufficiently robust seedlings to withstand the abiotic conditions or grazing or both of a mangrove swamp. However, Corlett (1986) argued that Janzen's (1985) statements were oversimplified. He showed that in Singapore and Southern Malaysia there are mangroves with understories which tend to be in areas with abundant year-round rainfall and freshwater runoff. In Bintuni Bay there also sometimes occurred a mangrove understory but mainly on open higher ground.

4.5.2.2 Tree height and diameter distribution

The Bintuni bay mangrove, like most mature mangroves (Watson 1928; de Haan 1931; van Steenis 1958; Chapman 1976, 1977b), is apparently single-storeyed, with narrow-crowned trees 10 - 30 m or more high and with a trunk diameter 10 - 30 cm, occurring from about 100 m from the sea landwards. The outer edges, *Sonneratia* and *Avicennia* (facing the sea or estuaries), or *Rhizophora mucronata* (facing the creeks and rivers) are always shorter and more bushy and even-aged especially for *Sonneratia* and *Avicennia.*

The even-aged structure of the pioneer species *Avicennia* and *Sonneratia* may be because they are light demanders (Chapman 1944), though *Avicennia germinans* L. (Stearn) does not regenerate under shade. Clarke & Hannon

(1970) stated that young seedlings of *Avicennia marina* (Forsk.) Vierh. are extremely sensitive to water-logging.

Odum *et al.* (1982) discussed the possibility that a large-scale disturbances will destroy large tracts of forest, which then regenerate at about the same time. He hypothesized that mangroves in Florida have adapted to a 25-year disturbance cycle, the return time for major hurricanes. Smith & Duke (1987) also found a positive relationship between large-scale disturbances (cyclones) and species richness in mangrove forests of northeastern Queensland which had one cyclone every 5 years. Blasco (1975) reported that (tall) *Rhizophoraceae* are minor components of the forest community in the Sundarbans mangroves of Bangladesh which have up to 40 cyclones a year. However, major disturbances cannot account for even-aged stands in areas which are not subjected to hurricanes. In Bintuni Bay, the forest is tall for mangroves and this can at least be partly related to the absence of hurricane-force winds in Irian Jaya.

Without a detailed knowledge of the autecology of the mangrove species we cannot hope to explain differences in species distribution in terms of soil chemistry and the soil investigation (chapter 3) reported here was not designed to do this.

Appendix 1 List of mangrove and mangrove adjacent species observed outside the Floristic Plots and Floristic Transects in Bintuni Bay, Irian Jaya.

No.	Family	Species	Growth form	Habitat
1	Acanthaceae	*Acanthus ilicifolius* L.	Shrub	Upper mangrove[1]
2	Arecaceae	*Metroxylon sagu*	Palm tree	Upper brackish areas
3	Arecaceae	*Nypa fruticans* (Thun.) Wurmb.	Rhizomatous palm	Lower brackish areas
4	Avicenniaceae	*Avicennia marina* (Forsk.) Vierh.	Tree	Mangrove, lower intertidal zone
5	Avicenniaceae	*Avicennia officinalis* L.	Tree	Mangrove, riverbank
6	Bignoniaceae	*Dolichandrone spathacea* (L.f.) K. Sch.	Shrub	Brackish areas
7	Caesalpiniaceae	*Caesalpinia bonduc* (L.) Roxb.	Climber / vine	Upper mangrove
8	Combretaceae	*Lumnitzera littorea* (Jack) Voight.	Tree	Brackish areas
9	Malvaceae	*Hibiscus tiliaceus* L.	Tree	Upper mangrove or brackish areas
10	Euphorbiaceae	*Excoecaria agalocha* L.	Tree	Brackish areas
11	Meliaceae	*Xylocarpus mekongensis* Pierre	Tree	Upper mangrove, mid intertidal zone
12	Myrsinaceae	*Aegiceras corniculatum* L. Blanco	Shrub/ tree	Mangrove, riverbank
13	Myrtaceae	*Malaleuca* sp.	Tree	Upper brackish areas to higher grassland
14	Orchidaceae	*Dendrobium* sp.	Epiphyte	Mangrove, especially on aged *Sonneratia* trees
15	Pandanaceae	*Pandanus* sp.	Shrub/ tree	Brackish areas, adjacent to lower grassland
16	Pteridaceae	*Acrostichum aureum* L.	Fern	Upper mangrove [1]
17	Rhizophoraceae	*Bruguiera sexangula* (Lour.) Poir.	Tree	Mangrove, mid intertidal zone
18	Rhizophoraceae	*Ceriops tagal* (Perr.) C.B. Robinson	Shrub/ tree	Mangrove, mid intertidal zone
19	Rhizophoraceae	*Rhizophora stylosa* Griff.	Tree	Mangrove, lower to mid intertidal zone
20	Rubiaceae	*Myrmecodia tuberosa* Jack	Epiphyte ant-plant	Brackish areas, especially on *Lumnitzera* trees
21	Rubiaceae	*Scyphiphora hydrophyllaceae* Gaertn. f.	Shrub	Brackish areas
22	Sonneratiaceae	*Sonneratia caseolaris* (L.) Engler	Tree	Brackish areas, sometimes scattered in Nypa areas
23	Sterculiaceae	*Heritiera* sp.	Tree	Upper mangrove to brackish areas

Note : [1] including mounds built by the mud lobster *Thalassina anomala.*

A

B

Plate 6 **A** Nypa (*Nypa fruticans*) vegetation along the lower Bintuni River with patchily distributed *Sonneratia caseolaris* in between. **B** Typical vegetation behind mangrove in Babo, near Bintuni Bay, dominated by grasses and *Pandanus* sp.

A

B

Plate 7 Two common species in back mangrove vegetation in Babo, near Bintuni Bay: **A** *Lumnitzera littorea*, **B** *Schypiphora hydrophillacea*.

Plate 8 **A** *Malaleuca* spp. (Myrtaceae) are common in higher grassland behind mangrove in Babo, near Bintuni Bay. **B** The "ant-plant" *Myrmecodia tuberosa* (**My**), one of several mangrove epiphytes in Bintuni Bay.

V SMALL LITTERFALL AND LEAF-LITTER DECOMPOSITION

5.1 Introduction

Mangroves are ecosystems in which the rate of above-ground litterfall is usually high and hence which contribute much energy by this pathway to the detritus-based marine food webs (Heald 1969; Odum & Heald 1972; Boto & Bunt 1981). Litterfall is the shedding of dead plant parts and a distinction is usually made between small litterfall (leaves, twigs ≤ 2cm diameter, reproductive parts, and small trash) and large litterfall (woody parts ≥ 2cm diameter). Large litterfall is dificult to quantify and this chapter is concerned with small litterfall. Correlations between litterfall and net primary production vary but measurements of litterfall are a useful index of production and quantify an important carbon flux in the ecosystem (Clough 1985).

Medwecka-Kornas (1970) differentiated between standing crop or litter layer and litterfall:

- Litter present at a given moment in a definite area is called the standing crop or litter layer and is expressed in weight or energy units per area (e.g., g / m^2).
- Litterfall is the rate of litter shed per unit area within a definite time period (e.g. g / m^2 / day).

Most of the energy from primary production becomes available to support consumer production after it has been fragmented and processed through decomposer pathways (Newell 1982). Decomposition of mangrove litter therefore, is an important stage in nutrient cycling and the supply of organic matter to the estuarine and mangrove food web, and is a function of the substratum characteristics including the availability of oxygen and animal and microorganism activity (Lugo & Snedaker 1974).

5.2 Methods

5.2.1 Small litterfall

Litterfall was collected according to the methods described by Brown (1984) using traps which were made by attaching a nylon mesh (2 mm) to a 1 m X 1 m wooden frame (Plate 9). One trap was randomly located within each of ten 10 m X 10 m subplots in each of FP1, FP2 and FP3, and positioned about 1.5 m above the mean high water level at spring tide (MHWS). The trap were set up on 1 June 1993 and litterfall was collected from each trap on the 15th and on the last day of each month from 15 June 1993 to 31 May 1994. The litterfall was bulked by month before sorting into leaves, branches, fruits and flowers, and a miscellaneous fraction (Proctor 1983). The fractions were subsequently dried to a constant weight at 70 °C for 24 h and then ground using a mill before chemical analysis.

Plate 9 **A** and **B** The 1 m x 1 m litter traps in FP1-3, Sikoroti Island, Bintuni Bay.

5.2.2 Small litter layer

The small litter layer was collected from 1 m x 1 m wooden frames which were laid on the forest floor. The frames were positioned in the same 10 m x 10 m subplots as for the litterfall collection (FP1-3), but they were only collected on the last day of each month. Only leaf, stipule, reproductive part, and small wood litter layer were collected. No attempt was made to collect a trash fraction from the litter layer since it was felt that it would have been impossible to avoid contamination with soil. The litter layer was cleaned, dried, sorted and weighed using the same methods as for litterfall.

5.2.3 Litterfall leaf chemical analysis

Subsamples of about 0.15 g dry weight of each ground sample were digested in a sulphuric acid / hydrogen peroxide mix (Allen 1989). Total nitrogen and phosphorus were determined by colorimetry using a Kontron Uvikon 860 spectrophotometer, following an indophenol-blue method (Rowland 1983) for nitrogen, and a stannous chloride - molybdenum-blue method (Allen 1989) for phosphorus. Analyses of potassium, sodium, calcium and magnesium were made using a Varian AA-575 S atomic absorption spectrophotometer with an air-acetylene flame for potassium and sodium, and a nitrous-oxide - acetylene flame for calcium and magnesium.

5.2.4 Leaf-litter decomposition experiment

Decomposition was studied using freshly-fallen leaf litter (collected from the forest floor at low tide) of *Avicennia eucalyptifolia* , *Bruguiera gymnorrhiza, B.*

parviflora, Rhizophora apiculata, and *Sonneratia alba.* Ten to 15 g of this leaf-litter were enclosed separately in 30 cm X 30 cm 2-mm mesh nylon bags. The bags were left on the forest floor (tied to plant roots or trunks) in sites which were dominated by the same species as the leaves that were used in the bags (see chapter 2).

Collections were made at 0, 2, 4, and 6 days, then weekly for six occasions and then 2-weekly for six occasions. There were four replicate bags for every collection. Litter remaining in the bags at every collection time was washed carefully with fresh water and air-dried. After the final collection the litter was oven-dried at 85 ° C for 48 h and weighed.

No chemical analyses were made for the litter because it was impossible to clear off the remnants of adhering mud without altering the chemical composition of the sample.

5.3 Data Analysis

Comparisons of the annual data of any fraction of small litterfall mass among the floristic plots were made using a nested-balanced analysis of variance design, considering litterfall fraction (random factor) and plot (fixed factor) (Zar 1996). The differences in the annual small litterfall concentration data among the plots and among the fractions were tested using a one-way analysis of variance.

To test the differences with time (month) in the small litterfall mass and nutrient concentration pattern between the plots, an analysis of variance with a repeated measures design was applied. For these analyses, time (month) was considered as the within-subject factor and plot the between-subject factor. The Mauchly's sphericity test (Kinnear & Gray 1995) was applied to evaluate the homogeneity of covariance assumption, which is important for the univariate approach. Whenever a significant difference was detected, a nested-balanced design of analysis of variance and a one-way analysis of variance were applied for a further determination.

The litterfall *decomposition rate* (or, in the case of mangroves, *litterfall loss-rate,* since there may be removal by the tides) was calculated as the ratio of annual litterfall mass (L) to litter layer or standing crop (X_{ss}), $k = L / X_{ss}$. *Turnover rate,* the rate of the amount of a substance released by or entering into a compartment in a given time was defined as the inverse form of *decomposition rate* ($1/k$). *Half-lives* ($t_{0.5}$) (assuming an exponential model applies), were calculated as $0.693/k$ (Olson 1963).

For leaf-litter decomposition experiments linear and exponential regression models (Jenny *et al.* 1949, Olson 1963, Wieder & Lang 1982, Ezcurra & Becerra 1987), were applied to observed decomposition rates (k):

Linear regression : $W_t / W_0 = -kt$

Exponential regression : $Wt / W0 = e^{-kt}$

where W_t and W_0 are weight of leaf-litter at time t and time 0, k is decomposition rate, and t is time. A Student t-test was applied to determine the species effect on the decomposition processes.

The homogeneity of the data was tested before every statistical analysis, and where necessary data were arcsine, square root, or log (n + 1) transformed. The Tukey test was used for data comparison and the differences were considered statistically significant at ≤ 0.05. The MINITAB Release 10.2 (Minitab Inc. 1995) and SPSSx Release 6.1 (SPSS Inc. 1996) for MS WINDOWS packages were used for the most of the calculations.

5.4 Results

5.4.1 Small litterfall

The total small litterfall was 11.09 t ha^{-1} y^{-1} (Table 5.1 and Fig. 5.1), and leaf litterfall was by far the biggest contributor (56.2 %), followed by reproductive parts (23.6 %), stipules (10.1 %), wood (8.1 %) and trash (1.9 %). The production of litterfall was not different between FP1, FP2 and FP3 ($p > 0.1$), but there were significant differences between months and between litterfall parts ($p < 0.001$). Double peaks of litterfall occurred: from November 1993 to January 1994, and in May 1994. The lowest litterfall was in July 1993.

In general litterfall production was least just before the driest time of the year (Fig. 5.2). The litterfall production increased with increasing rainfall up to December 1993, decreased during the high rainfall of January to February 1994 and then showed an increase again during a slight increase of rainfall up to May 1994.

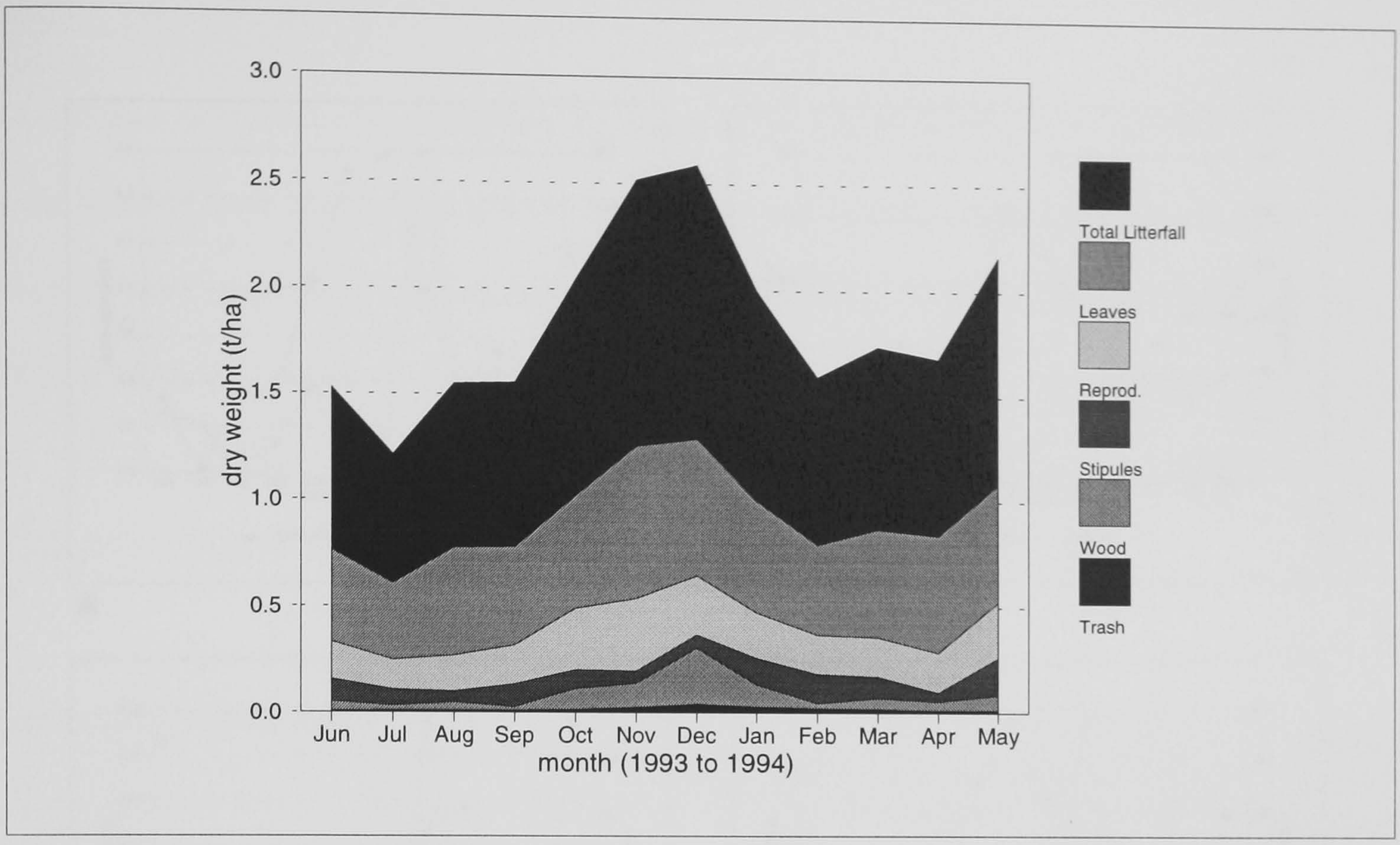


Fig. 5.1 The monthly distribution of mangrove litterfall (t / ha) from June 1993 to May 1994 in Bintuni Bay, Irian Jaya.

	Litterfall (t / ha)					
	Leaves	**Stipules**	**Reprod.**	**Wood**	**Trash**	**Total**
Jun	**0.43** (0.401 - 0.469)	**0.10** (0.094 - 0.111)	**0.18** (0.124 - 0.216)	**0.04** (0.025 - 0.067)	**0.01** (0.005 - 0.012)	**0.76** (0.698 - 0.840)
Jul	**0.36** (0.333 - 0.384)	**0.08** (0.058 - 0.085)	**0.14** (0.116 - 0.152)	**0.02** (0.015 - 0.030)	**0.01** (0.007 - 0.012)	**0.61** (0.555 - 0.653)
Aug	**0.51** (0.428 - 0.601)	**0.05** (0.047 - 0.052)	**0.17** (0.136 - 0.204)	**0.04** (0.020 - 0.055)	**0.01** (0.008 - 0.011)	**0.78** (0.640 - 0.905)
Sep	**0.46** (0.430 - 0.517)	**0.11** (0.088 - 0.123)	**0.18** (0.145 - 0.254)	**0.02** (0.013 - 0.023)	**0.01** (0.007 - 0.015)	**0.78** (0.752 - 0.811)
Oct	**0.53** (0.517 - 0.554)	**0.09** (0.075 - 0.099)	**0.29** (0.234 - 0.390)	**0.10** (0.041 - 0.186)	**0.02** (0.011 - 0.021)	**1.02** (0.888 - 1.101)
Nov	**0.72** (0.687 - 0.759)	**0.06** (0.042 - 0.073)	**0.34** (0.276 - 0.422)	**0.11** (0.079 - 0.139)	**0.03** (0.020 - 0.032)	**1.26** (1.161 - 1.401)
Dec	**0.65** (0.610 - 0.693)	**0.06** (0.053 - 0.066)	**0.28** (0.215 - 0.324)	**0.27** (0.158 - 0.346)	**0.04** (0.029 - 0.047)	**1.29** (1.186 - 1.464)
Jan	**0.53** (0.471 - 0.559)	**0.13** (0.094 - 0.145)	**0.21** (0.123 - 0.293)	**0.10** (0.082 - 0.132)	**0.03** (0.027 - 0.034)	**1.00** (0.980 - 1.035)
Feb	**0.43** (0.399 - 0.452)	**0.14** (0.095 - 0.161)	**0.19** (0.135 - 0.238)	**0.03** (0.002 - 0.045)	**0.02** (0.013 - 0.028)	**0.80** (0.735 - 0.892)
Mar	**0.51** (0.492 - 0.538)	**0.10** (0.097 - 0.102)	**0.19** (0.144 - 0.228)	**0.05** (0.029 - 0.089)	**0.02** (0.014 - 0.021)	**0.87** (0.806 - 0.912)
Apr	**0.55** (0.546 - 0.569)	**0.04** (0.032 - 0.061)	**0.19** (0.163 - 0.221)	**0.04** (0.022 - 0.064)	**0.01** (0.008 - 0.020)	**0.84** (0.818 - 0.854)
May	**0.56** (0.528 - 0.583)	**0.18** (0.162 - 0.197)	**0.27** (0.218 - 0.319)	**0.07** (0.048 - 0.088)	**0.01** (0.010 - 0.017)	**1.08** (1.007 - 1.169)
Total	**6.24** (6.095 - 6.462)	**1.12** (1.083 - 1.163)	**2.62** (2.103 - 3.030)	**0.90** (0.862 - 0.955)	**0.21** (0.181 - 0.264)	**11.09** (11.500 - 11.669)

Table 5.1 The mean (n = 3) monthly distribution data of mangrove litterfall (t / ha) from June 1993 to May 1994 in Bintuni Bay, Irian Jaya. Ranges are given in parentheses.

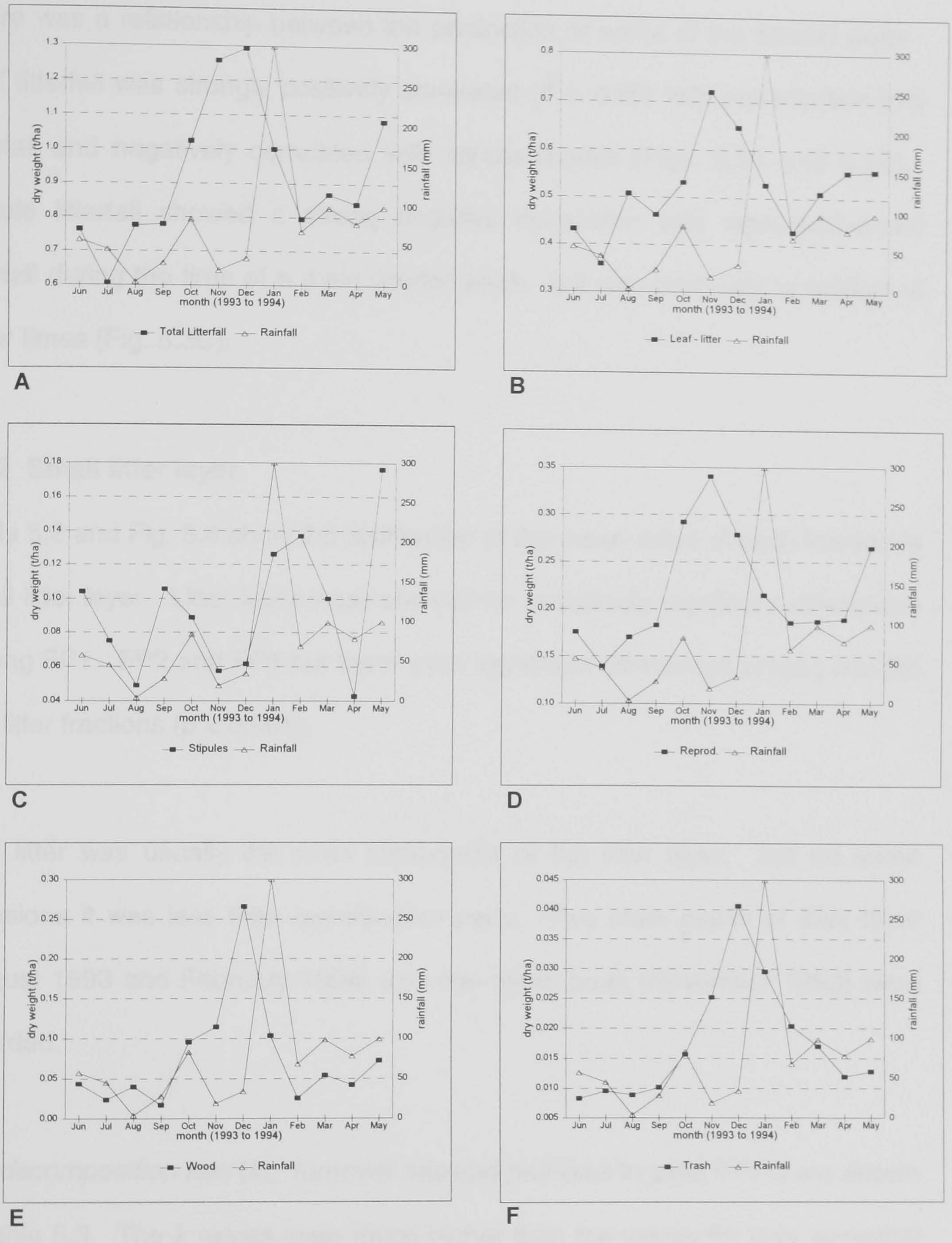


Fig. 5.2 Monthly rainfall and litterfall distribution from June 1993 to May 1994 in Bintuni Bay, Irian Jaya.

There was a relationship between the production of some of the litterfall parts. Leaf litterfall was strongly positively correlated ($r^2 = 0.86$) with reproductive-part litterfall and negatively correlated with stipule litterfall (Figs. 5.3A and 5.3B). Stipule litterfall showed a strong negative correlation with reproductive-part litterfall during the time of a main litterfall peak, but was positively correlated at other times (Fig. 5.3C).

5.4.2 Small litter layer

Table 5.2 and Fig. 5.4 show the distribution of the mean value of each fraction of small litter layer. Litter layer mass showed no statistically significant differences among FP1, FP2 and FP3 but there were significant differences among months and litter fractions ($p < 0.001$).

Leaf litter was usually the main component of the litter layer, but on some occasions it was less than reproductive parts. Two main peaks of litter layer (August 1993 and February 1994) and one minor peak (November 1993) were recorded.

The *decomposition rate* (*k*), *turnover rate* and *half-lives* in plots FP1-3 are shown in Table 5.3. The *k* values were much higher than the values for truly terrestrial tropical rain forests (Olson 1963, Anderson & Swift 1983) because of the removal of litter by sea water and hence the *k* values are not really comparable. The removal by sea water will differ with the tides and will be offset to some extent by an inflow as well as the outflow.

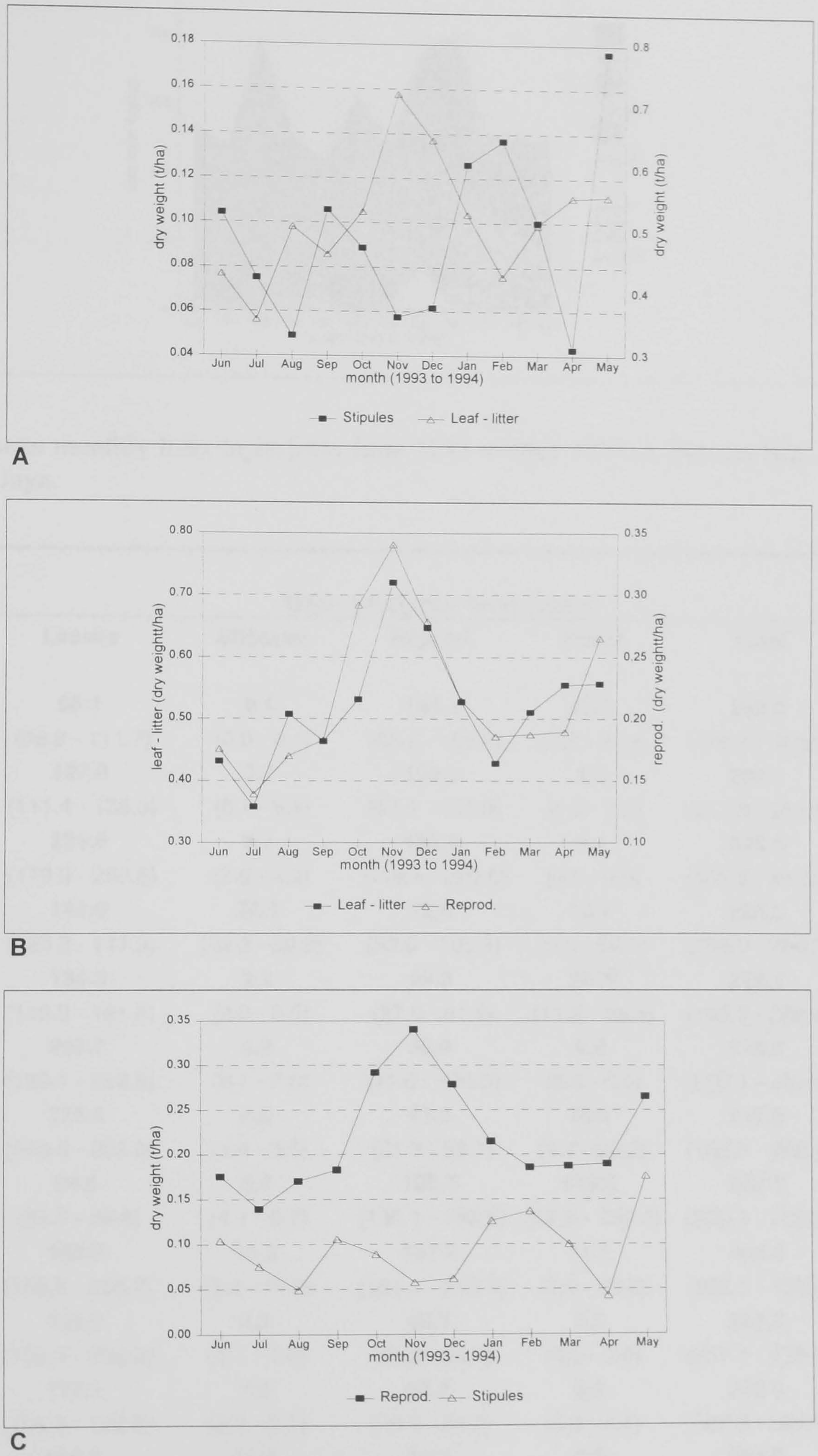


Fig. 5.3 Monthly distribution of some litterfall fractions from June 1993 to May 1994 in Bintuni Bay, Irian Jaya. A. stipules and leaf litter, B. leaf litter and reproductive parts, C. reproductive parts and stipules.

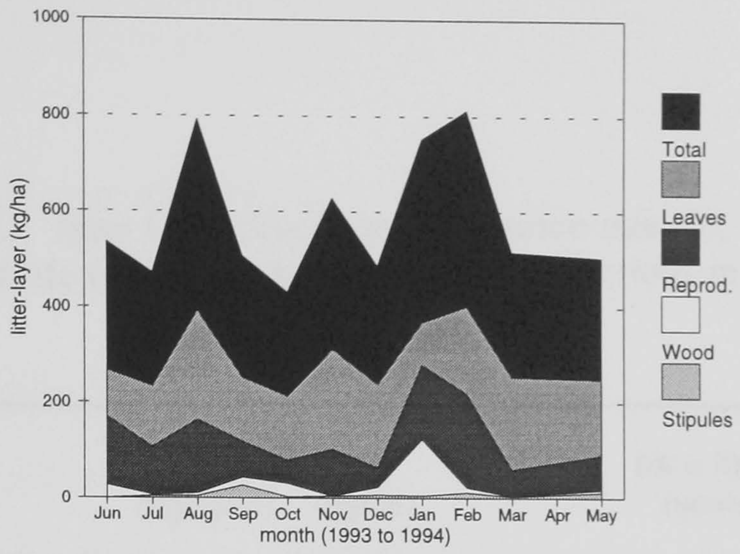


Fig. 5.4 The mean monthly litter-layer from June 1993 to May 1994 in Bintuni Bay, Irian Jaya.

	Mean small-litter layer (kg/ha)				
	Leaves	**Stipules**	**Reprod.**	**Wood**	**Total**
Jun	**96.1**	**0.1**	**143.4**	**27.5**	**269.0**
	(86.9 - 111.7)	(0.0 - 0.1)	(65.2 - 198.9)	(3.2 - 61.2)	(155.6 - 350.7)
Jul	**127.0**	**3.7**	**100.9**	**2.5**	**238.1**
	(111.4 - 135.3)	(0.7 - 5.4)	(67.0 - 135.8)	(0.0 - 7.2)	(211.8 - 251.6)
Aug	**228.6**	**3.7**	**155.0**	**6.1**	**398.9**
	(179.9 - 259.8)	(2.9 - 4.2)	(119.4 - 223.6)	(0.0 - 9.6)	(383.6 - 412.2)
Sep	**133.0**	**26.1**	**75.9**	**16.7**	**255.3**
	(120.3 - 141.9)	(22.3 - 39.3)	(53.8 - 105.3)	(0.0 - 50.0)	(234.0 - 280.3)
Oct	**134.8**	**2.2**	**48.3**	**28.7**	**218.1**
	(113.3 - 161.8)	(2.0 - 3.5)	(37.0 - 61.4)	(11.5 - 38.4)	(192.8 - 266.6)
Nov	**209.7**	**4.2**	**98.6**	**0.0**	**316.6**
	(120.1 - 256.9)	(2.7 - 7.0)	(31.6 - 188.5)	(0.0 - 0.0)	(200.1 - 453.4)
Dec	**175.2**	**6.6**	**41.3**	**16.4**	**247.8**
	(148.6 - 202.0)	(4.4 - 9.5)	(21.3 - 58.1)	(4.7 - 25.2)	(188.5 - 289.1)
Jan	**89.6**	**5.4**	**155.3**	**119.2**	**382.1**
	(89.5 - 89.8)	(4.1 - 6.7)	(130.1 - 180.5)	(57.8 - 180.7)	(335.3 - 429.0)
Feb	**183.8**	**11.3**	**197.2**	**11.1**	**409.3**
	(158.8 - 208.7)	(5.4 - 17.2)	(181.1 - 213.3)	(2.2 - 20.0)	(365.1 - 453.5)
Mar	**194.2**	**3.3**	**56.7**	**0.3**	**262.3**
	(188.3 - 206.0)	(2.1 - 5.6)	(49.2 - 60.4)	(0.0 - 0.9)	(257.1 - 272.7)
Apr	**177.1**	**7.3**	**64.7**	**3.2**	**258.5**
	(166.5 - 190.3)	(5.3 - 9.1)	(35.9 - 81.2)	(0.8 - 4.4)	(227.5 - 288.8)
May	**160.0**	**11.4**	**72.7**	**6.0**	**254.6**
	(142.8 - 192.4)	(8.5 - 13.1)	(22.6 - 102.0)	(0.8 - 8.8)	(182.3 - 320.5)

Table 5.2 The mean (n = 3) monthly data of mangrove litter-layer from June 1993 to May 1994 in Bintuni Bay, Irian Jaya. Ranges are given in parentheses.

Table 5.3 The litterfall (*L*), litter layer (*Xss*), decomposition rate (*k*), turnover rate (1 / *k*) and half-life ($t_{0.5}$) of each of the litterfall fractions in Bintuni Bay, Irian Jaya.

		L (kg/ha/yr)	***Xss*** (kg/ha)	***k = L/Xss***	***1/k = Xss/L*** (years)	**Half-lives** *(0.6931/k)*
FP1	Leaves	6462	162.8	39.7	0.03	0.017
	Stipules	1125	5.6	200.5	0.00	0.003
	Reprod.	3030	124.3	24.4	0.04	0.028
	Wood	872	18.0	48.3	0.02	0.014
	Total	11489	310.8	37.0	0.03	0.019
FP2	Leaves	6150	152.2	40.4	0.02	0.017
	Stipules	1163	9.6	121.0	0.01	0.006
	Reprod.	2727	73.7	37.0	0.03	0.019
	Wood	862	21.8	39.6	0.03	0.018
	Total	10903	257.3	42.4	0.02	0.016
FP3	Leaves	6095	162.3	37.6	0.03	0.018
	Stipules	1083	6.1	178.8	0.01	0.004
	Reprod.	2103	104.5	20.1	0.05	0.034
	Wood	955	19.6	48.7	0.02	0.014
	Total	10236	292.4	35.0	0.03	0.020
Mean	Leaves	6236	159.1	39.2	0.03	0.018
	Stipules	1124	7.1	158.4	0.01	0.004
	Reprod.	2620	100.8	26.0	0.04	0.027
	Wood	896	19.8	45.2	0.02	0.015
	Total	10876	286.8	37.9	0.03	0.018

5.4.3 Small litterfall mineral-elements

5.4.3.1 Mineral-element concentration

In general, the concentrations of each element analysed from the litterfall were significantly different with time ($p = 0.017$), and among the litterfall fractions by time ($p = 0.019$), but they were not different among the plots (FP1-3).

In the leaf litterfall only the concentrations of calcium and magnesium showed no significant differences with time (Tables 5.4 and 5.5). Nitrogen usually had the highest concentration but was occasionally exceeded by calcium or sodium (Fig. 5.5A). Among all the litterfall fractions, the leaf litter had the highest concentrations of sodium and magnesium (Figs. 5.6 D and F).

Stipules had a similar element concentration distribution pattern with time as the leaf litter but the concentrations were lower (Fig. 5.5 B). Stipular nitrogen and calcium concentrations were not significantly different with time (Tables 5.4 and 5.5).

The concentrations of all elements in the reproductive parts were significantly different with time (Tables 5.4 and 5.5). Nitrogen had the highest concentrations (Fig. 5.5C) ranging from 37.1 mg g^{-1} in April to 16.1 mg g^{-1} in January. Calcium and sodium were more or less at the same concentration throughout. Phosphorus had the lowest concentration. Potassium had its highest concentrations in all months in the reproductive parts (Fig. 5.6C).

Table 5.4 The mean (n = 3) monthly data of each litter fraction elements from June 1993 to May 1994 in Bintuni Bay, Irian Jaya. Ranges are given in parentheses.

	Leaves						Stipules					
	N (mg/g)	P (mg/g)	K (mg/g)	Na (mg/g)	Ca (mg/g)	Mg (mg/g)	N (mg/g)	P (mg/g)	K (mg/g)	Na (mg/g)	Ca (mg/g)	Mg (mg/g)
Jun	**18.2**	**0.5**	**4.4**	**15.3**	**22.4**	**6.1**	**10.0**	**0.4**	**3.8**	**13.4**	**9.6**	**2.9**
	(13.6-21.9)	(0.4-0.6)	(4.0-5.1)	(13.9-16.2)	(21.0-23.5)	(5.1-6.8)	(8.2-13.4)	(0.4-0.4)	(3.7-3.9)	(10.5-17.	(9.1-10.7)	(2.8-3.3)
Jul	**13.4**	**0.5**	**3.3**	**12.5**	**23.5**	**5.4**	**10.2**	**0.3**	**2.8**	**7.3**	**10.5**	**2.4**
	(10.3-18.0)	(0.5-0.6)	(2.8-3.7)	(11.5-14.0)	(21.7-24.5)	(4.3-6.0)	(9.2-11.6)	(0.3-0.4)	(2.7-3.0)	(5.9-8.8)	(9.0-12.2)	(2.4-2.5)
Aug	**21.2**	**0.5**	**4.6**	**25.7**	**23.9**	**6.8**	**11.4**	**0.4**	**4.0**	**13.8**	**9.4**	**3.0**
	(17.1-27.2)	(0.4-0.6)	(4.2-5.2)	(20.6-30.1)	(23.3-24.6)	(6.0-7.3)	(8.4-16.1)	(0.4-0.5)	(3.6-4.7)	(11.5-16.	(7.5-11.6)	(2.9-3.1)
Sep	**17.9**	**0.4**	**4.2**	**16.9**	**15.9**	**6.5**	**12.2**	**0.4**	**4.2**	**14.4**	**9.7**	**2.7**
	(15.5-19.8)	(0.3-0.6)	(3.5-4.9)	(13.0-19.4)	(11.6-24.0)	(5.6-7.0)	(10.2-15.	(0.4-0.4)	(4.1-4.6)	(11.6-17.	(9.1-10.2)	(2.5-2.8)
Oct	**19.5**	**0.5**	**3.8**	**15.0**	**23.4**	**6.3**	**8.4**	**0.4**	**3.3**	**9.8**	**10.7**	**2.6**
	(18.5-20.3)	(0.4-0.6)	(3.4-4.0)	(13.0-16.5)	(23.2-23.6)	(5.4-6.8)	(0.0-13.6)	(0.3-0.4)	(3.1-3.5)	(9.6-10.1)	(10.2-11.	(2.4-2.6)
Nov	**18.6**	**0.5**	**4.3**	**16.3**	**22.9**	**6.2**	**14.4**	**0.4**	**3.4**	**9.7**	**11.1**	**2.6**
	(17.8-19.3)	(0.4-0.6)	(3.5-5.1)	(13.5-19.2)	(22.0-23.9)	(4.9-6.8)	(12.4-17.	(0.3-0.4)	(3.3-3.6)	(8.7-11.1)	(10.5-11.	(2.4-2.7)
Dec	**23.6**	**0.7**	**4.0**	**12.3**	**19.3**	**5.6**	**13.0**	**0.4**	**3.1**	**8.0**	**12.1**	**2.8**
	(18.7-30.0)	(0.6-0.8)	(3.7-4.4)	(8.8-17.4)	(14.3-23.3)	(4.4-6.6)	(6.1-16.8)	(0.4-0.5)	(2.9-3.1)	(7.3-8.5)	(11.1-13.	(2.8-2.9)
Jan	**27.4**	**0.7**	**3.6**	**11.9**	**23.0**	**5.5**	**12.2**	**0.3**	**3.1**	**8.8**	**10.5**	**2.4**
	(25.4-30.0)	(0.6-0.7)	(3.3-3.9)	(9.8-12.9)	(21.5-24.4)	(4.8-6.0)	(9.4-16.0)	(0.3-0.4)	(2.9-3.3)	(7.4-9.6)	(9.5-11.7)	(2.4-2.5)
Feb	**16.5**	**0.6**	**4.2**	**13.7**	**23.2**	**6.0**	**6.3**	**0.4**	**3.6**	**10.6**	**9.9**	**3.6**
	(14.5-17.6)	(0.5-0.7)	(3.3-4.7)	(11.3-16.4)	(19.3-26.4)	(4.8-6.8)	(0.0-10.3)	(0.4-0.5)	(3.4-4.1)	(9.4-12.7)	(8.1-11.8)	(2.6-5.3)
Mar	**28.5**	**0.4**	**2.9**	**10.2**	**21.9**	**4.7**	**18.8**	**0.3**	**2.5**	**7.5**	**10.3**	**2.3**
	(26.9-30.4)	(0.3-0.5)	(2.7-3.0)	(9.8-10.8)	(19.4-23.4)	(3.8-5.3)	(18.7-18.	(0.2-0.3)	(2.3-2.6)	(5.5-8.8)	(9.1-11.1)	(2.2-2.4)
Apr	**25.5**	**0.3**	**3.7**	**15.2**	**21.7**	**5.7**	**17.0**	**0.3**	**2.9**	**11.6**	**10.7**	**2.9**
	(24.9-26.1)	(0.3-0.4)	(3.4-4.0)	(14.4-15.8)	(19.2-23.1)	(4.7-6.4)	(16.6-17.	(0.3-0.3)	(2.7-3.0)	(7.9-17.3)	(9.2-12.1)	(2.5-3.4)
May	**27.3**	**0.3**	**3.5**	**13.6**	**23**	**5.4**	**13.6**	**0.2**	**3.2**	**10.6**	**9.3**	**2.3**
	(24.7-29.8)	(0.3-0.4)	(3.2-3.7)	(12.5-14.7)	(21.9-24.6)	(4.8-5.9)	(8.0-16.8)	(0.2-0.3)	(3.1-3.3)	(9.1-12.8)	(8.3-10.4)	(2.2-2.4)

Cont.

cont.

	Reproductive parts						Wood					
	N (mg/g)	P (mg/g)	K (mg/g)	Na (mg/g)	Ca (mg/g)	Mg (mg/g)	N (mg/g)	P (mg/g)	K (mg/g)	Na (mg/g)	Ca (mg/g)	Mg (mg/g)
Jun	**18.7**	**0.9**	**5.8**	**12.1**	**9.4**	**2.8**	**20.9**	**0.3**	**1.1**	**2.3**	**28.2**	**1.9**
	(17.7-19.7)	(0.9-1.0)	(5.6-6.0)	(10.8-13.5)	(8.3-11.4)	(2.5-3.3)	(14.3-27.3)	(0.3-0.4)	(0.8-1.4)	(1.1-3.8)	(25.9-31.5)	(1.5-2.3)
Jul	**20.6**	**0.8**	**4.5**	**8.2**	**12.1**	**3.1**	**21.3**	**0.3**	**1.1**	**2.2**	**32.3**	**1.6**
	(18.7-22.2)	(0.7-0.9)	(4.3-4.7)	(7.5-9.1)	(9.0-14.6)	(2.2-3.6)	(17.7-27.2)	(0.2-0.3)	(0.9-1.3)	(1.7-3.2)	(27.9-38.6)	(1.6-1.7)
Aug	**21.5**	**0.8**	**5.9**	**12.2**	**9.8**	**3.0**	**18.3**	**0.3**	**1.4**	**4.4**	**25.7**	**2.1**
	(16.9-24.8)	(0.8-0.9)	(5.3-6.4)	(8.8-14.7)	(8.6-10.7)	(92.6-3.5)	(17.3-19.2)	(0.2-0.5)	(1.0-2.0)	(3.1-5.7)	(16.4-31.9)	(1.6-2.4)
Sep	**21.9**	**0.9**	**6.0**	**12.4**	**11.2**	**3.5**	**24.8**	**0.4**	**1.3**	**2.7**	**30.6**	**2.2**
	(17.6-26.1)	(0.8-0.9)	(5.4-6.5)	(9.6-15.2)	(10.0-12.1)	(3.0-3.8)	(16.8-30.6)	(0.3-0.5)	(1.3-1.3)	(2.1-3.4)	(26.9-34.3)	(2.0-2.3)
Oct	**18.4**	**0.8**	**5.9**	**13.8**	**12.5**	**3.5**	**18.3**	**0.3**	**1.4**	**4.8**	**32.9**	**2.0**
	(15.7-21.5)	(0.8-0.8)	(5.6-6.2)	(10.7-18.7)	(9.5-14.3)	(2.6-4.0)	(11.3-22.2)	(0.2-0.4)	(1.2-1.5)	(1.6-10.1)	(20.7-55.5)	(1.0-3.6)
Nov	**19.0**	**0.8**	**5.6**	**11.8**	**11.5**	**3.1**	**16.9**	**0.2**	**1.4**	**4.5**	**28.4**	**1.8**
	(12.1-22.9)	(0.7-0.9)	(5.4-5.8)	(10.5-12.8)	(11.1-12.0)	(2.7-3.5)	(12.7-19.5)	(0.2-0.3)	(1.2-1.6)	(3.8-5.4)	(24.7-32.7)	(1.6-2.2)
Dec	**21.8**	**0.9**	**4.7**	**8.5**	**8.9**	**2.4**	**20.6**	**0.3**	**1.4**	**3.6**	**26.0**	**1.9**
	(17.1-26.7)	(0.9-1.0)	(4.7-4.7)	(8.2-8.9)	(8.3-10.0)	(2.0-2.6)	(17.2-26.4)	(0.3-0.3)	(1.4-1.5)	(3.1-3.9)	(22.0-28.4)	(1.7-2.1)
Jan	**16.1**	**0.9**	**4.6**	**8.3**	**8.8**	**2.2**	**18.4**	**0.3**	**1.6**	**3.5**	**25.7**	**1.8**
	(12.5-21.9)	(0.9-1.1)	(4.3-4.9)	(6.4-11.0)	(7.4-10.0)	(2.1-2.4)	(14.3-23.2)	(0.3-0.4)	(1.6-1.7)	(2.7-4.7)	(18.4-31.9)	(1.6-2.0)
Feb	**22.4**	**0.9**	**5.0**	**9.6**	**8.2**	**2.2**	**18.5**	**0.3**	**1.3**	**2.6**	**30.1**	**1.8**
	(17.0-29.1)	(0.7-1.0)	(4.7-5.5)	(7.2-12.3)	(7.3-8.9)	(2.1-2.4)	(16.1-20.0)	(0.2-0.3)	(1.3-1.3)	(2.3-2.8)	(21.2-35.5)	(1.6-2.1)
Mar	**30.8**	**0.6**	**3.8**	**7.1**	**5.5**	**1.3**	**25.1**	**0.2**	**1.3**	**2.6**	**27.2**	**1.5**
	(22.0-37.0)	(0.5-0.7)	(2.6-4.8)	(5.0-9.2)	(5.1-6.0)	(1.1-1.5)	(20.0-30.1)	(0.2-0.3)	(1.2-1.4)	(2.2-3.1)	(24.5-29.1)	(1.5-1.6)
Apr	**37.1**	**0.8**	**4.6**	**10.1**	**5.4**	**1.5**	**30.2**	**0.3**	**1.4**	**3.2**	**33.1**	**2.2**
	(34.3-39.0)	(0.7-0.8)	(4.2-4.8)	(6.7-12.0)	(4.6-6.9)	(1.4-1.7)	(24.2-40.1)	(0.2-0.6)	(1.2-1.7)	(3.0-3.6)	(21.5-45.4)	(1.4-2.9)
May	**36.5**	**0.8**	**4.2**	**8.0**	**5.7**	**1.5**	**28.9**	**0.3**	**1.4**	**3.0**	**28.8**	**1.6**
	(34.9-37.4)	(0.8-0.8)	(4.1-4.4)	(7.1-8.5)	(4.5-7.4)	(1.3-1.7)	(26.8-30.9)	(0.3-0.4)	(1.0-1.7)	(2.1-3.6)	(24.1-31.7)	(1.3-2.0)

cont.

cont.

	Trash					
	N (mg/g)	P (mg/g)	K (mg/g)	Na (mg/g)	Ca (mg/g)	Mg (mg/g)
Jun	**39.4** (37.1-42.1)	**0.7** (0.7-0.8)	**3.4** (3.1-3.9)	**9.2** (8.8-9.9)	**23.3** (20.9-25.	**4.1** (3.3-4.7)
Jul	**40.0** (24.1-55.1)	**1.2** (0.6-2.1)	**2.6** (2.5-2.7)	**5.3** (5.3-5.3)	**31.2** (17.1-53.	**4.4** (3.1-5.8)
Aug	**45.7** (36.9-52.2)	**0.9** (0.6-1.1)	**3.5** (3.1-3.8)	**15.8** (10.1-0.2)	**19.4** (16.8-22.	**4.9** (4.2-5.5)
Sep	**53.3** (43.5-60.3)	**0.9** (0.7-1.2)	**3.7** (3.3-4.3)	**9.7** (8.8-10.9)	**25.4** (18.3-30.	**4.7** (4.0-5.8)
Oct	**51.3** (39.0-62.8)	**1.2** (0.6-2.4)	**3.1** (2.7-3.4)	**8.1** (6.7-9.1)	**25.6** (14.6-40.	**4.4** (3.8-4.7)
Nov	**47.1** (42.0-56.0)	**1.1** (0.7-1.4)	**3.2** (2.6-3.6)	**7.3** (6.0-9.3)	**30.3** (26.3-38.	**4.1** (3.7-4.3)
Dec	**50.1** (46.1-54.6)	**1.2** (0.8-2.0)	**3.5** (3.1-4.3)	**6.7** (5.5-7.9)	**32.3** (20.7-51.	**4.4** (3.2-6.4)
Jan	**48.1** (36.2-55.7)	**1.3** (1.2-1.5)	**3.1** (3.1-3.3)	**6.3** (5.6-7.1)	**34.4** (31.9-37.	**5.0** (4.1-5.9)
Feb	**48.7** (36.1-72.1)	**1.9** (1.0-3.3)	**3.3** (2.8-3.9)	**7.4** (6.9-7.8)	**53.7** (32.4-66.	**6.0** (4.8-7.3)
Mar	**52.8** (38.7-77.3)	**1.4** (1.2-1.7)	**2.6** (1.9-3.2)	**5.0** (3.9-6.0)	**39.5** (21.0-52.	**2.5** (0.0-4.1)
Apr	**54.4** (44.6-71.1)	**0.5** (0.3-1.0)	**2.9** (2.7-3.2)	**12.2** (7.3-15.5)	**25.5** (18.2-30.	**3.6** (2.4-5.2)
May	**53.1** (37.7-83.8)	**0.9** (0.6-1.1)	**3.1** (2.9-3.4)	**9.2** (5.2-14.7)	**20.8** (17.7-23.	**3.6** (3.0-4.7)

Table 5.5 The significance of differences in mangrove litterfall element concentrations among monthly collections from June 1993 - May 1994 in Bintuni Bay, Irian Jaya.

	N	P	K	Na	Ca	Mg
Leaves	0.000**	0.001**	0.012*	0.000**	0.079^{NS}	0.302^{NS}
Stipules	0.084^{NS}	0.000**	0.000**	0.000**	0.385^{NS}	0.035*
Reprod.	0.000**	0.002**	0.000**	0.000**	0.000**	0.000**
Wood	0.067^{NS}	0.817^{NS}	0.514^{NS}	0.125^{NS}	0.975^{NS}	0.864^{NS}
Trash	0.950^{NS}	0.395^{NS}	0.107^{NS}	0.000**	0.091^{NS}	0.201^{NS}

$^{**} = P \leq 0.01$, $^{*} = P \leq 0.05$, ^{NS} = not significant

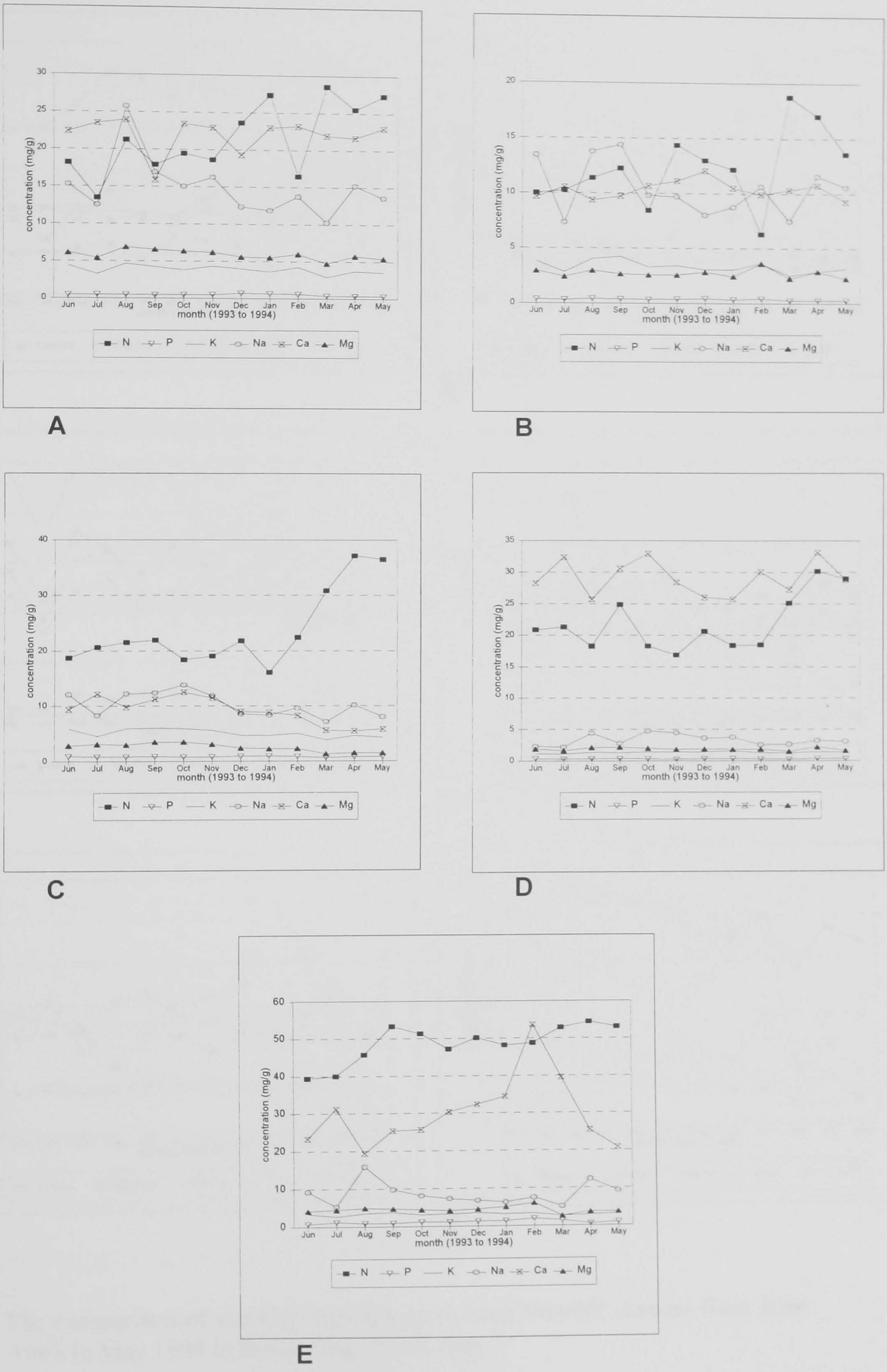


Fig. 5.5 The monthly distribution of each element on each litter fraction from June 1993 to May 1994 in Bintuni Bay, Irian Jaya: A Leaves, B Stipules, C Reproductive parts, D Wood, E Trash.

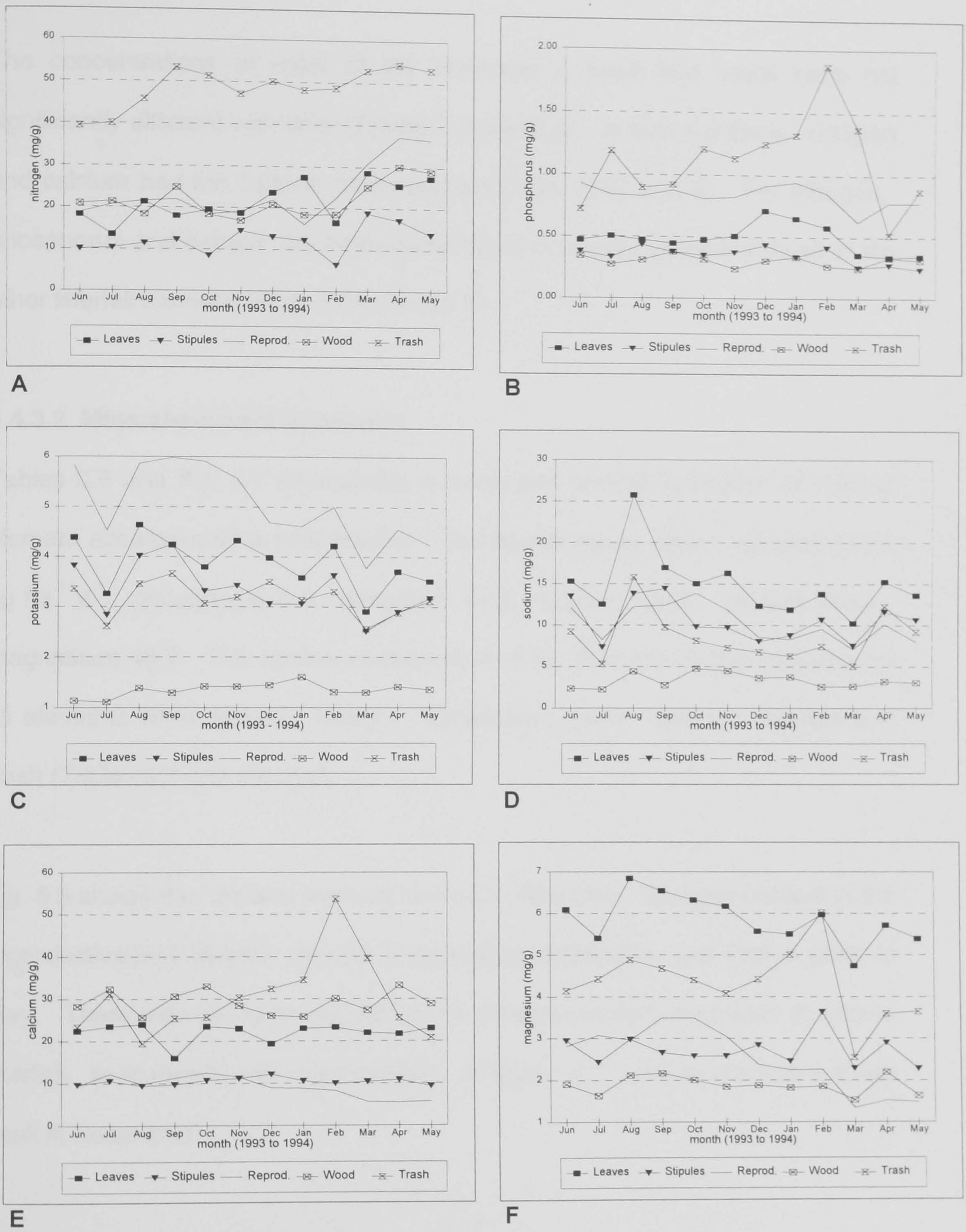


Fig. 5.6 The comparison of monthly distribution of each litterfall element from June 1993 to May 1994 in Bintuni Bay, Irian Jaya.

The concentrations of most of the elements in trash and wood were not significantly different with time (Tables 5.4 and 5.5). In both fractions, nitrogen and calcium had the highest concentrations (Figs. 5.5D and E). For nitrogen, phosphorus and calcium the trash concentrations usually exceeded those in the other litterfall fractions (Figs. 5.6A, B and E)

5.4.3.2 Mineral-element accession

Tables 5.6 and Fig. 5.7 showed the monthly and annual estimation of mineral element accession from total litterfall. The litterfall fluxes were: nitrogen 240.4 kg ha^{-1} y^{-1}, phosphorus 6.1, potassium 43.2, sodium 136.2, calcium 204.4, magnesium 48.7. The relative contributions of the different litterfall fractions for all elements were ranked: leaves, reproductive parts, woods, stipules and trash (Tables 5.7 and Fig. 5.8).

Fig. 5.9 shows the mineral-element accession with time. Nitrogen content in the reproductive-part litterfall showed a fluctuating distribution and had a peak in May. There was no temporal pattern of mineral-element accession in stipule litterfall. In the trash and wood fraction, nitrogen and calcium showed a sharp peak in December.

5.4.4 Leaf-litter decomposition

Fig. 5.10 shows the leaf litter decomposition of the five main mangroves species. *Sonneratia alba* decomposed very fast with only 3.2 % of the initial mass

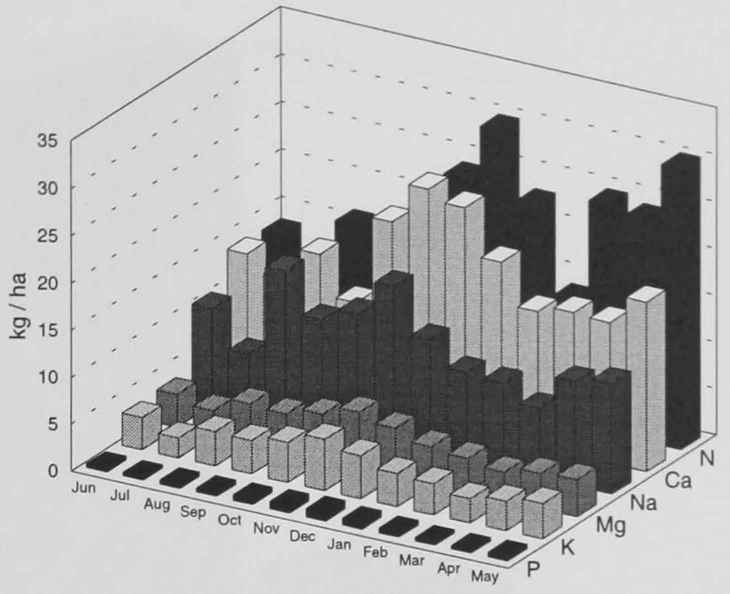


Fig. 5.7 The monthly distribution of litterfall element accession from June 1993 to May 1994 in Bintuni Bay, Irian Jaya.

	Litterfall elements (kg/ha)					
	N	P	K	Na	Ca	Mg
Jun	13.4	0.4	3.4	10.3	13.7	3.6
	(10.4 - 15.1)	(0.4 - 0.5)	(3.3 - 3.6)	(9.0 - 11.2)	(12.6 - 14.7)	(2.8 - 4.2)
Jul	9.3	0.3	2.1	6.3	11.9	2.6
	(7.4 - 11.2)	(0.3 - 0.4)	(1.9 - 2.3)	(5.6 - 7.4)	(10.8 - 13.9)	(2.1 - 3.1)
Aug	16.2	0.4	3.6	16.0	15.4	4.2
	(11.7 - 18.8)	(0.3 - 0.5)	(3.0 - 4.0)	(13.8 - 18.5)	(12.5 - 18.1)	(3.7 - 5.2)
Sep	14.6	0.4	3.6	11.7	11.5	4.0
	(13.6 - 16.2)	(0.3 -0.5)	(3.0 - 3.9)	(9.8 - 13.8)	(9.2 - 15.4)	(3.4 - 4.5)
Oct	18.7	0.6	4.2	13.2	20.4	4.9
	(17.2 - 20.7)	(0.5 - 0.6)	(3.8 - 5.0)	(11.2 - 14.5)	(16.8 - 22.5)	(3.8 - 5.6)
Nov	23.9	0.7	5.4	17.0	25.0	5.9
	(21.1 - 27.1)	(0.7 - 0.8)	(5.2 - 5.6)	(14.4 - 20.4)	(23.2 - 26.1)	(4.7 - 6.9)
Dec	29.3	0.9	4.6	12.2	23.9	5.1
	(24.2 - 35.6)	(0.8 - 1.0)	(4.1 - 5.4)	(9.1 - 16.9)	(18.7 - 30.3)	(3.9 - 6.5)
Jan	22.9	0.7	3.5	9.6	18.8	4.0
	(20.6 - 25.0)	(0.6 - 0.7)	(3.3 - 3.7)	(8.0 - 11.5)	(18.1 - 19.4)	(3.6 - 4.4)
Feb	13.9	0.5	3.3	9.3	14.5	3.6
	(9.4 - 17.9)	(0.5 - 0.6)	(3.2 - 3.4)	(9.0 - 9.9)	(13.4 - 16.2)	(2.9 - 4.3)
Mar	24.3	0.4	2.5	7.5	15.4	3.0
	(23.8 - 24.7)	(0.3 - 0.4)	(2.4 - 2.6)	(7.3 - 7.6)	(13.2 - 16.5)	(2.4 - 3.4)
Apr	23.8	0.4	3.1	11.2	15.1	3.7
	(22.3 - 24.8)	(0.3 - 0.4)	(3.1 - 3.2)	(10.7 - 11.7)	(14.1 - 16.0)	(3.2 - 4.0)
May	29.9	0.5	3.8	11.9	18.2	3.9
	(27.0 - 32.5)	(0.4 - 0.5)	(3.5 - 4.0)	(10.3 - 13.2)	(17.2 - 20.3)	(3.4 - 4.3)
Total	240.4	6.1	43.2	136.2	204.4	48.7
	(230.7 - 246.1)	(5.9 - 6.4)	(42.2 - 44.2)	(123.7 - 145.5)	(186.7 - 216.2)	(39.8 - 53.2)

Table 5.6 The mean (n = 3) monthly data of litterfall element accession from June 1993 to May 1994 in Bintuni Bay, Irian Jaya. Ranges are given in parentheses.

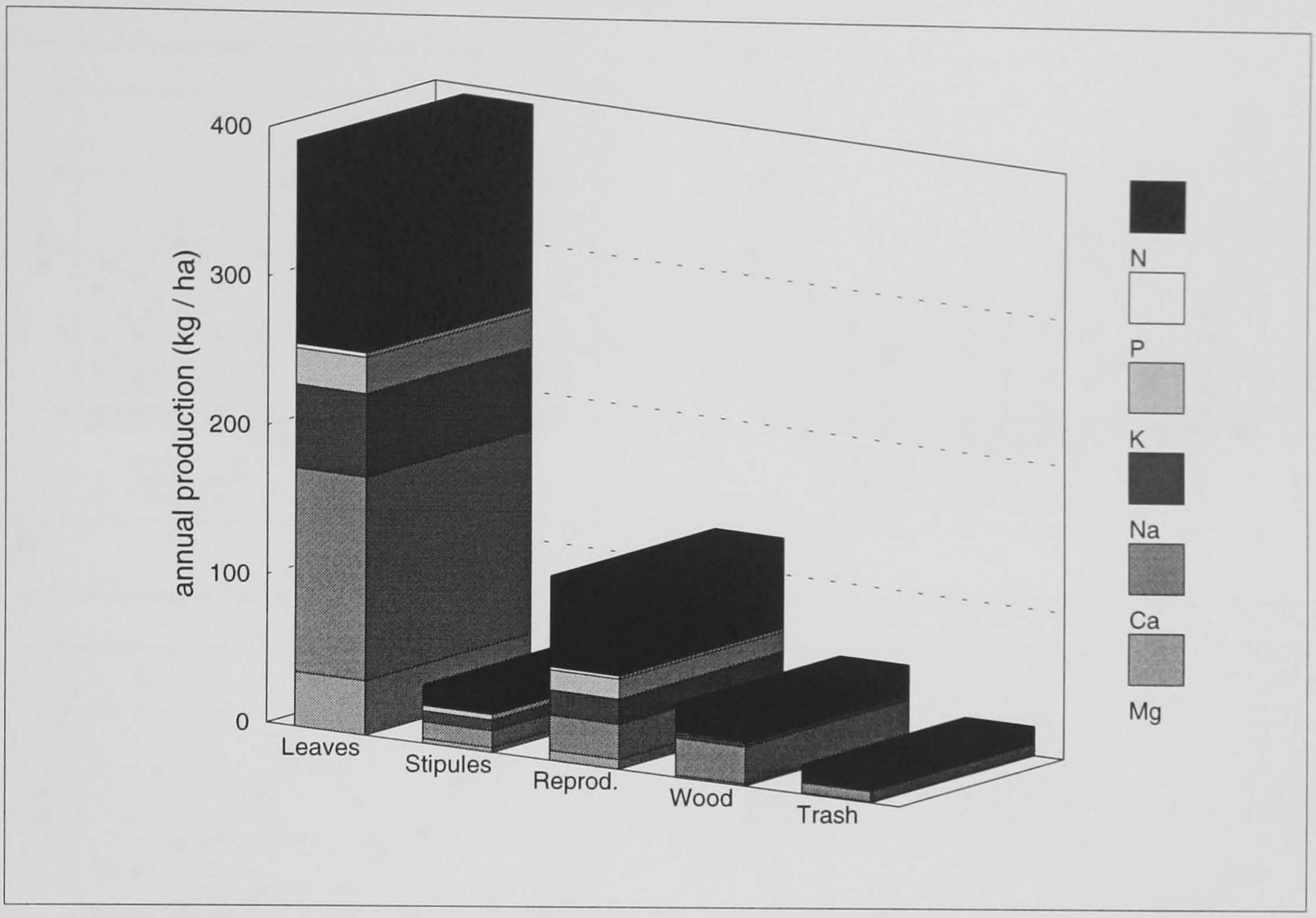


Fig. 5.8 The mean annual accession (June 1993 - May 1994) of chemical elements in each litterfall fraction in Bintuni Bay, Irian Jaya.

	Litterfall elements (kg/ha)					
	N	P	K	Na	Ca	Mg
Leaves	136.1 (133.3 - 138.9)	3.1 (2.7 - 3.5)	24.3 (22.2 - 25.8)	93.0 (83.3 - 99.8)	137.0 (126.1 - 147.0)	36.5 (29.6 - 40.6)
Stipules	13.4 (11.4 - 16.4)	0.4 (0.4 - 0.4)	3.8 (3.6 - 3.8)	11.7 (11.3 - 12.1)	11.4 (10.8 - 12.3)	3.0 (2.8 - 3.4)
Reprod.	61.8 (51.9 - 72.5)	2.2 (1.8 - 2.4)	13.3 (11.1 - 14.6)	26.8 (23.9 - 28.7)	24.1 (18.9 - 26.8)	6.6 (4.8 - 7.7)
Wood	18.8 (16.6 - 20.5)	0.3 (0.2 - 0.3)	1.3 (1.2 - 1.3)	3.1 (2.7 - 3.7)	25.2 (21.5 - 26.9)	1.7 (1.5 - 1.8)
Trash	10.3 (7.6 - 15.9)	0.3 (0.2 - 0.4)	0.7 (0.5 - 0.9)	1.6 (1.3 - 2.2)	6.7 (5.2 - 7.9)	0.9 (0.8 - 0.9)
Total	240.4 (230.7 - 246.1)	6.1 (5.9 - 6.4)	43.2 (42.2 - 44.2)	136.2 (123.7 - 145.5)	204.4 (186.7 - 216.2)	48.7 (39.8 - 53.2)

Table 5.7 The mean ($n = 3$) annual (June 1993 - May 1994) litterfall element accession in Bintuni Bay, Irian Jaya. Ranges are given in parentheses.

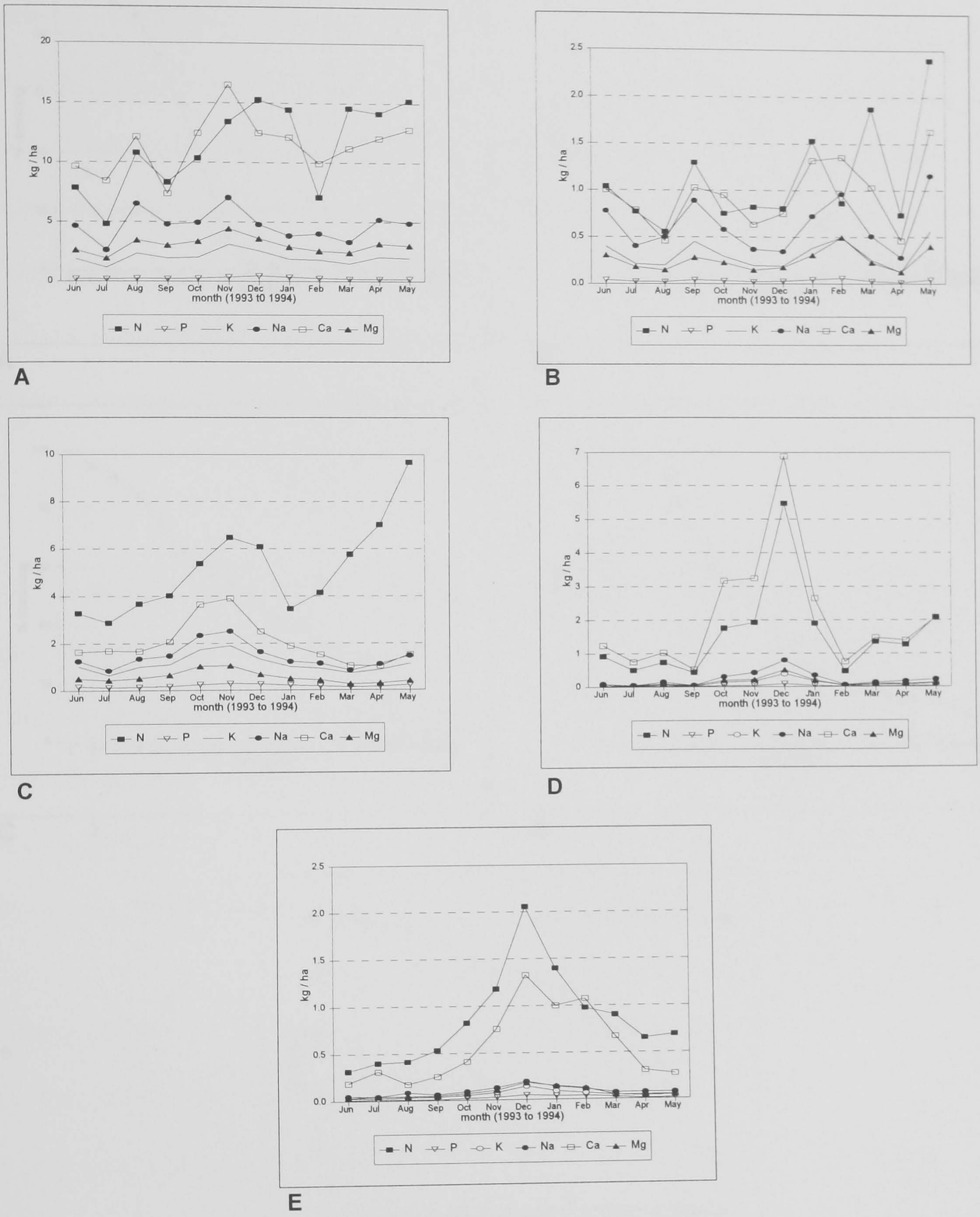


Fig. 5.9 The monthly accession distribution of each element in each litter fraction from June 1993 to May 1994 in Bintuni Bay, Irian Jaya: A. Leaves, B. Stipules, C. Reproductive parts, D. Wood, E. Trash.

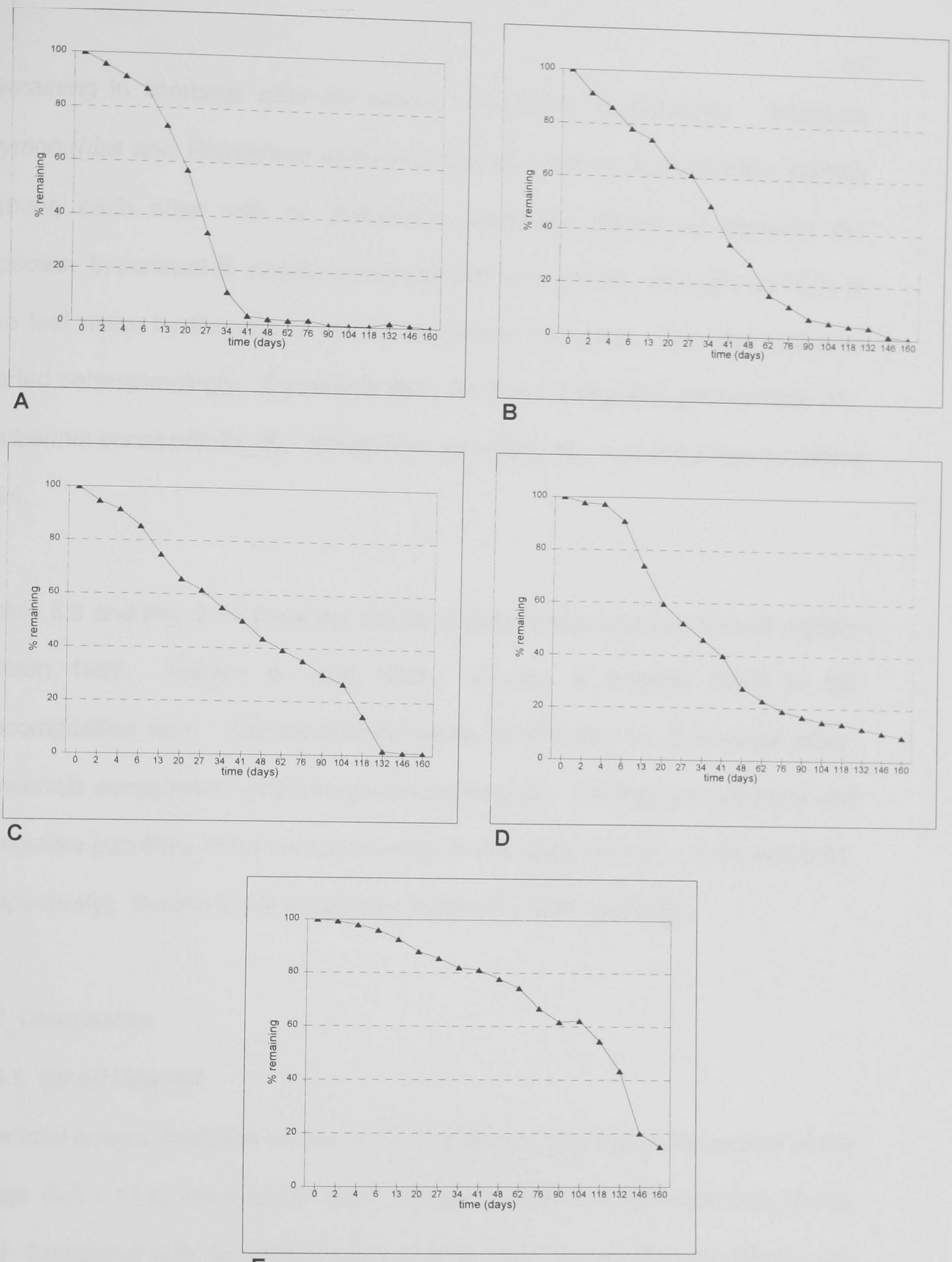


Fig. 5.10 The percentage of leaf litter remaining by time during the decomposition experiment of five main mangrove species in Bintuni Bay, Irian Jaya: A. *Sonneratia alba*, B. *Avicennia eucalyptifolia*, C. *Rhizophora apiculata*, D. *Bruguiera gymnorrhiza*, E. *Bruguiera parviflora*.

remaining in litterbags after six weeks. *Avicennia eucalyptifolia*, *Bruguiera gymnorrhiza* and *Rhizophora apiculata* showed a similar decomposition pattern among each other with no statistically significant differences between the species. In contrast *B. parviflora* decomposed more slowly, and still had 15 % of the leaf mass by the end of the experiment at 160 days. The litter half-lives varied correspondingly: *Sonneratia alba*, 24 days; *Bruguiera gymnorrhiza*, 31; *Avicennia eucalyptifolia*, 35; *Rhizophora apiculata*, 42; and *Bruguiera parviflora* 124.

Table 5.8 and Fig. 5.11 show the results of fitting linear and exponential models (Olson 1963, Wieder & Lang 1982, Ezcurra & Becerra 1987) to the decomposition data. The exponential model fitted better for *Sonneratia alba, Avicennia eucalyptifolia* and *Bruguiera gymnorrhiza*. *Rhizophora apiculata* and *Bruguiera parviflora* fitted the exponential model quite well (r^2 = 0.84 and 0.81, respectively), but the linear model was better (r^2 = 0.94 and 0.95).

5.5 Discussion

5.5.1 Small litterfall

The total annual litterfall of 11.09 t ha^{-1} y^{-1} at Bintuni Bay was in the middle of the range (5.5 - 15.8) reported for other mangrove sites in south-east Asia (Table 5.9). Compared with terrestrial tropical primary rain forests (Proctor 1984), the litterfall from the Bintuni Bay mangroves was higher than in much of primary lowland evergreen rain forest in south-east Asia and New Guinea.

Table 5.8 The linear and exponential regression parameters fitted to the decomposition data of five main mangrove species in Bintuni Bay, Irian Jaya. All regressions were significant ($p \leq 0.001$), i = intercept, k = decomposition rate.

		Linear				Exponential			
		i	*k*	r-sqr	f	*i*	*k*	r-sqr	f
Sonneratia alba	**1**	70.9	0.621	0.63	26.8	70.4	0.044	0.73	44.2
	2	65.6	0.579	0.59	22.6	54.7	0.041	0.69	35.8
	3	72.2	0.641	0.59	23.3	50.3	0.045	0.68	33.3
	4	58.6	0.519	0.61	25.4	80.1	0.051	0.93	224.7
	Mean	66.8	0.590	0.61	25.1	71.4	0.045	0.81	66.8
Avicennia eucalyptifolia	**1**	73.6	0.595	0.80	64.4	113.9	0.034	0.91	168.0
	2	78.6	0.619	0.82	73.2	113.5	0.029	0.93	221.8
	3	73.1	0.594	0.83	76.9	142.9	0.041	0.86	101.6
	4	81.8	0.637	0.87	110.5	157.6	0.036	0.75	49.0
	Mean	76.8	0.611	0.84	82.9	119.6	0.032	0.93	224.0
Rhizophora apiculata	**1**	98.8	0.613	0.92	192.4	176.5	0.028	0.70	38.0
	2	81.7	0.587	0.87	106.0	140.5	0.029	0.80	63.2
	3	74.3	0.557	0.88	114.5	110.8	0.027	0.90	144.8
	4	81.8	0.617	0.87	109.2	121.2	0.027	0.92	192.4
	Mean	84.2	0.593	0.94	231.3	135.1	0.027	0.84	83.6
Bruguiera gymnorrhiza	**1**	78.3	0.492	0.67	32.6	75.7	0.011	0.80	62.5
	2	77.7	0.591	0.81	69.9	92.2	0.021	0.98	686.8
	3	78.5	0.572	0.77	53.8	81.9	0.016	0.90	151.5
	4	79.2	0.582	0.78	58.1	130.2	0.030	0.57	21.1
	Mean	78.4	0.559	0.78	55.8	82.5	0.015	0.94	252.7
Bruguiera parviflora	**1**	97.1	0.459	0.80	63.9	124.5	0.013	0.57	21.2
	2	100.0	0.470	0.99	1362.1	108.3	0.008	0.93	217.1
	3	98.4	0.422	0.94	242.8	106.1	0.007	0.86	97.2
	4	106.0	0.528	0.94	272.6	122.4	0.011	0.79	60.6
	Mean	100.4	0.470	0.95	324.0	112.2	0.009	0.81	66.8

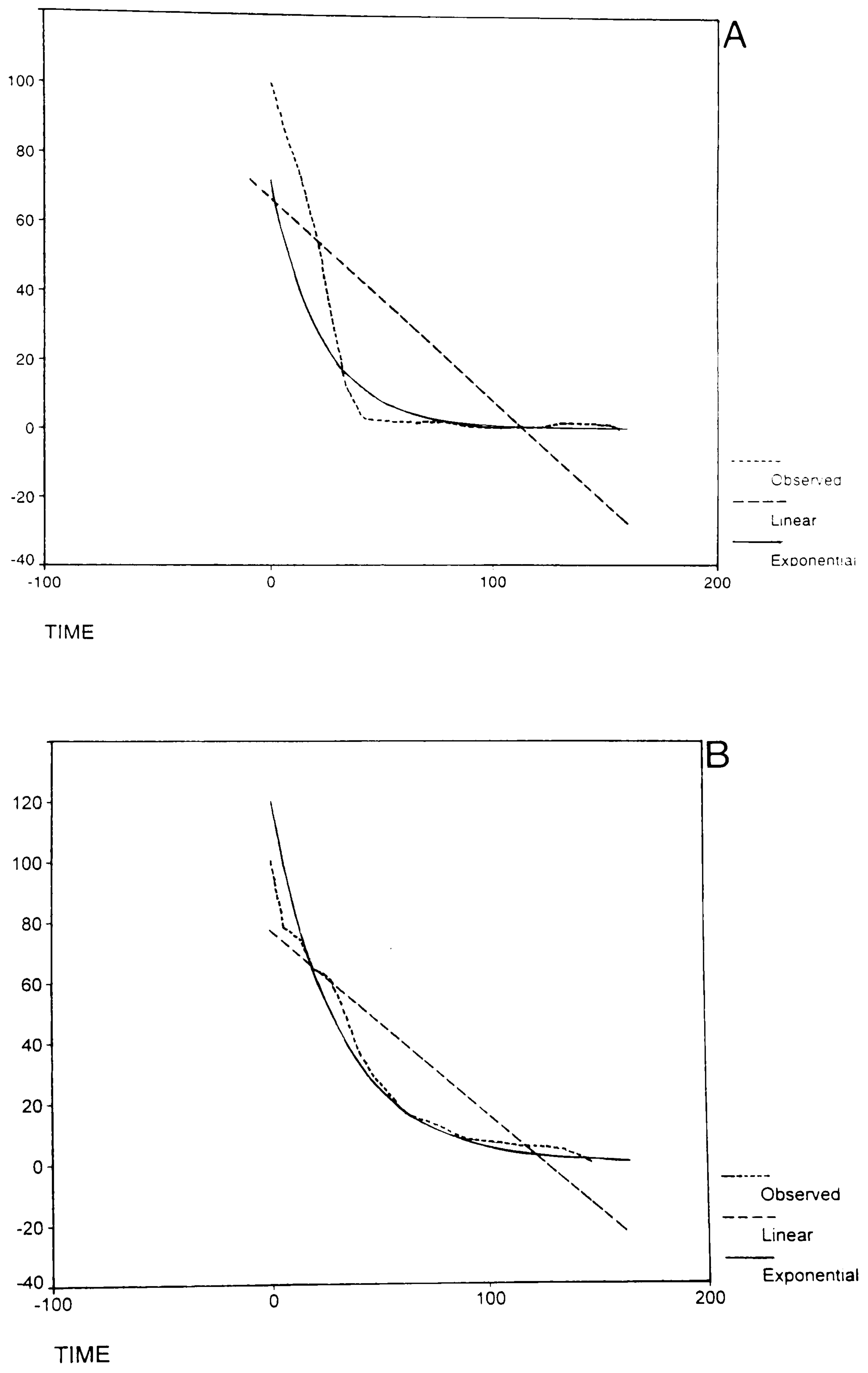


Fig. 5.11 A-B The linear and exponential regression lines fitted to the leaf litter decomposition data: A. *Sonneratia alba*, B. *Avicennia eucalyptifolia*.

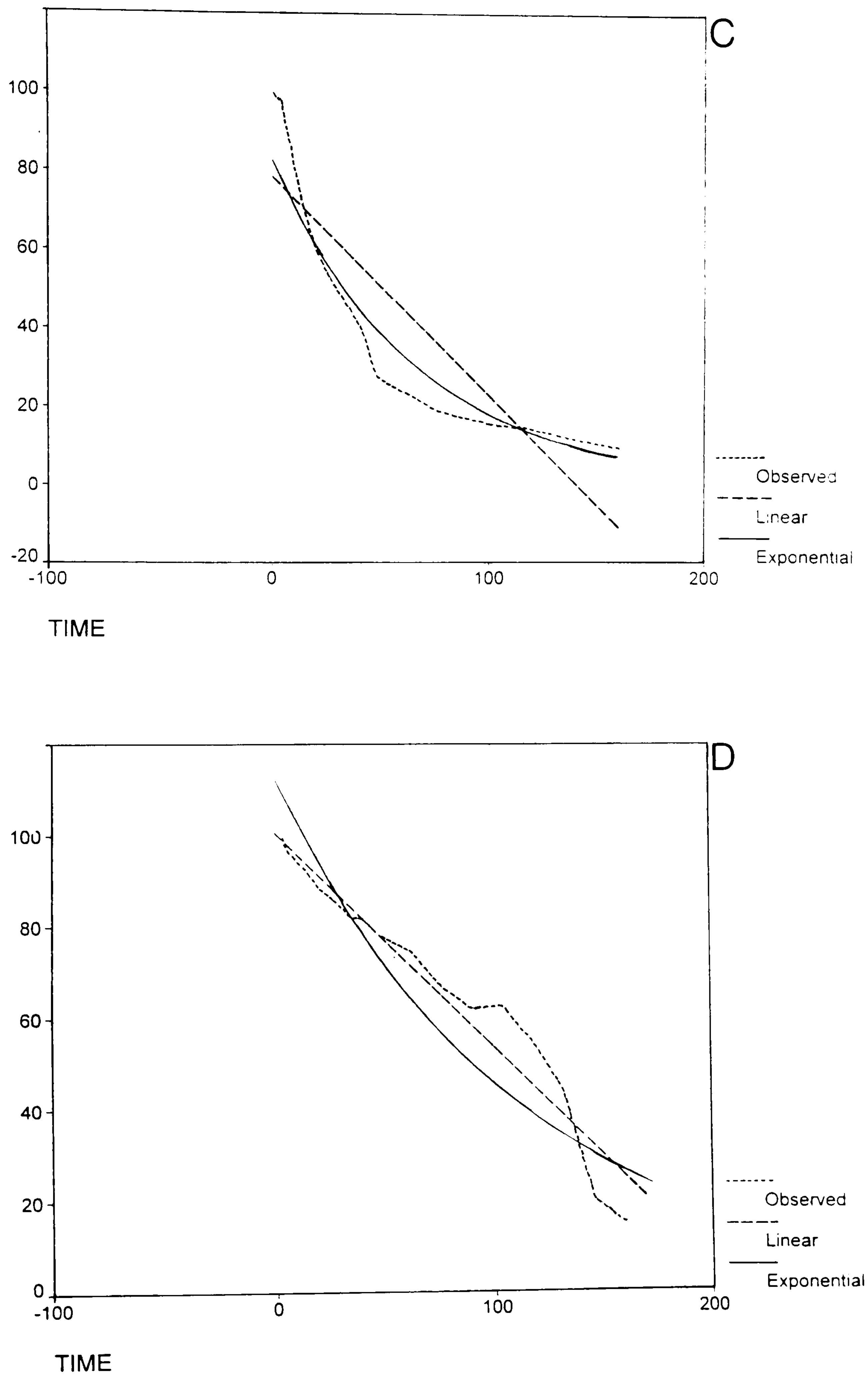


Fig. 5.11 C-D The linear and exponential regression lines fitted to the leaf litter decomposition data: C. *Bruguiera gymnorrhiza*, D. *Bruguiera parviflora*.

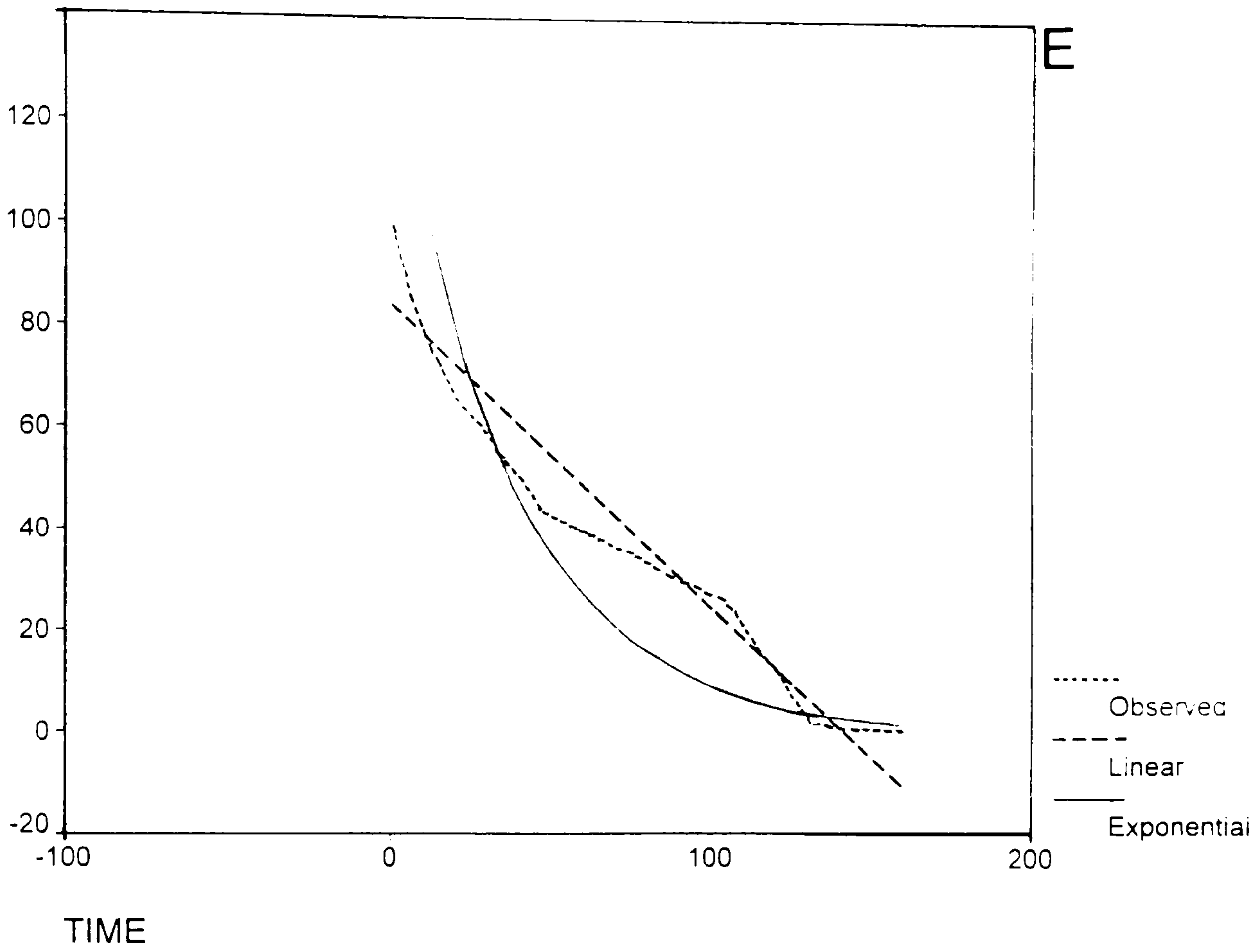


Fig. 5.11 E The linear and exponential regression lines fitted to the leaf litter decomposition data: E. *Rhizophora apiculata.*

Table 5.9 The comparison data of total small litterfall in some mangrove areas.

Location	Mangrove type	Total small litterfall (dry weight t ha^{-1} yr^{-1})	References and comments
Beechwood Mangrove Swamp, Mgeni Estuary, Durban, South Africa (30° S, 32° E)	*Avicennia marina* (height 9 m) *Bruguiera gymnorrhiza* (height 7 m)	4.8 - 9.5 7.8 - 9.5	Steinke & Charles (1984) Annual rainfall 1013 mm Mean annual temperature 21° C Flooded only by spring tides Salinity 16 - 32 ‰
Misionary Bay, Hinchinbrook Island, Australia (18°15' S, 146°15'E)	*Rhizophora* spp. (height up to 20 m)	9.8	Duke *et al.* (1981) Annual rainfall 2127 mm Mean annual temperature 29° C Tidal amplitude 2 - 3 m Substantial additional freshwater run-off from surrounding rivers Salinity 34 - 37‰ Substratum: well sorted silt containing organic matter
Motupore Island, Papua New Guinea (9° 31' 34" S, 147° 17' 02" E)	*Rhizophora stylosa* (dominant) (height 10 m)	14.30	Leach & Burgin (1985) Monsoonal climate Annual rainfall 1200 mm Annual temperature: max 29.6 - 32.6° C min 20.9 - 24.1° C Salinity 30 - 35 ‰ Flushed daily by tide, but a little freshwater input Substratum: coarse sand, coral rubble and a little silt
Vaitupu, Tuvalu, South Pacific (7° 28' S, 178° 42' E)	*Rhizophora stylosa* (height 4-6 m)	7.8	Woodroffe & Moss (1984) Annual rainfall 3000 mm Mean annual temperature 29° C Microtidal ± 1.5 m Substratum: organic-rich silt over dissected limestones
Bintuni Bay, Irian Jaya, Indonesia (02° 02' - 02° 97' S, 132° 55' - 134° 02' E)	Mixed *Rhizophora* - *Bruguiera* forest (height up to 40 m)	11.1	This study Monsoonal climate Annual rainfall 2500 - 3000 mm Mean annual temperature 26° C Tidal amplitude 1 - 5.6 m Substratum: saline peats, sands and silt High fresh water run-off from rivers Salinity 27 ‰
Muara Angke-Kapuk, Jakarta, Indonesia (06° 05' 08" S, 106° 51' 42" E)	*Avicennia -Rhizophora* community (height 10.2 - 14.5 m)	14.0	Sukardjo (1989). Annual rainfall 1783 mm Mean annual temperature 28.4° C Frequently inundated by tides Salinity 29 - 34 ‰
Lundu, Sarawak, Malaysia (01°44' N, 109°52' E)	*Rhizophora mucronata - Rhizophora apiculata* forest	5.7	Othman (1989) Annual rainfall 4260 mm Seasonally wet & strong winds Frequently to seasonally tidal inundation Mean annual temperature 25 - 28° C Substratum: soil derived from biotite and adamellite rocks

Cont.

Cont.

Kuala Selangor, Malaysia (03°15′ N, 101°18′ E)	*Rhizophora* forest (height 10 - 15 m)	15.8	Sasekumar & Loi (1983) Annual rainfall 1900 mm Mean annual temperature 26.6° C Salinity 28 - 35 ‰ Semidiurnal tides, max. 4.9 m Substratum mostly clay and silt
Matang Mangrove Reserve, Perak, Malaysia (04° 50′ N, 100° 35′ E)	Mixed species of Virgin Jungle Reserve (height up to 40 m)	7.6	Gong *et al.* (1984) Mean annual temperature Watson's innundation class 1 to5 (flooded almost every tide - just awashed during spring tide only) Substratum: Sandy loam
	25 yr old *Rhizophora apiculata* stands (height 15 - 30 m)	11.4	
Phang-nga Bay, Thailand (08° 20′ N, 98° 32′ E)	Mixed youngmangrove forest dominated by *Rhizophora mucronata, R.. apiculata, , Avicennia* spp., *Sonneratia griffithii* and *Ceriops tagal* (height 2-5 m)	5.5	Angsupanich & Aksornkoae (1994) Annual temperature 25 - 33° C Salinity 26 - 33 ‰
Ranong Mangrove Forest, Thailand (09° 50′ N, 98° 35′ E)	*Rhizophora apiculata* (height > 30 m)	6.23 - 10.88	Aksornkoae *et al.* (1991) Monsoonal climate Annual rainfall 4000 - 5000 mm Annual temperature 25.5 - 28.4 ° C Predominantly semi-diurnal tides, Mean tidal amplitude 2.5 m Salinity 15.0 - 27.4‰ (wet), 30.1 - 32.1‰ (dry) Substratum firm clay, sandy, loam
Amphoe Khlung, Changwat Chantaburi, Thailand (12-13° N, 102-103°E)	*Rhizophora apiculata* (dominant species) (height > 30 m)	9.3	Aksornkoae & Khemnark (1984) Monsoonal climate Monthly rainfall max. 590 mm (Sept), min. 11 mm (Dec) Mean annual temperature 27° C Diurnal , tidal amplitude 0.6 - 2.4 m Substratum sandy loam
Dutch Bay, Sri Lanka (8° 15′ N, 79° 50′ E)	*Avicennia marina* and *Rhizophora mucronata* (Height 3 - 4 m)	4 - 6	Amarasinghe & Balasubramaniam (1992) Annual rainfall 1000 - 1100 mm Dry climate prevails with two distinct dry season, low freshwater input, Semi-diurnal tides, max. 79 cm Salinity 0.0 - 45.0 ‰
Ten-Thousand Island, Florida, USA (25°50′ N, 81°41′ W)	*Rhizophora mangle, Avicennia germinans, Laguncularia racemosa* (height 7 - 20 m)	10.8	Pool *et al.* (1975) Annual rainfall 1371 mm Mean annual temperature 23.6° C Seasonal high intensity of rainfall and windstorm frequency High freshwater run-off Max tidal amplitude 80 cm

There are several factors which influence litterfall in mangroves: latitude (Saenger & Snedaker 1993); freshwater input (Pool *et al.* 1975, Flores-Verdugo *et al.* 1987); salinity (Clough *et al.* 1982, Clough 1984); radiation, the degree of cloudiness, and the ratio of precipitation to evaporation (Clough *et al.* 1982, Clough 1984); soil nutrients (Boto & Wellington 1983); and the age or state of maturity of the forest (Clough 1985).

The mangroves of Bintuni Bay were not extreme as far as the above factors are concerned and not surprisingly produced a high litterfall. It should be noted that there may be overriding factors which can influence litterfall in the short term. For example, in the State of Baja, Mexico, Espinosa *et al.* (1981) reported total mangrove litterfall of 9.5 to 16.3 t ha^{-1} y^{-1} in an area with an annual rainfall of only 250 mm. Similarly, Flores-Verdugo *et al.* (1987) reported a litterfall production of 11 t ha^{-1} y^{-1} from mangrove forests in an arid region of El Verde, Mexico. Both locations had a high freshwater input from the surrounding ephemeral inlets. The highest mean litter yield for *Rhizophora stylosa* in Australia was recorded in the arid zone (Bunt 1995). An example of high mangrove litterfall at high latitude was found by Woodroffe (1982) who showed that mangroves near their southern latitudinal limit in the Tuff Crater (36° 48' S), New Zealand, were as productive as mangroves in tropical Queensland and Florida. Bunt (1995) concluded that it seems likely that full response to any favourable climate becomes possible only where other local conditions are not limiting.

The preponderance of leaf litterfall is typical of forests, and its percentage is much related to the type and the age of the forest (Pool *et. al.* 1975, Duke *et al.* 1981, Sasekumar & Loi 1983, Steinke & Charles 1984, Gong *et al.* 1984, Mackey & Smail 1995) (Table 5.10). The Bintuni Bay data were similar to the results from tropical Australia (Duke et al. 1981) and the virgin forest of Matang, Malaysia (Gong *et al.* 1984).

There was a clear seasonality in litterfall production in Bintuni Bay, which may be caused by any of the following factors which have been reported elsewhere: climate especially rainfall (Pool *et al.* 1975, Leach & Burgin 1985, Bunt 1995), temperature (Gill & Tomlinson 1971, Pool *et al.* 1975, Leach & Burgin 1985) and strong winds (Lugo & Snedaker 1974, 1975, Pool *et al.* 1975), ground water salinity (Pool *et al.* 1975, Wium-Andersen & Christensen 1978, Wium-Andersen 1981, Twilley 1988, Bunt 1995). These factors may act alone or in combination and interact with internal tree physiology, and the timing of pollination and propagule dispersal (Borchert 1983, Duke et al. 1984).

The effect of temperature, for example, was determined by Pool *et al.* (1975) for mangrove forest in Southern Florida and Puerto Rico. They stated that mangroves have developed a leaf fall strategy whereby leaves are dropped continuously throughout the year with the higher rates occurring during the wet season and lower rates during the cooler dry season. When temperature increases and freshwater becomes increasingly available, photosynthetic rates are expected to be higher than corresponding rates at lower temperatures and

Table 5.10 The proportion (%) of litter fractions in some mangrove areas.

Location & Vegetation Type	Leaves	Stipule	Reprod.	Wood	Misc.	Authors
Kuala Selangor, Malaysia *Rhizophora* forest Height 10 - 15 m	63.5	7.4	8.5	16.4	4.2	Sasekumar & Loi 1983
Missionary Bay, Hinchinbrook I., Australia *Rhizophora* spp. Height up to 20 m	57.4	8.7	16.3 (seasonal up to 36.7)	9.9	7.2	Duke *et al.* 1981
Mgeni Estuary, Durban South Africa *Bruguiera gymnorrhiza* Height 5 - 7 m	64.9	5.0	26.3	3.8		Steinke & Charles 1984
Vaitupu, Tuvalu, South Pacific *Rhizophora stylosa* Height 4 - 6 m	84	13	2	1		Woodroffe & Moss 1983
Dutch Bay, Sri Lanka *Rhizophora mucronata* Height 3 - 4 m	83.5	88	2.2	3.3	2.2	Amarasinghe & Balasubramaniam 1992
Matang Mangrove Forest, Malaysia *Rhizopora apiculata* (Virgin Jungle Reserve)	59.3		3.2	37.5		Gong *et al.* 1984
Bintuni Bay, Irian Jaya, Indonesia Mixed *Rhizophora - Bruguiera* forest Height up to 40 m	52.4	10.1	23.6	8.1	1.9	This study
Lothian I., Sunderbans, West Bengal, India *Avicennia officinalis*	80 - 90		20 - 30	3 - 10	1 - 5	Yadav & Choudhury 1985
Ten Thousand I., South Florida, USA *Rhizophora mangle, Avicennia germinans & Laguncularia racemosa* Height 7 - 20 m	68 - 86			3 - 15	8 - 21	Pool *et al.* 1975

higher salinities. It is hypothesised that leaf fall patterns are sensitive to stresses such as salinity which increase the energetic cost of maintaining photosynthetic tissue. There must be an environmental threshold beyond which it is metabolically less costly to drop leaves than to overcome the stress. At this point, leaf fall rates increase above normal. Under normal conditions, leaf fall occurs in phase with the production of new leaves such that the photosynthetic rates remain constant. However, Steinke & Charles (1984) argued if this assumption is correct, then perhaps this seasonal variation in leaf fall is not a response which one would expect from tropical mangroves.

5.5.2 Small litter layer

The high value of decomposition rate (k) indicates the high ratio of litterfall and litter layer. However, this finding is a common phenomenon in the mangrove forest since high tide normally removes most of the litterfall from the forest floor. Leach & Burgin (1985) found that k was high (28.6) for *Rhizophora stylosa*-dominated forest in Matupore Island, Papua New Guinea. Robertson (1986), Robertson & Daniel (1989) and Robertson (1991) reported that in tropical Australia the k values varied from 6.19 for *Avicennia* in a high intertidal area to 280 for *Rhizophora* in the mid-intertidal area.

Leach & Burgin (1985) noted although there is a relatively high litterfall (14.3 t ha^{-1} y^{-1}), it appears that only a small proportion of this remains to decompose in the forest. The general observation throughout the study was that the mangrove floor was relatively free of litter. Twilley (1985) reported that in infrequently flooded basin mangroves in south-west Florida with an estimated tidal amplitude of 0.08 m, only 20% of litterfall was exported. In the fringe mangroves along the waterways in south Florida at tidal amplitude of 0.05 m Heald (1969) found the exportation was 45%. For Australian mangroves, with a tidal amplitude of 3 m, Boto & Bunt (1981) found the leaf litter on the forest floor was negligible.

Recent work in Australia, south-east Asia, Africa, the Caribbean and South America proved that a large proportion of the leaf and other litter reaching the floor of mangrove forests is consumed or buried by crabs (Sasekumar & Loi 1983, Loke 1984, Leh & Sasekumar 1985, Robertson 1986, 1991, Robertson & Daniel 1989, Lee 1989, Japar 1989, Smith *et al.* 1989, Micheli *et al.* 1991, and Emmerson & McGwynne 1992). Leh (1982), for example, reported that about 10% of the total litterfall in the high mangrove shore in a Malayan mangrove swamp is consumed by two grapsid crabs *Chiromanthes onychophorum* (de Mann) and *C. eumolpe* (de Mann). In a *Rhizophora stylosa*-dominated forest at Chunda Bay, Queensland, Robertson (1986) found that almost 30% of annual leaf fall in low to mid-low intertidal was taken underground and consumed by the leaf-eating crabs *Sesarma messa* (Campbell). The removal rates reach almost 80% in high intertidal forests (Robertson & Daniel 1989). In a warm-temperate Southern African mangrove, Emmerson & McGwynne (1992) reported that *Sesarma meinertii* consumed 43.6% of the *Avicennia marina* leaf fall. So far, there has been no specific research on crab consumption in Bintuni Bay, but Erftemeijer *et al.* (1989) reported that the densities of fiddler crabs *Uca seismella* and *Uca coarctata* reached of 20 - 30 individuals m^{-2} along river banks in the mangroves. *Sesarmid* crabs (*Chiromantes*) were frequently observed in the Nypa forest at Bintuni Bay.

5.5.3 Small litterfall mineral-elements

5.5.3.1 Mineral-element concentration

In general the litterfall mineral-element concentrations from Bintuni Bay fall within the range of those from mangroves elsewhere (Table 5.11). The mean nitrogen concentration was higher compared with values from other areas, but this is mainly because of the outstandingly high value for 'trash' nitrogen caused by its high content of insect remains and frass. A similar high mangrove trash-nitrogen concentration was found by Bunt (1982) and Wafar *et al.* (1997).

Potassium concentration was highest in the reproductive parts. Teas (1986) found a similar result in Puerto Rico, Panama and Florida and this phenomenon has been discussed by de Lacerda *et al.* (1988) who believed that the high potassium in mangrove propagules was a device to overcome the difficulty in absorbing K from Na-rich sediments.

In Bintuni Bay, calcium concentrations were always higher and magnesium always lower than sodium in all litter parts. This result was similar to those of Golley *et al.* (1978) and Gong *et al.* (1984), but was in contrast to Aksornkoae & Khemnark (1984) and de Lacerda *et al.* (1986). Joshi *et al.* (1975) and Bidwell (1979) mentioned that the uptake of Ca and Mg is greatly affected by the antagonistic effect of Na. The high leaf litterfall calcium concentrations in Bintuni

Table 5.11 The litterfall elements concentration (mg/g) from some mangrove areas.

Location / sample type	N	P	K	Na	Ca	Mg	Author(s)
Amphoe Khlung, Changwat Chantaburi, Thailand:							Aksornkoae & Khemnark 1984
R. apiculata							
- leaves	19.5	0.9	11.4	40.0	6.1	2.8	
- branches	10.0	0.8	4.1	24.0	2.8	1.1	
Matang , Malaysia,							Gong *et al.* 1984
R. apiculata (leaf litter)	5.3	1.1	2.8	5.1	11.3	4.0	
Bintuni Bay, Irian Jaya, Indonesia:							This study
Mixed *Rhizophora-Bruguiera* forest:							
- reproductive parts	23.7	0.8	5.0	6.5	9.1	2.5	
- leaves	21.5	0.5	3.9	9.1	22.0	5.8	
- stipules	12.3	0.3	3.3	6.7	10.3	2.7	
- wood/twigs	21.8	0.3	1.3	2.8	29.1	1.9	
- trash	48.7	1.1	3.2	5.6	30.1	4.3	
Missionary Bay, Hinchinbrook I., Australia:							Bunt 1982
Rhizophora spp. :							
- leaves	4.4	0.4					
- stipules	2.2						
- flower buds	5.6	0.3					
- twigs	4.4						
- debris	6.4						
Mandovi - Zuari Estuaries, Central West-coast, India:							Wafar *et al.* 1997
R. apiculata							
- leaves	6.8	0.6					
- stipules	8.5	0.1					
- flowers	7.0	0.8					
- fruits	8.3						
- wood	10.1						
- debris	21.8	0.1					
Puerto Rico, Panama & Florida:							Teas 1985
Rhizophora							
- leaves		0.9	8.0	9.8	12.2	4.7	
- propagules		0.7	10.1	9.6	5.9	2.9	
- wood litter		0.9	3.0	5.5	12.9	1.0	
Panama:							Golley *et al.* 1978
R. mangle (leaves)			8.4	9.8	12.2	4.7	
Florida:							Snedaker & Brown 1981
R. mangle (leaves)			16.0		17.0	7.0	
South-eastern Brazilian Coast, Brazil:							Lacerda, de *et al.* 1986
R. mangle (sun leaves)			15.8	22.9	1.3	7.6	

Bay compared with other areas was consistent with the soil analytical results (Tables 3.1, 3.2 and 3.4). The high accumulation of mollusc shells on the forest floor was the likely source of this high soil calcium concentration.

5.5.3.2 Mineral-element accession

The amounts of nutrient returned through small litterfall were estimated to be (kg / ha / yr): N 240.4, P 6.1, K 43.2, Na 136.2, Ca 204.4 and Mg 48.7. These values are higher than those reported by Gong *et al.* (1984) for Matang mangrove forest, Malaysia: N 46.6, P 4.7, K 25.6, Na 31.8, Ca 99.3, Mg 34.1, and Lim (1978) for Pasoh lowland dipterocarp forest, Malaysia: N 74.9, P 2.5, K 24.3 , Ca 57.3, Mg 42.4. The lower values for both these Malaysian forests must be viewed in the light of their lower annual litterfall (Matang 7.8 t / ha, Pasoh 8.9 t / ha) than in Bintuni Bay (11.1 t / ha).

5.5.4 Leaf-litterfall decomposition

Except in *Bruguiera parviflora*, the decomposition rate was faster in the first 4 - 12 weeks, and then slowed until week 22 (the end of the experiment). These results more or less agreed with previous studies, even though different species were used and the sites were different. In Tuff Crater, New Zealand, Woodroffe (1982) found that rapid decomposition of *Avicennia marina* leaves occurred during the first six weeks, and similarly Singh & Steinke (1992) reported a significant decrease of *Bruguiera gymnorrhiza* leaves up to week seven in Durban, South Africa. In Hong Kong, Hodgkiss & Leung (1986) found that the decomposition of *Kandelia candel* leaves was faster in the first six weeks.

Fell & Newel (1981) suggested that extracellular enzymes from fungi that are lytic to plant structural compounds may be important for litter breakdown. Hodgkiss & Leung (1986) discovered that the highest fungal cellulolytic enzyme activity was found during the first six weeks of decomposition, indicating that microbial cellulolytic activity is likely to reach a peak at this time. They also noticed that time was also required for the leaching of tannins and the build up of microbial biomass. Benoit & Starkey (1968) and Swift (1976) had pointed out that the presence of tannins in mangrove leaves can probably delay the colonisation by fungi and bacteria.

Decomposition rates were ranked: *Sonneratia alba* > *Avicennia eucalyptifolia* > *Rhizophora apiculata* > *Bruguiera gymnorrhiza* > *Bruguiera parviflora*. The exposure of the litterbags at the lowest high water level (LD5, chapter 2) was perhaps one among several factors in causing faster decomposition of *Sonneratia*. At this lowest high water level the litterbags are washed twice daily by sea water. In contrast, the decomposition rates of *Bruguiera parviflora* leaves was the lowest because of their higher exposure at the LD1 site. Sasegolo & Lana (1991) found that decomposition rates of *Rhizophora mangle, Avicennia schaueriana* and *Laguncularia racemosa* leaves were four to six times faster in their submerged state. They suggested that this pattern was most probably related to higher levels of litter mechanical fragmentation and transport by tidal forces. In Thailand, Aksornkoae & Khemnark (1984) noted that the rates of litter decomposition decreased from the area at the forest margin to the inland sites.

Choong *et al.* (1992) reported that *Sonneratia alba* has a relatively a high ratio of protein (% N) to fibre, which they believed to be a good predictor of leaf palatability and digestibility.

Decomposition rates of *Avicennia eucalyptifolia*, *Bruguiera gymnorrhiza* and *Rhizophora apiculata* were not significantly different. Previous studies, however, found that in South Africa, *Avicennia marina* leaves decomposed faster than *Bruguiera gymnorrhiza* (Steinke et al. 1983, 1990, 1993), and in south-eastern Brazil, Sasegolo & Lana (1991) found that the decomposition of *Avicennia schaueriana* was faster than *Rhizophora mangle* and *Laguncularia racemosa.* This may reflect differences in morphology, anatomy and chemistry within the genus *Avicennia* or differences in experimental methods. In Bintuni Bay each litterbag was placed on the forest floor under trees of the same species used in the litterbags to simulate their natural physical environment. In South Africa (Steinke *et al.* 1983, 1990, 1993) and Brazil (Sasegolo & Lana 1991) the studies were made with all species under the same conditions.

Steinke *et al.* (1983, 1990, 1993) attributed differences in decomposition rates to differences in leaf morphology, anatomy and chemistry. *B. gymnorrhiza* has glabrous leaf surfaces which are covered with a thick cuticle which would impede the entry of water and degradative organisms. In contrast, only the adaxial surface of *A. marina* leaves has a thick cuticle; the lower (abaxial) surface is covered with numerous fine, non-glandular hairs. Fahn & Shimony (1977) have shown that the non-glandular hairs are covered by a very thin cuticle which may be absent in parts. It is suggested that water and microbes may enter readily through the leaf underside.

The decomposition data of all the species fitted a single exponential decay model ($r^2 \geq 0.81$) similar to other decomposition studies in mangroves (Sasegolo & Lana 1991, Mackey & Smail 1996). The assumption underlying this model can be expressed in two ways: either the absolute decomposition rate decreases linearly as the amount of remaining substrate declines, or the relative decomposition remains constant (Wieder & Lang 1982). This assumption corresponds well with the knowledge and understanding of the biology of litter decomposition. As decomposition proceeds, soluble components and relatively easily degraded compounds such as sugars, starches, and protein will be rapidly utilised by decomposers, while more recalcitrant material such as cellulose, fats, waxes, tannins, and lignins will be lost at slower rates. Thus, with time, the relative proportion of these recalcitrant materials will increase and the absolute decomposition rate will decrease (Wieder & Lang 1982).

VI LEAF HERBIVORY

6.1 Introduction

The notion that the majority of mangrove primary production enters the detritus food chain through natural senescence (Heald 1971, Odum & Heald 1975) is widely accepted by mangrove researchers. However, a substantial proportion of mangrove leaves is partially eaten by herbivores while still attached to the tree. Thus, mangroves are supporting populations other than those of the detritus-based food chain and direct herbivore activity is held by some to be more important than the detrital food chain (Johnstone 1981).

Leaf herbivory will cause a series of chemical and physical changes in trees, affecting their quality and quantity of litter, productivity and reproductive performance (Belsky 1986, Choudhury 1988, Crawley 1983, Owen 1978, Pullin 1987). Leaf herbivores reduce tree growth by depleting the plant's carbohydrate reserves, by tapping its current photosynthesis, or by reducing its photosynthetic leaf area (Crawley 1983). Differences in the vulnerability of component plant species to herbivory may influence community structure (Harper 1979, Weis & Berenbaum 1989). It is possible to visualise more complex effects. If photosynthesis is 'sink limited', removing leaf area will have no effect on overall production; herbivory can increase the light falling on leaves whose photosynthesis may be light limited; also herbivory might speed up the cycling of nutrients.

The rate of foliar herbivory may be affected by factors such as leaf age, leaf quality, plant size (Coley 1983, Marquis 1987, Ernest 1989, Kursar & Coley 1992, Nascimento & Hay 1993), and by the composition, density and diversity of the surrounding vegetation (Brown & Ewel 1987). While the impact of herbivory will vary with intrinsic variables such as plant phenostage, the relative contribution of photosynthate by leaves of different ages, and the amounts of foliage eaten, it will also vary with extrinsic variables such as competing neighbours, and light and soil conditions (Dirzo 1984).

6.2 Methods

Leaf herbivory was studied in two main mangrove species in Bintuni Bay : *Rhizophora apiculata* and *Bruguiera gymnorrhiza.* The study sites were those mentioned in chapter II: LH1, positioned beneath the canopy of mature mixed *Rhizophora-Bruguiera* forest ('shaded' site) and LH2, located in an open area of forest clear-felled 7 years ago ('unshaded' site).

There were three different plant height categories sampled (< 1 m , 1 - 3 m and 3 - 5 m) and two leaf age categories: young and mature. It was impracticable to sample trees greater than 5 m high. Young leaves were defined as being near the tip of the branch, light-green in colour, tender and sometimes not fully expanded; mature or older leaves were located further from the branch tip, darker in colour and tougher in texture.

Ten plants of each height category were randomly selected from LH1 and LH2, all their leaves were collected and sorted into young and mature groups. They were then assessed for bites (incisions along the leaf margin) and holes (within the leaf). All leaves were measured for breadth and length from the base of the drip tip and not including the petiole. For the damaged leaves paper templates were constructed to assess the original breadth and length. Sub-samples of 25% of randomly selected leaves from both the undamaged and damaged leaf collections were measured (using an electronic area meter) for total leaf area and total remaining leaf area.

6.3 Data analysis

Regression analysis was used to determine the relationship between the leaf breadth and length and the leaf area of each undamaged leaf type. The regression equation was then used to estimate the original leaf area of damaged leaves. After substracting the measured damaged leaf area from the estimated initial leaf area, the area lost owing to herbivory was established.

An ANOVA General Linear Model (GLM) was applied to assess the site, species, plant height and leaf-age effects and their interactions on herbivory. Whenever a significant difference was detected, a one-way analysis of variance was applied for a further determination.

All herbivory data (in %) were arcsine and square root transformed prior to the statistical analyses. The MINITAB release 10.2 (Minitab Inc. 1995) for WINDOWS package was used for most of the calculations.

6.4 Results

Table 6.1 shows the total number and percentage of leaves sampled. Most of leaf loss was in the form of holes within the lamina or small bites / incisions along the leaf margin. More than 50% of the leaves had bites or holes or both. The shaded *Rhizophora apiculata* leaves had more herbivory (mean 68.8%, range 53.1% to 86.4%) than the unshaded (mean 61.8%, range 34.0% to 95.8%). In *Bruguiera gymnorrhiza*, the values from the unshaded site (LH2) varied greatly, from 11% in the young leaves of the tallest plants to 92% in the young and mature leaves in the shortest plants, and the values were lower than those from the shaded site (LH1) (mean 70.8%, range 48.4% to 90.7%).

Regression analyses showed that leaf breadth and length of undamaged leaf were highly correlated to leaf area ($p \leq 0.01$, mean $r^2 = 0.95$), hence the regression equations of each leaf type were valid to access the leaf area loss in damaged leaves.

The mean percentages of leaf area loss to herbivory in both species of *Rhizophora apiculata* and *Bruguiera gymnorrhiza* under different conditions are shown in Table 6.2. Statistical analyses in general indicated that the herbivory levels were varied and significantly different ($p \leq 0.05$) among different sites, species, plant height and leaf-age examined. However the interactions site x species, site x age, and age x height were not significant.

Figs 6.1 and 6.2 show the distribution of the values with regard to the herbivory. In all cases, the greatest numbers were in the lowest herbivory class (< 2.5%)

Table 6.1 Total numbers and percentages of leaf herbivory samples from Bintuni Bay, Irian Jaya.

Species	Site	Plant height	Leaf age	Leaf condition	n	% of sample	Species	Site	Plant height	Leaf age	Leaf condition	n	% of sample
Rhizophora	Shaded	<1 m	Young	Damaged	96	60.4	*Bruguiera*	Shaded	<1 m	Young	Damaged	64	62.7
				Undamaged	63	39.6					Undamaged	38	37.3
			Mature	Damaged	175	74.2				Mature	Damaged	263	90.7
				Undamaged	61	25.8					Undamaged	27	9.3
		1 - 3 m	Young	Damaged	366	65.0			1 - 3 m	Young	Damaged	222	48.4
				Undamaged	197	35.0					Undamaged	237	51.6
			Mature	Damaged	1203	86.4				Mature	Damaged	1843	86.8
				Undamaged	189	13.6					Undamaged	281	13.2
		3 - 5 m	Young	Damaged	757	53.1			3 - 5 m	Young	Damaged	506	49.1
				Undamaged	669	46.9					Undamaged	525	50.9
			Mature	Damaged	2422	81.2				Mature	Damaged	3517	87.2
				Undamaged	561	18.8					Undamaged	518	12.8
	Unshaded	<1 m	Young	Damaged	398	73.3		Unshaded	<1 m	Young	Damaged	268	92.1
				Undamaged	145	26.7					Undamaged	23	7.9
			Mature	Damaged	613	95.8				Mature	Damaged	431	92.5
				Undamaged	27	4.2					Undamaged	35	7.5
		1 - 3 m	Young	Damaged	1231	47.4			1 - 3 m	Young	Damaged	467	22.2
				Undamaged	1364	52.6					Undamaged	1639	77.8
			Mature	Damaged	2743	68.1				Mature	Damaged	1822	51.6
				Undamaged	1283	31.9					Undamaged	1709	48.4
		3 - 5 m	Young	Damaged	2486	34.0			3 - 5 m	Young	Damaged	446	11.5
				Undamaged	4818	66.0					Undamaged	3448	88.5
			Mature	Damaged	7426	52.4				Mature	Damaged	3751	37.0
				Undamaged	6759	47.6					Undamaged	6390	63.0

Table 6.2 The mean percentages of leaf area loss to herbivory in *Rhizophora apiculata* and *Bruguiera gymnorrhiza* in Bintuni Bay, Irian Jaya. Ranges are given in the parentheses. All differences involving site, plant height, leaf age, and species are significantly different ($p \leq 0.05$). The significance of interactions is given in the text.

Species	Plant height (m)	Shaded site (LH1)		Unshaded site (LH2)	
		Young leaves	Mature leaves	Young leaves	Mature leaves
Rhizophora	**<1**	**1.92** (0.2 - 10.13)	**3.77** (0.19 - 28.92)	**2.90** (0.08 - 14.06)	**4.37** (0.21 - 16.99)
	1-3	**3.02** (0.02 - 19.95)	**4.89** (0.11 - 35.30)	**3.50** (0.05 - 34.39)	**3.93** (0.01 - 52.73)
	3-5	**6.99** (0.01 - 69.17)	**6.64** (0.04 - 92.19)	**5.23** (0.02 - 42.77)	**4.69** (0.01 - 38.41)
Bruguiera	**<1**	**2.02** (0.06 - 13.91)	**5.25** (0.01 - 33.34)	**3.20** (0.29 - 10.20)	**4.49** (0.07 - 17.59)
	1-3	**1.61** (0.06 - 8.55)	**4.71** (0.03 - 60.15)	**1.85** (0.04 - 18.26)	**3.63** (0.01 - 90.40)
	3-5	**3.73** (0.13 - 28.86)	**4.94** (0.01 - 90.88)	**1.84** (0.09 - 18.06)	**3.53** (0.01 - 49.97)

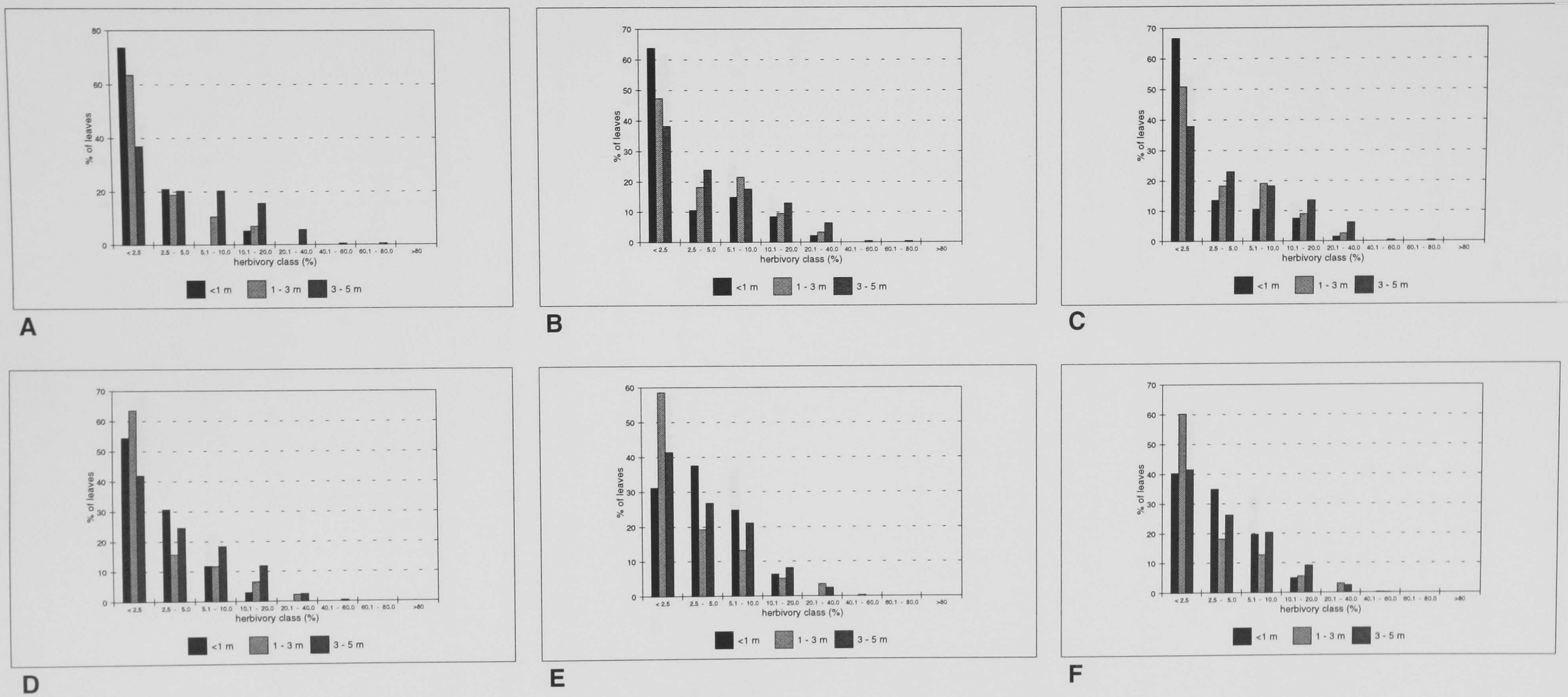


Fig. 6.1 The percentage of damaged leaves in a range of herbivory classes in *Rhizophora apiculata*. Shaded site: A young leaves, B mature leaves, C total young and mature leaves. Unshaded site: D young leaves, E mature leaves, F total young and mature leaves.

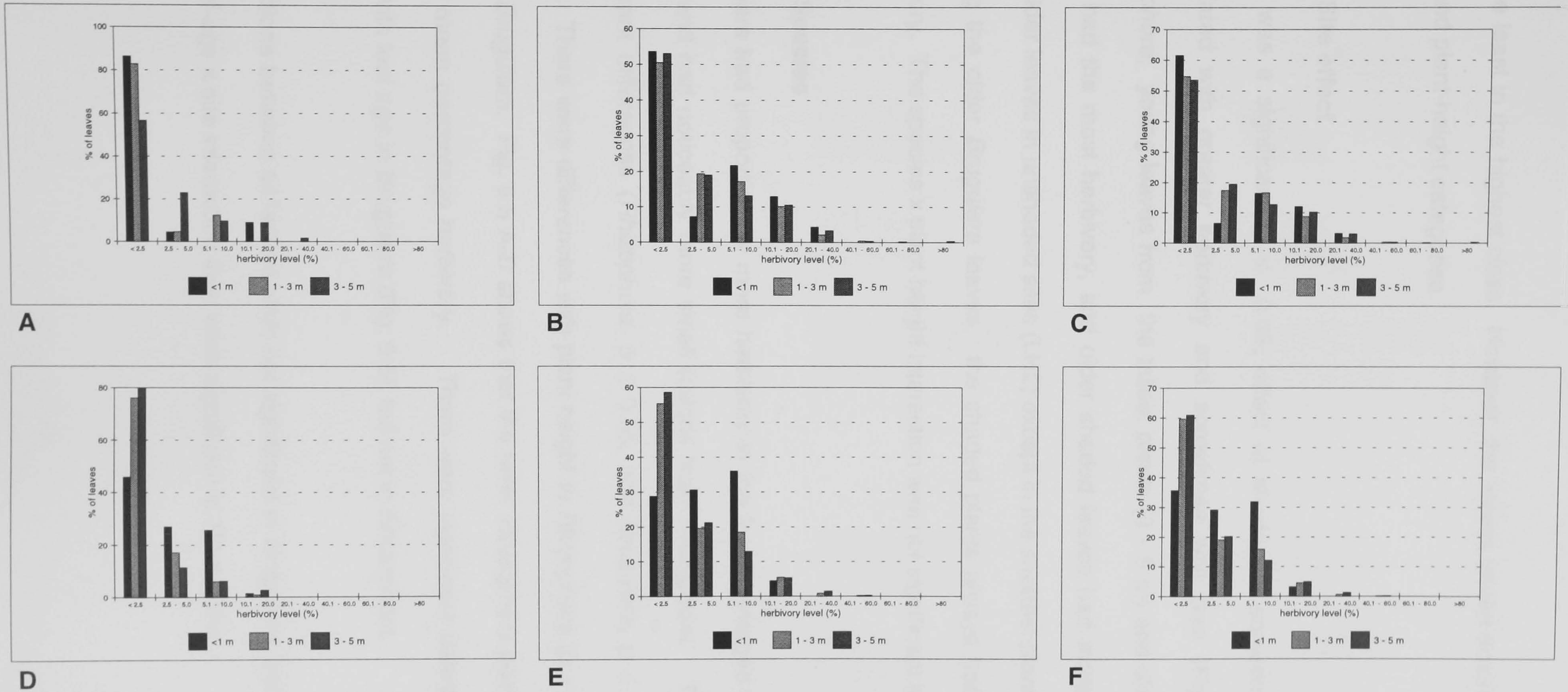


Fig. 6.2 The percentage of damaged leaves in a range of herbivory classes in *Bruguiera gymnorrhiza*. Shaded site: A young leaves, B mature leaves, C total young and mature leaves. Unshaded site: D young leaves, E mature leaves, F total young and mature leaves.

and the least in the highest class. However, the values varied among species, sites and plant-height categories.

6.4.1 Site effect

There was a significant ($p \leq 0.05$) effect of shade but sometimes it was associated with greater herbivory and sometimes with less (Fig. 6.3). In *Rhizophora*, young leaves from the tallest plants (3 - 5 m) and shaded sites (LH1) had the most herbivory, and older shaded leaves had more herbivory than older leaves in unshaded sites (LH2) except in the shortest plants (< 1 m). Among the older *Bruguiera* leaves, the shaded plants always had the most herbivory. The species x plant height interaction was not significant in LH2.

6.4.2 Species

Bruguiera had proportionally more herbivory in the least damaged class (Fig. 6.4), and had noticeably more small lesions than *Rhizophora*. There were significant differences (*Rhizophora,* $p \leq 0.05$, and *Bruguiera,* $p \leq 0.01$) with shade. There were differences with plant height in *Rhizophora* ($p \leq 0.05$), but not in *Bruguiera*. Fig. 6.5 A-D shows that the taller *Rhizophora* plants had the higher mean percentage herbivory. There were significant differences ($p \leq 0.01$) with leaf age in *Bruguiera* (Fig. 6.5), but not in *Rhizophora*.

Interactions between all factors were not significant in *Bruguiera*, but except for the leaf-age x site interaction they were significant in *Rhizophora*.

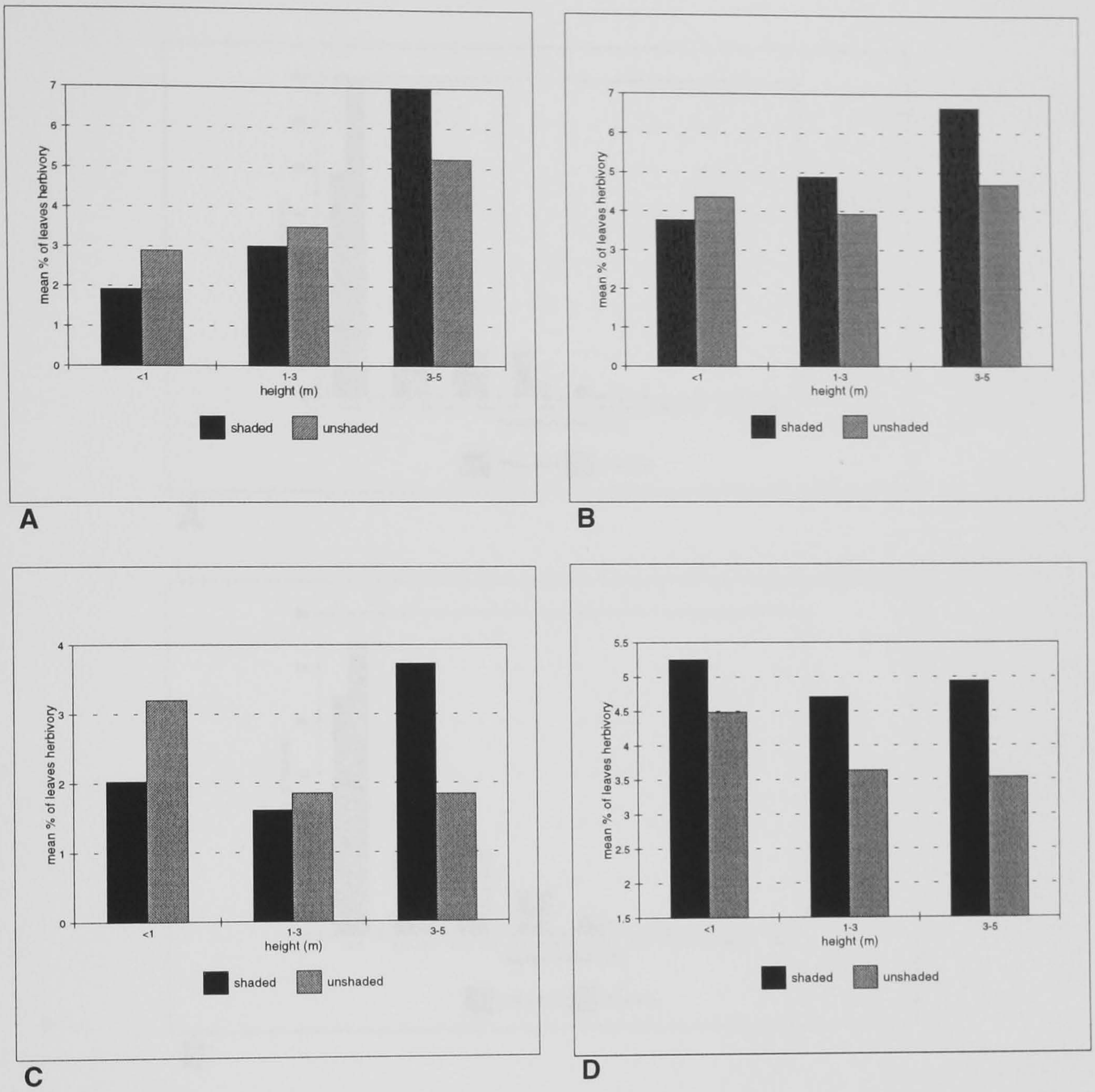


Fig. 6.3 The mean percentage of leaf herbivory on each site and plant-height classes. *Rhizophora apiculata*: A young leaves, B mature leaves. *Bruguiera gymnorrhiza*: C young leaves, D mature leaves.

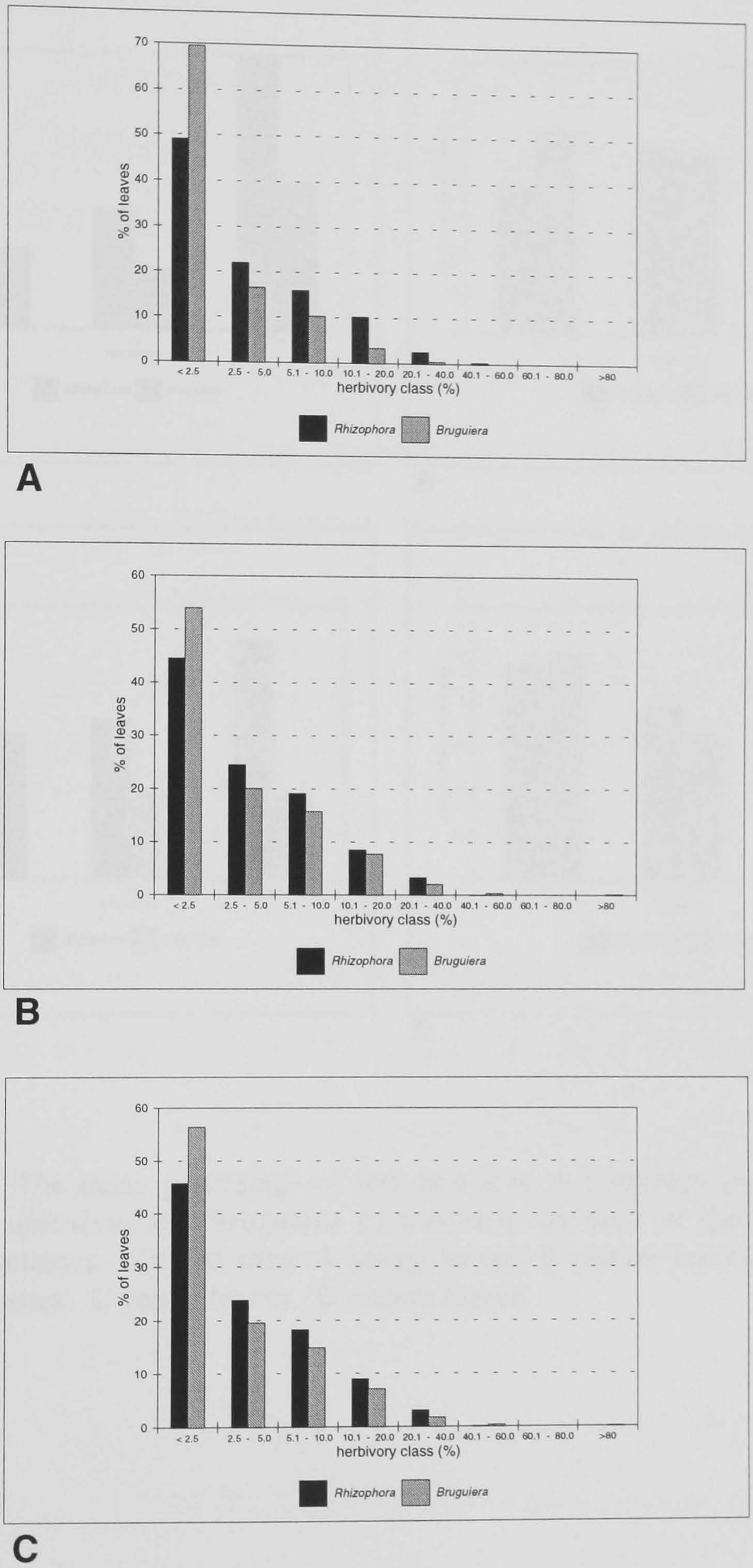


Fig. 6.4 The mean percentage of leaves on each herbivory classes of *Rhizophora apiculata* and *Bruguiera gymnorrhiza* in Bintuni Bay, Irian Jaya. A young leaves, B mature leaves, C total young and mature leaves.

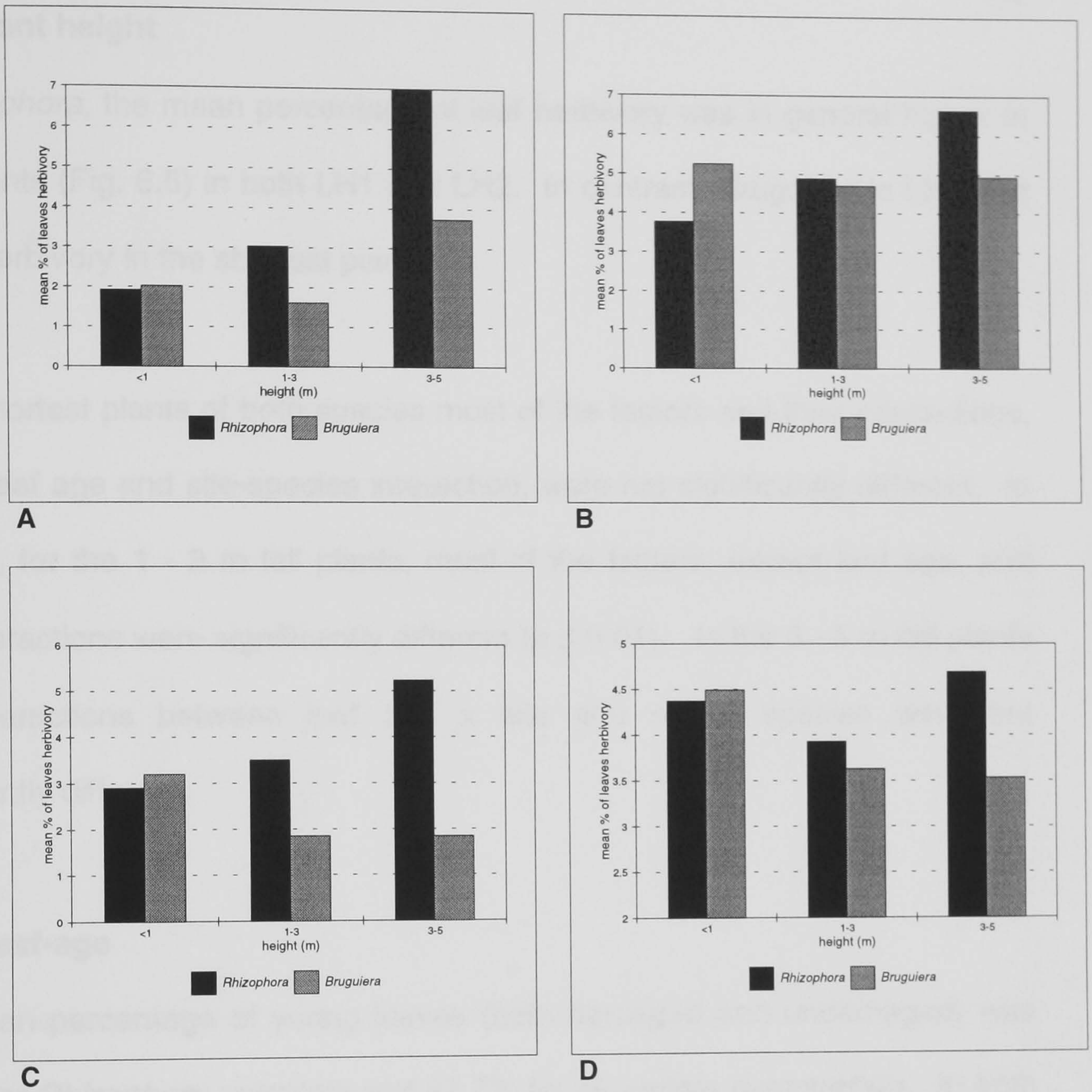


Fig.6.5 The mean percentage of leaf area loss to herbivory in *Rhizophora apiculata* and *Bruguiera gymnorrhiza* on each of the plant-height classes. Shaded sites: A young leaves, B mature leaves. Unshaded sites: C young leaves, D mature leaves.

6.4.3 Plant height

In *Rhizophora*, the mean percentage of leaf herbivory was in general higher in taller plants (Fig. 6.5) in both LH1 and LH2. In contrast, *Bruguiera* in LH2 had higher herbivory in the shortest plants.

In the shortest plants of both species most of the factors and their interactions, except leaf age and site-species interaction, were not significantly different. In contrast, for the 1 - 3 m tall plants, most of the factors, except leaf age, and their interactions were significantly different ($p \leq 0.01$). In the 3 - 5 m tall plants only interactions between leaf age x site and site x species were not significantly different.

6.4.4 Leaf-age

The mean percentage of young leaves (both damaged and undamaged) was 34.9% for *Rhizophora apiculata* and 27.7% for *Bruguiera gymnorrhiza*. In both species the percentage of young leaves was higher in LH2 than in LH1 (35.6% against 31.7% for *Rhizophora*, and 30.8% against 19.8% for *Bruguiera*)

Fig. 6.6 showed that in general the mature leaves had more herbivory, except for the tallest *Rhizophora*. Of the interactions, only site x species in young leaves, and species and site x plant height in mature leaves were not significant.

The mature leaves from LH1, except in the smallest *Rhizophora*, had more herbivory than the mature leaves from LH2. In contrast, the young leaves from

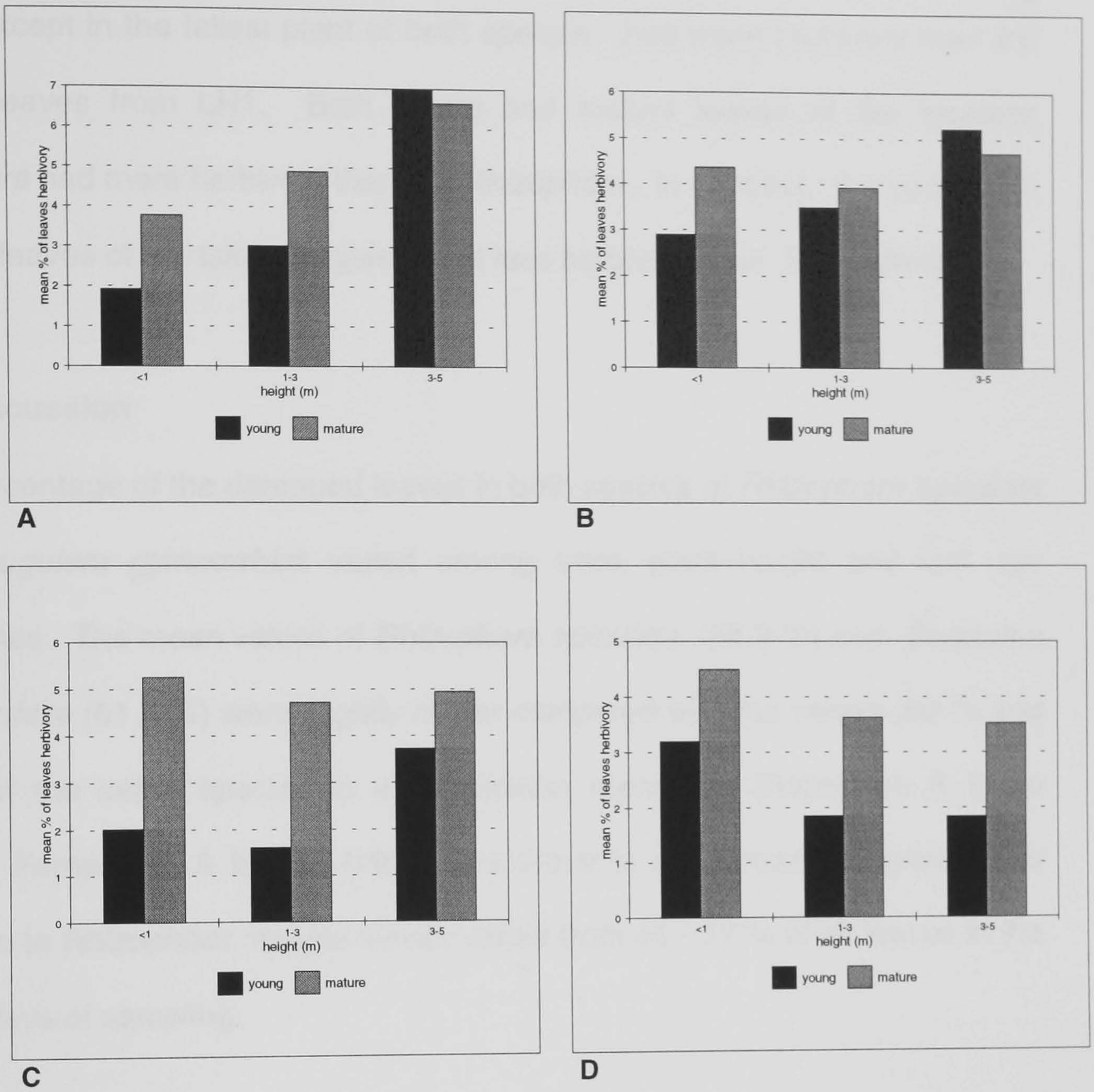


Fig. 6.6 The mean percentage of leaf area loss to herbivory for each leaf-age and plant -height class. *Rhizophora apiculata*: A shaded, B unshaded. *Bruguiera gymnorrhiza*: C shaded, D unshaded.

LH2, except in the tallest plant of both species, had more herbivory than the young leaves from LH1. Both young and mature leaves of the smallest *Bruguiera* had more herbivory than the *Rhizophora*. In contrast, the young and mature leaves of the taller *Bruguiera* had less herbivory than *Rhizophora*.

6.5 Discussion

The percentage of the damaged leaves in both species of *Rhizophora apiculata* and *Bruguiera gymnorrhiza* varied among sites, plant height and leaf age categories. The mean values of *Rhizophora apiculata* (65.3 %) and *Bruguiera gymnorrhiza* (61.0 %) were slightly higher compared with the values (63 % and 51%) of the same species in an Australian mangrove (Robertson & Duke 1987). Farnsworth & Ellison (1991) found that in a Belizean mangrove, the damage to *Rhizophora mangle* leaves varied from 46 - 77 % of all leaves in the first 4 days of sampling.

In terms of mean percentage of leaf area loss to herbivory, the values from Bintuni Bay (*Rhizophora apiculata* 4.3 %, *Bruguiera gymnorrhiza* 3.5%) were more or less similar to an Australian site (*Rhizophora apiculata* 5.8 %, *Bruguiera gymnorrhiza* 3.7 %) (Robertson & Duke 1987), but somewhat lower than in a New Guinean mangrove (*Rhizophora apiculata* 8.6% *Bruguiera gymnorrhiza* 4.9 %)(Johnstone 1981) (Table 6.3).

There has been some explanation about herbivory differences within the same species in different sites. Robertson & Duke (1987) believed that different insect communities were one of the causes. Onuf *et al.* (1977), working with

Table 6.3 Mean percentage of leaf area loss to herbivory in some mangrove areas.

Location / site / vegetation type	No. of leaves examined	Mean percentage of leaf herbivory	Authors
Port Moresby, Papua New Guinea			Johnstone (1981)
- *Bruguiera gymnorrhiza*	150	4.9	
- *Heritiera littoralis*	25	14.2	
- *Rhizophora apiculata*	175	8.6	
- *Xylocarpus moluccensis*	25	0.2	
- Mean (all 23 species)	2200	6.8	
Missionary Bay, North Queensland, Australia			Robertson & Duke (1987)
- *Bruguiera gymnorrhiza*	239	3.7	
- *Excoecaria agalocha*	204	0.3	
- *Heritiera littoralis*	163	35.0	
- *Rhizophora apiculata*	477	5.8	
- *Rhizophora stylosa*	583	5.1	
Bako National Park, Sarawak, Malaysia			Cooke *et al.* (1984)
- *Avicennia marina*	200	10.2	
- *Sonneratia alba*	200	14.3	
Pichavaram, southeast India			Kathiresan (1992)
- *Avicennia officinalis*	50	12.0	
- *Avicennia marina*	50	9.3	
- *Rhizophora apiculata*	50	2.6	
- *Rhizophora lamarckii*	50	0.8	
- *Bruguiera cylindrica*	50	2.3	
- *Excoecaria agalocha*	50	0.8	
- *Ceriops decandra*	50	0.7	
Placencia Lagoon, Belize			Farnsworth & Ellison (1991)
- *Rhizophora mangle*			
- adults			
- LW	524	6.9	
- MW	720	5.5	
- HHW	540	16.6	
- seedlings			
- LW	45	4.3	
- MW	63	9.2	
- HHW	70	25.3	
- *Avicennia germinans* (HHW)			
- adults	1347	14.0	
- seedlings	75	15.1	

Rhizophora mangle in Indian River, Florida, found that soil nutritional status may also influence herbivory. However, this was argued against by Johnstone (1981) and Farnsworth & Ellison (1991) who both failed to detect differences in herbivory in fertilised and nutrient-enriched mangrove sites.

6.5.1 Site

There was no general trend of shade effect on herbivory in Bintuni Bay, this possibly because the observations were confounded by other factors. Several studies have been done to assess shade effects on herbivory. Farnsworth & Ellison (1991) reported that in Belizean mangrove swamps seedlings of *Rhizophora mangle* growing under a monospecific canopy of *Rhizophora* trees showed significantly higher damage than seedlings growing in full sun. They believed that understory seedlings simply may have experienced higher recruitment of herbivores dropping directly from the adult canopy.

Lowman (1985) and Lowman & Box (1983), working with two species of Australian rain forest trees, found that shade leaves had significantly higher grazing levels than those in the sun. They believed that the difference was caused because of the higher phenol concentrations in the sun leaves. Similarly, in a tropical rain forest in French Guiana, Newbery & de Foresta (1985) reported lower phenols and condensed tannins in young leaves of primary forest understory than in the pioneer vegetation and forest gaps.

6.5.2 Species

Previous studies of herbivory in Australasian and neotropical mangroves have raised questions about interspecific variability in damage (Onuf *et al.* 1977, Beever *et al.* 1979, Johnstone 1981, de Lacerda *et al.* 1986, Robertson & Duke 1987, Smith *et al.* 1989). Farnsworth & Ellison (1991) concluded that different interspecific levels of herbivory could result from variation in leaf palatability, texture, or nutrient content.

In Bintuni Bay, even though *Rhizophora apiculata* and *Bruguiera gymnorrhiza* are both from the *Rhizophoraceae* of which most of the members contain high concentrations of soluble tannins and have high C : N ratios (Giddins 1984, Hogg & Gillian 1984, Ghosh *et al.* 1985, de Lacerda *et al.* 1986), they showed a different pattern of herbivory. *Bruguiera* had proportionally more herbivory in the least damaged class (Fig. 6.4), and had many more small lesions than *Rhizophora*, suggesting that the species may have different herbivores (Plate 10). Moreover the differences of herbivory between these two species with plant height and shade (Fig. 6.5) suggested that they may have different defence strategies.

6.5.3 Plant height

Lowman (1985) reported that insects generally preferred to graze leaves in the lower canopy of some Australian rain forest trees. This difference with height in the canopy may be partially an interaction between nearness to ground level (and higher humidity) (many insects appear to live near the ground) and light regime.

Plate 10 Typical leaf herbivory in **A** *Rhizophora apiculata* and **B** *Bruguiera gymnorrhiza* in Bintuni Bay.

In mangroves, this plant-height factor becomes more crucial since there is also a tidal inundation factor which according to Newbery (1980), de Lacerda et al. (1983) and Schoener (1988), may change chemical or physical properties or both, of the submerged leaves which in turn can affect the herbivory.

Robertson & Duke (1987) found that leaves on seedlings of *Avicennia marina* in Australian mangroves suffer greater leaf loss to insects than saplings or mature trees and this also appeared to be true for *Xylocarpus granatum*. Leaf loss to insects often leads to the death of seedlings of these two species.

Farnsworth & Ellison (1991) in contrast reported that damage to *Rhizophora* seedlings was significantly lower than for mature trees. This agrees with Stowe (1995) who studied the effect of periodic submersion of leaves on the herbivory of white mangrove *Laguncularia racemosa* along Rio Tempisque, Costa Rica. He found that exposed foliage was significantly more damaged than submerged foliage. He believed that submerged leaves may be less damaged than those which are not, because they are exposed to terrestrial herbivores for a shorter time.

In Bintuni Bay, leaves from the smallest *Rhizophora apiculata* plants, which are always submerged by sea water during spring high tide, were mostly less damaged than leaves from the taller plants. However, in contrast, most of the smallest *Bruguiera gymnorrhiza* (within the size range of *Rhizophora*) had a higher herbivory. It seems that there are some other factors which had a stronger influence than plant-height on herbivory. Statistical analysis at least showed that plant-height x species and plant-height x site interaction factors were significantly different ($p \leq 0.01$).

There is a possibility that taller *Bruguiera gymnorrhiza* plants were more resistant to herbivory because they already experienced it when they were small. Karban (1987) hypothesised that if a seedling or sapling survives an initial attack it is subsequently more resistant. This resistance is retained long after the direct effects of early herbivory have disappeared. Acquired resistance is not absolute but would make the host less suitable for herbivores.

Other evidence suggests that changes caused by herbivore attack, rather than other plant age-related effects, are involved. Overhulser *et al.* (1972), working on Sitka spruce (*Picea sitchensis* (Bong.) Carriere) , noticed that more weevils *Pissodes strobi* (Coleoptera: Curculionidae) hatch from twelve year old trees attacked for the first time than from trees of the same age previously attacked by weevils. Furthermore, female weevils prefer to oviposit in previously unattacked trees.

6.5.4 Leaf age

Mature leaves in both LH1 and LH2, except in the tallest *Rhizophora* had more herbivory than young leaves. This finding agrees with Newbery & de Foresta (1985). They also found that mature leaves of the primary forest understory, with the lowest concentrations of total phenols and condensed tannins, were more defoliated than the mature leaves of pioneer plants with higher concentrations of these secondary compounds. They suggested that leaves with greater concentrations of defence chemicals deter herbivores. Turner (1995), investigating the foliar defences of three woody plant communities in Singapore, found that total phenols and condensed tannins of immature leaves of *Rhizophora apiculata* were higher than in mature leaves. *Bruguiera gymnorrhiza*, in contrast, had a higher concentration of both these defence chemicals in the mature leaves.

Coley (1983) and Crawley (1983), however, found that in general nutritional quality declines in older, tougher leaves, and many herbivores preferentially attack newly emerging leaflets. Lowman & Box (1983), working with five species of Australian rain forest trees, believed that the young leaves were more heavily grazed since they were more palatable than the mature leaves which have tough, waxy surfaces and higher phenolic contents. Rockwood (1974), Scriber (1977), and White (1978) stated that young leaves are palatable probably due to higher nitrogen and water content and are more easily cut and chewed. In dipterocarp forest in Bako National Park, Sarawak, Cooke *et al.* (1984) found that the young leaves of *Eugenia ochneocarpa* and of *Shorea* spp. were as palatable as the mature leaves. It should be noted that the leaf age factor is blurred since there is usually no record of when the herbivory occurred or when the leaves became mature.

VII SEED PREDATION

7.1 Introduction

A number of marine animals may influence the mangrove forest indirectly. For instance crabs can destroy seedlings, and prevent regeneration (Tomlinson 1994) even though they depend on the mangrove for their habitat. There is no doubt that plant-animal interactions often play a major role in controlling population, community and ecosystem-level processes within mangrove forests.

The classic view that within-habitat zonation patterns of mangrove tree species are controlled solely by factors such as the degree of tidal inundation, pore-water salinities and competition for light (e.g., Watson 1928, Macnae 1968, Chapman 1976) has been challenged. Smith (1987a) and Smith *et al.* (1989) showed that post-dispersal predation, mostly by crabs, is an important mortality agent for trees in mangroves, and has a significant influence on distribution patterns and succession by selectively consuming propagules (Smith 1987b, 1988).

Smith (1987a) also found a negative correlation between the rate of predation on the propagules of a species and the dominance of that species in the canopy, with 'significantly higher losses of propagules in forests where conspecifics were rare or absent than in forest where conspecifics were dominant'. Smith et al. (1989) further proposed this 'dominance-predation' pattern might result from the differential distribution of seed predators and suggested that some differences among sites in the relationship between predation and dominance might arise from regional variations in the composition of the seed predators. McGuinness (1997) believed if this 'dominance-predation' model proved to be generally applicable to tropical mangroves, even if only for a few of species, it would represent an important step torwards an understanding of the factors structuring these forests. It would also contribute to the general understanding of the effect of seed predators on plant communities.

7.2 Methods

Experiments were done during the early dry season from May to June 1995 following the methods of Smith (1987a). Six species were chosen : *Avicennia alba*, *A. eucalyptifolia, Bruguiera gymnorrhiza, B. parviflora, Ceriops decandra* and *Rhizophora apiculata.* Twenty healthy, mature propagules of each species were collected from trees (*A. alba, A. eucalyptifolia, C. decandra*) and the forest flloor (*B. gymnorrhiza, B. parviflora, R. apiculata*), tied with a fine nylon string to the root of an established tree, and placed in the forest floor in each of the six 10 m x 10 m subplots within each of the five 10 m x 60 m plots. Three forest types were used : high intertidal zone of the *Rhizophora-Bruguiera-Avicennia alba* association (SP1), lower intertidal zone of the *Sonneratia-Avicennia* association (SP2), and the medium intertidal zone of *Rhizophora-Bruguiera* association (SP3). There were five subplots in each forest type.

The propagules were scored as viable (capable of growth) unless any of three criteria were met: 1) 50% of the mass consumed by predators, 2) pulled entirely down a crab burrow, or 3) the plumule and cotyledonary buds completely removed. The scoring was carried out at 2, 4, 6, 8, 10, 18 and 36 days after placement.

To study the effect of species dominancy on seed predation, the structure and composition of the trees inside the study sites were described using the same methods as in chapter 4. Seedling density and natural seeds available on each site were also recorded.

7.3 Data analysis

Repeated measures ANOVA (Zar 1996) was applied to determine the general effect of site and species factors and their interaction with time (days). For these analyses, time was considered as the within-subject factor and site and species as the between-subject factor. The Mauchly's sphericity test (Kinear & Gray 1995) was applied to evaluate the homogeneity of covariance assumption, which is important for the univariate approach.

Whenever a significant difference was detected, a nested-balanced design of analysis of variance and a one-way analysis of variance were applied for a further determination. A correlation analysis was also applied to investigate the possibility of a relationship between seed predation and species-dominance.

The homogeneity of the data was tested before every statistical analysis, and where necessary data were arcsine, square root, or log (n+1) transformed. The Tukey test was used for data comparison ($p \leq 0.05$). The MINITAB Release 10.2 (Minitab Inc., 1995) and SPSS^X Release 6.1 (SPSS^X Inc., 1996) for MS-WINDOWS™ packages were used for the most of the calculations.

7.4 Results

The mean percentages of non-viable seeds of the six mangrove species during the experiments are shown in Table 7.1. Averaged over all site and species, 62.1 (14 - 100) % of the seeds were non-viable by the end of the experiment (36 d). The repeated measures ANOVA showed that time, site, species and their interactional factors were significantly different ($p \leq 0.05$) against the seed predation. However, the significance of results of further specific analyses varied.

7.4.1 Site effect

Averaged over all species, the mean seed predation by 36 d in SP2 was 70.8%, followed by SP3 (66.8 %) and SP1 (48.7%). *A. alba* and *Bruguiera parviflora* (Fig. 7.1 A and D) were predated faster in SP3 and SP2 than in SP1. However, by the end of the experiment, *A. alba* reached similar values (mean SP1 97.0%, SP2 98.0% and SP3 100.0%), while *B. parviflora* in SP1 (45.0%) was still much lower than in SP3 (94.0%) and in SP2 (91.0%).

The predation of *A. eucalytifolia* (Fig. 7.1B) seeds in SP2 was faster and higher compared with SP3 and SP1. Similarly, *Ceriops decandra* and *R.*

Table 7.1. The seed predation (percentage of non-viable propagules among 20 viable propagules placed in the field) of six mangrove species in plots SP1-3, Bintuni Bay, Irian Jaya, in June 1995. Ranges are given in the parentheses (n = 5 sub-plots).

Time (days)	*Avicennia alba*			*Avicennia eucalyptifolia*			*Bruguiera gymnorrhiza*			*Bruguiera parviflora*			*Ceriops decandra*			*Rhizophora apiculata*		
	SP1	SP2	SP3	SP1	SP2	SP3	SP1	SP2	SP3	SP1	SP2	SP3	SP1	SP2	SP3	SP1	SP2	SP3
2	**23** (15 - 40)	**62** (35 - 85)	**55** (35 - 80)	**3** (0 - 5)	**51** (35 - 60)	**19** (5 - 40)	**0** (0 - 0)	**0** (0 - 0)	**2** (0 - 5)	**2** (0 - 5)	**27** (10 - 40)	**38** (0 - 80)	**0** (0 - 0)	**6** (0 - 15)	**3** (0 - 15)	**1** (0 - 5)	**6** (5 - 10)	**1** (0 - 5)
4	**50** (20 - 70)	**75** (55 - 95)	**77** (55 - 100)	**17** (0 - 45)	**75** (65 - 90)	**31** (10 - 60)	**1** (0 - 5)	**0** (0 - 0)	**2** (0 - 5)	**7** (0 - 15)	**40** (15 - 65)	**50** (5 - 95)	**0** (0 - 0)	**11** (0 - 20)	**5** (0 - 20)	**1** (0 - 5)	**9** (5 - 20)	**4** (0 - 10)
6	**63** (25 - 90)	**79** (55 - 100)	**88** (75 - 100)	**29** (10 - 50)	**84** (75 - 90)	**49** (20 - 80)	**2** (0 - 5)	**2** (0 - 5)	**5** (0 - 10)	**13** (5 - 20)	**51** (20 - 75)	**64** (15 - 95)	**0** (0 - 0)	**18** (10 - 25)	**9** (0 - 25)	**2** (0 - 5)	**16** (5 - 30)	**4** (0 - 10)
8	**74** (50 - 90)	**83** (65 -100)	**91** (75 - 100)	**34** (10 - 60)	**90** (85 - 95)	**51** (25 - 90)	**4** (0 - 5)	**4** (0 - 10)	**7** (0 - 20)	**18** (15 - 20)	**59** (20 - 85)	**68** (25 - 95)	**1** (0 - 5)	**24** (10 - 35)	**13** (0 - 30)	**4** (0 - 5)	**21** (5 - 30)	**7** (0 - 20)
10	**76** (50 - 95)	**86** (70 - 100)	**93** (80 - 100)	**41** (20 - 80)	**91** (85 - 95)	**58** (35 - 90)	**5** (0 - 10)	**8** (0 - 20)	**8** (0 - 20)	**20** (15 - 25)	**60** (20 - 85)	**73** (35 - 95)	**6** (0 - 15)	**30** (10 - 45)	**16** (5 - 30)	**9** (5 - 20)	**23** (10 - 35)	**9** (0 - 20)
18	**90** (65 - 100)	**91** (70 - 100)	**98** (90 - 100)	**52** (20 - 95)	**100** (100 -100)	**81** (70 - 95)	**12** (0 - 25)	**13** (5 - 25)	**16** (5 - 35)	**31** (25 - 35)	**74** (40 - 90)	**83** (55 - 100)	**16** (5 - 25)	**38** (25 - 55)	**26** (10 - 50)	**12** (5 - 25)	**27** (15 - 35)	**11** (5 - 20)
36	**97** (85 - 100)	**98** (90 - 100)	**100** (100 - 100)	**68** (45 - 100)	**100** (100 - 100)	**92** (75 - 100)	**37** (20 - 55)	**34** (15 - 50)	**36** (15 - 50)	**45** (35 - 60)	**91** (65 - 100)	**94** (80 - 100)	**30** (5 - 55)	**62** (55 - 75)	**55** (25 - 85)	**14** (5 - 30)	**41** (30 - 55)	**24** (15 - 35)

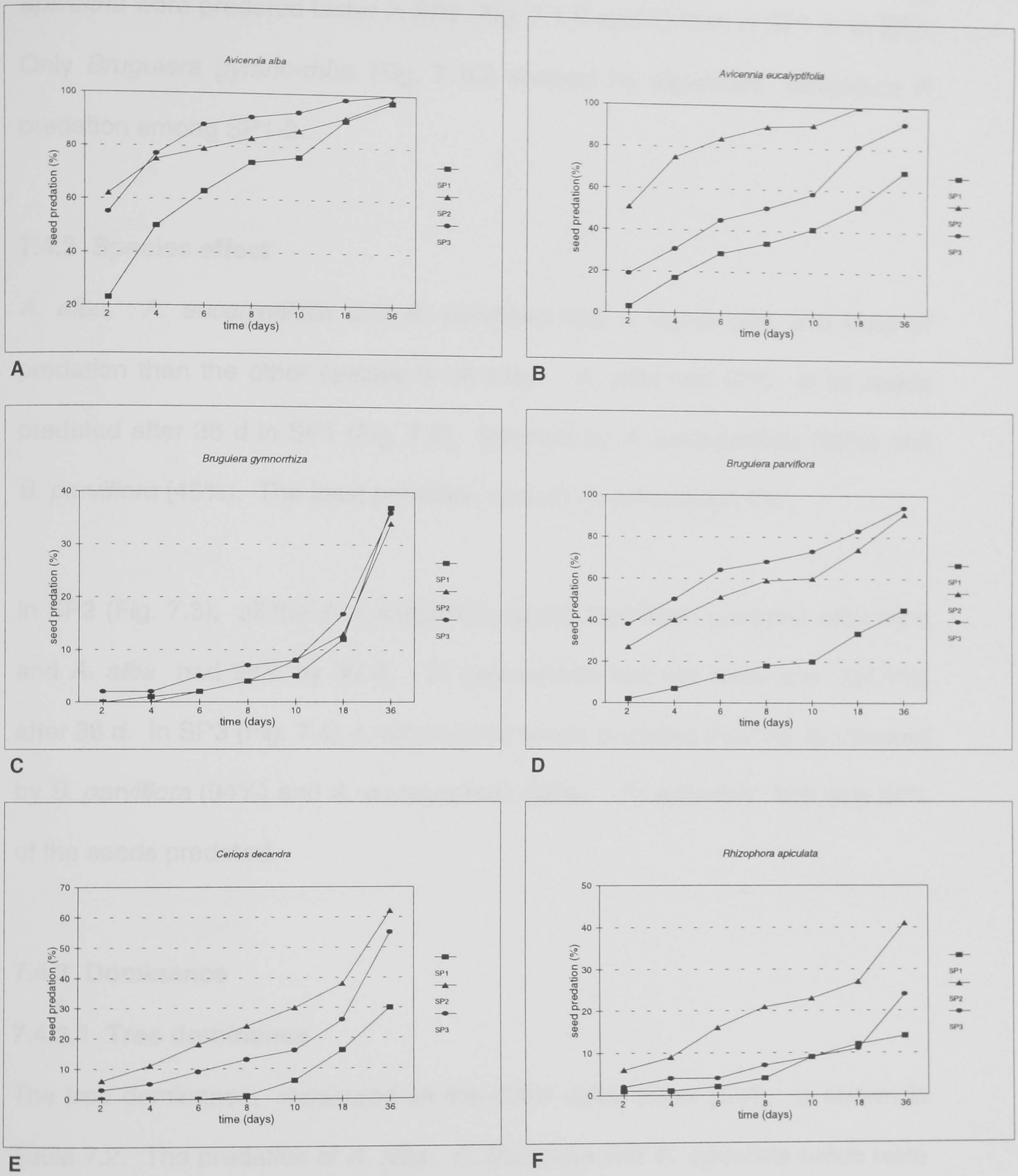


Fig. 7.1. The seed predation of six mangrove species in SP1-3, Bintuni Bay, Irian Jaya.

apiculata were predated faster in SP2 (Fig. 7.1 E and F) than in SP1 or in SP3. Only *Bruguiera gymnorrhiza* (Fig. 7.1C) showed no significant difference in predation among SP1-3.

7.4.2 Species effect

A. alba, A. eucalyptifolia and *B. parviflora* had a higher rate and level of predation than the other species in all sites . *A. alba* had 97% of its seeds predated after 36 d in SP1 (Fig. 7.2), followed by *A. eucalyptifolia* (69%) and *B. parviflora* (45%). The least predation was on *R. apiculata* (14%).

In SP2 (Fig. 7.3), all the *A. eucalyptifolia* seeds had been predated after 18 d and *A. alba* had 98% by 36 d. *B. gymnorrhiza* had the least rate (34.0%) after 36 d. In SP3 (Fig. 7.4) *A. alba* had all seeds predated after 36 d, followed by *B. parviflora* (94%) and *A. eucalyptifolia* (92%). *R. apiculata* had only 24% of the seeds predated.

7.4.3 Dominance

7.4.3.1 Tree dominance

The tree dominance, measured as the cover value index (CVI), is shown in Table 7.2. The predation of *A. alba, C. decandra* and *R. apiculata* seeds were highest on the sites where adults were absent or the least dominant and the predation of *A. alba* and *B. parviflora* were the lowest where the adult trees' dominance was highest (Fig. 7.5).

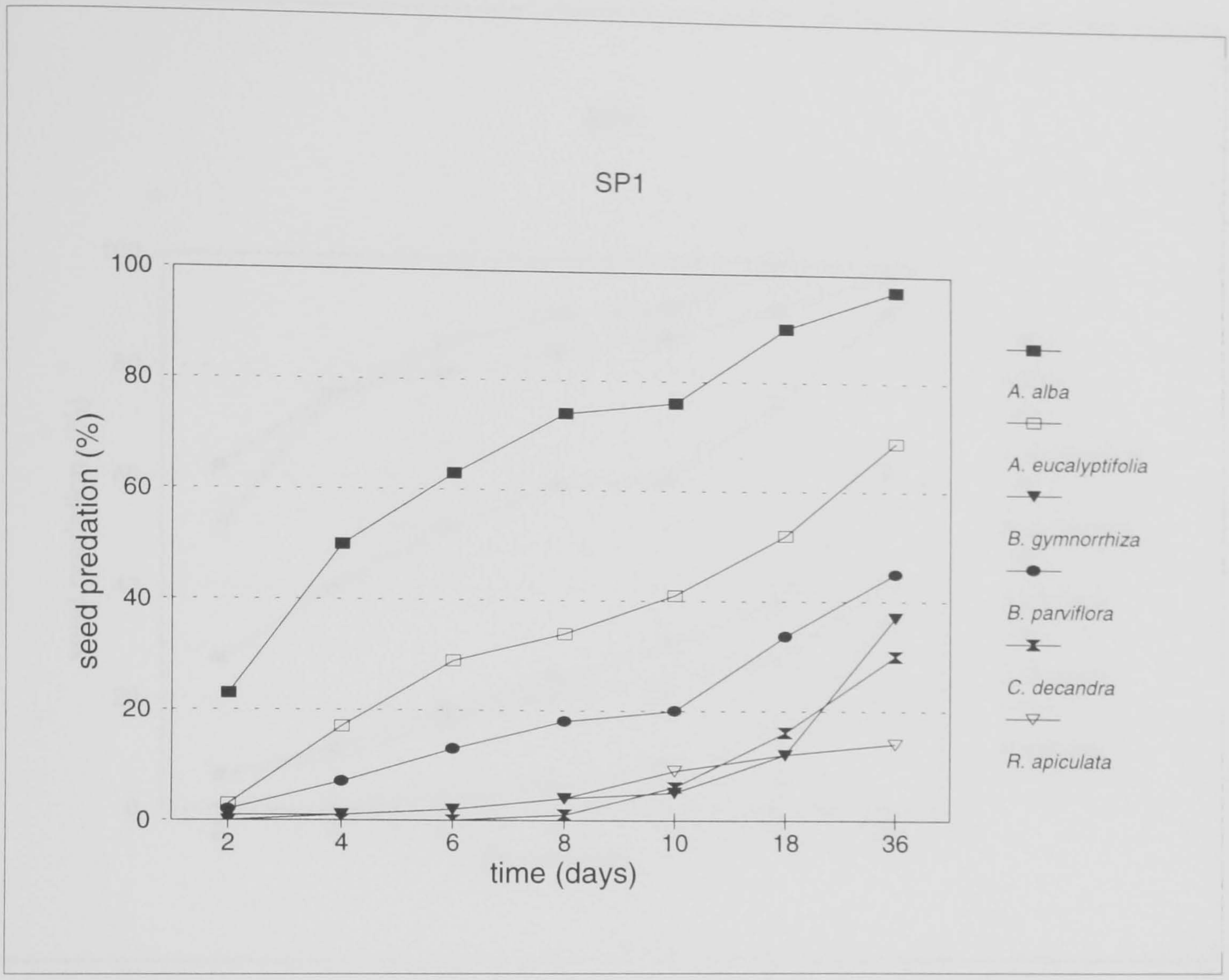


Fig. 7.2. The seed predation distribution of six mangrove species in SP1, Bintuni Bay, Irian Jaya.

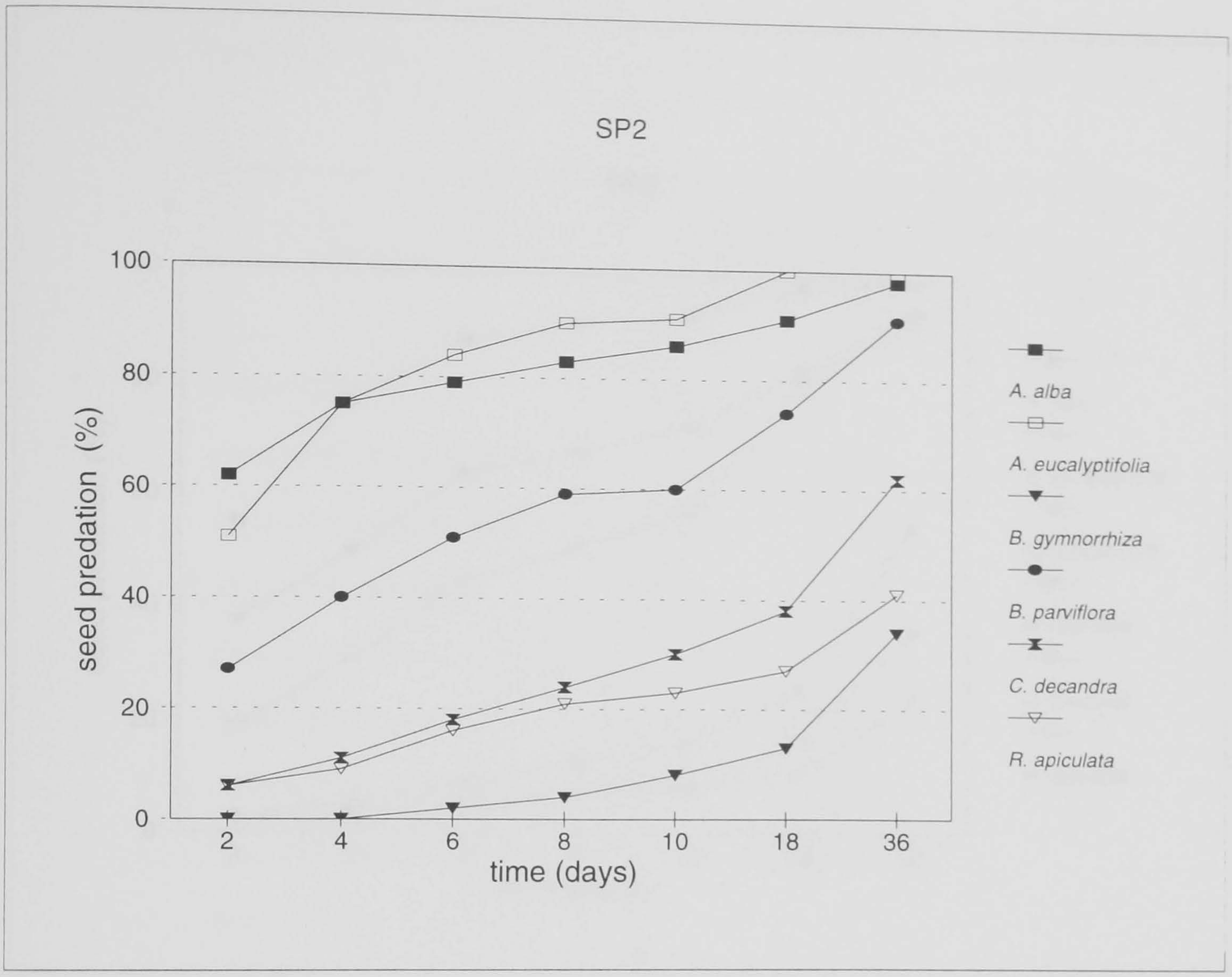


Fig. 7.3. The seed predation distribution of six mangrove species in SP2, Bintuni Bay, Irian Jaya.

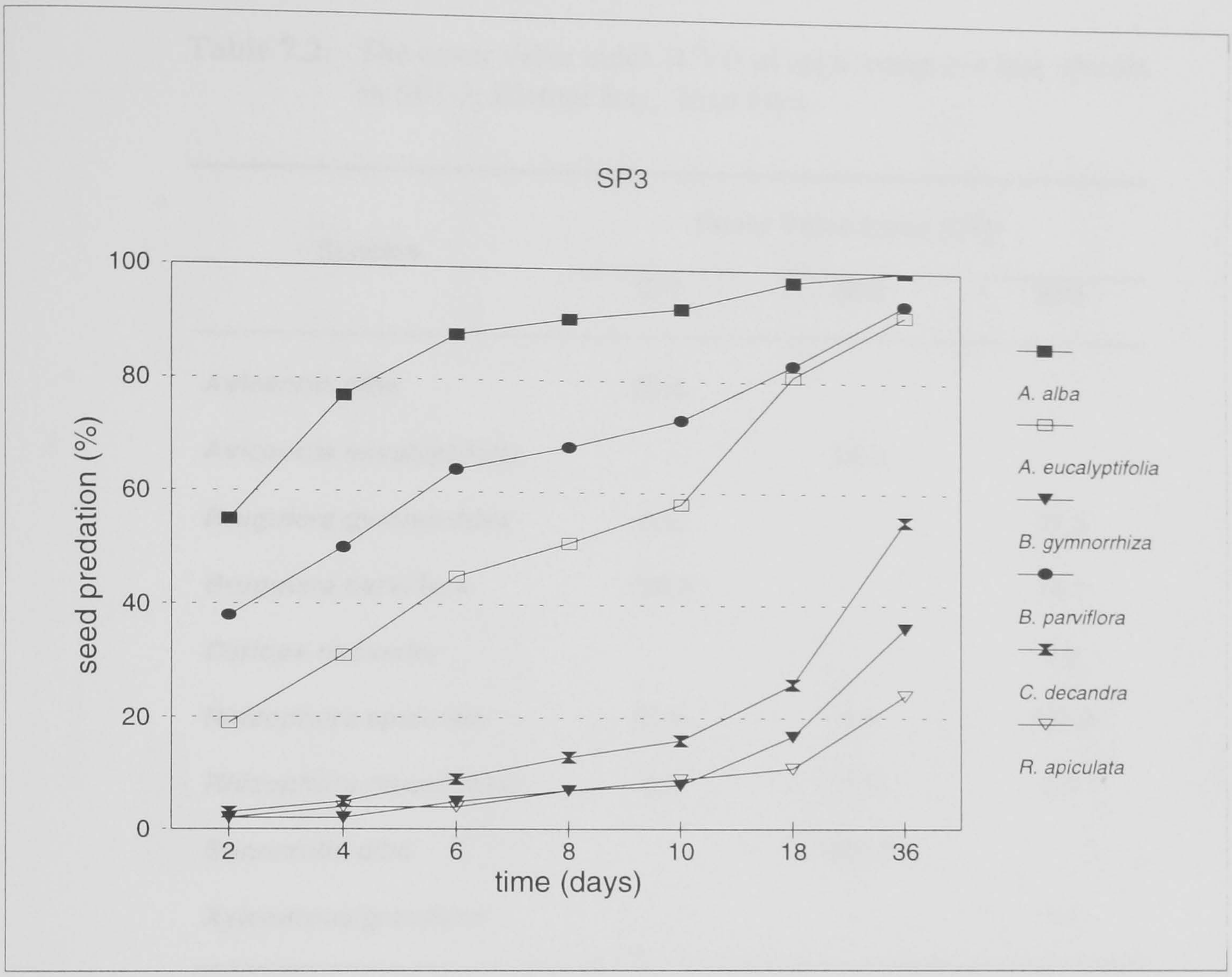


Fig. 7.4. The seed predation distribution of six mangrove species in SP3, Bintuni Bay, Irian Jaya.

Table 7.2. The cover value index (CVI) of each mangrove tree species in SP1-3, Bintuni Bay, Irian Jaya.

Species	Cover Value Index (CVI)		
	SP1	SP2	SP3
Avicennia alba	20.8		
Avicennia eucalyptifolia		20.2	
Bruguiera gymnorrhiza	8.8		37.3
Bruguiera parviflora	108.6		14.1
Ceriops decandra			3.9
Rhizophora apiculata	58.8	8.0	137.9
Rhizophora mucronata	2.9	16.5	5.7
Sonneratia alba		155.3	
Xylocarpus granatum			1.1

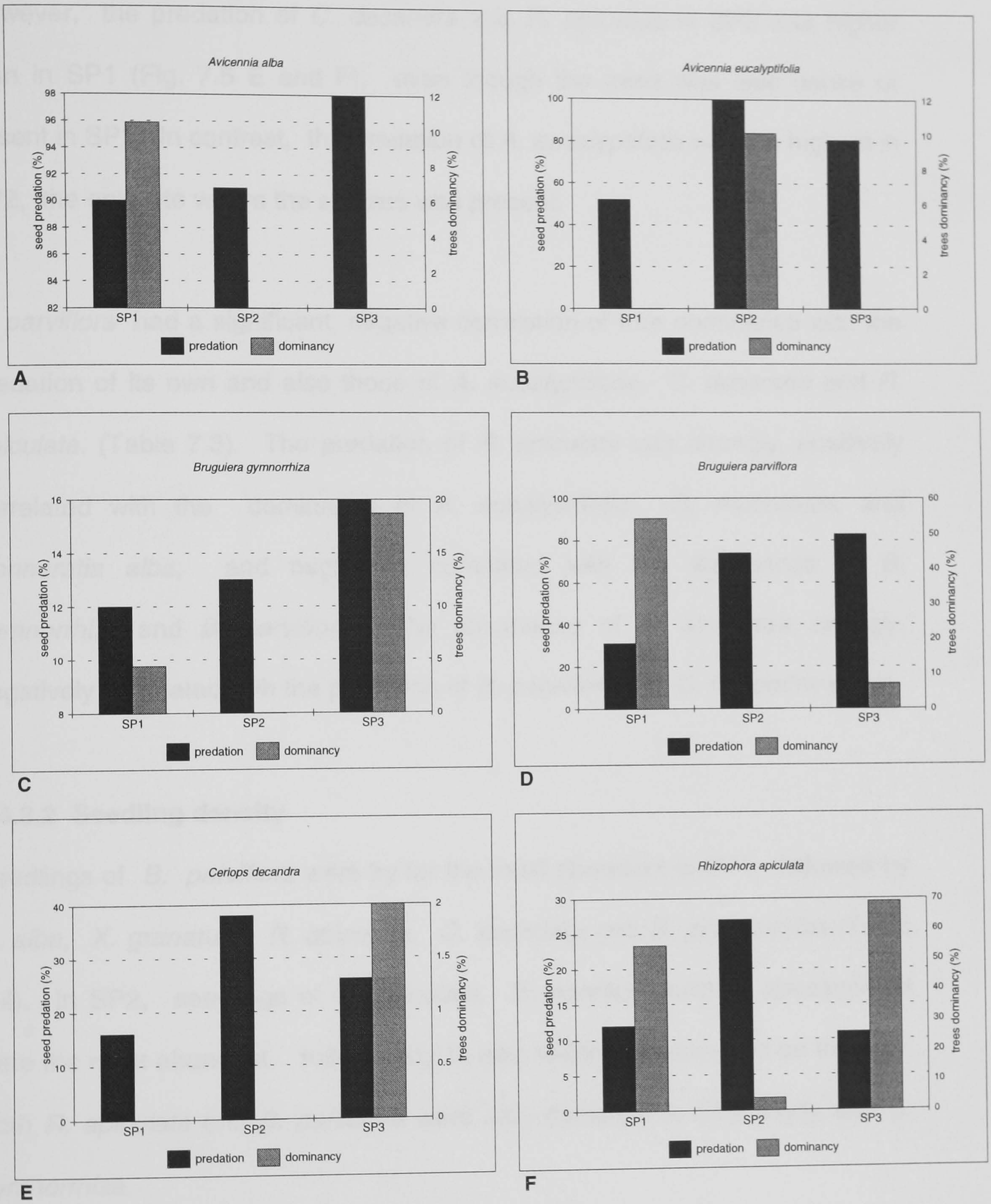


Fig. 7.5. Comparison of seed predation and tree dominance of each species in SP1-3, Bintuni Bay, Irian Jaya.

However, the predation of *C. decandra* and *R. apiculata* in SP3 was higher than in SP1 (Fig. 7.5 E and F), even though the trees was less dense or absent in SP1. In contrast, the predation of *A. eucalyptifolia* was the highest in SP2, the only site where the species was present.

B. parviflora had a significant, negative correlation of tree dominance with the predation of its own and also those of *A. eucalyptifolia, C. decandra* and *R. apiculata*. (Table 7.3). The predation of *R. apiculata* was strongly, positively correlated with the dominance of *A. eucalyptifolia, R. mucronata*, and *Sonneratia alba*, and negatively correlated with the dominance of *B. gymnorrhiza* and *B. parviflora*. The dominance of *A. alba* was strongly, negatively correlated with the predation of *B. parviflora* and *C. decandra* seeds.

7.4.3.2 Seedling density

Seedlings of *B. parviflora* were by far the most abundant in SP1, followed by *A. alba*, *X. granatum, R. apiculata, C. decandra* and *B. gymnorrhiza* (Table 7.4). In SP2, seedlings of *R. apiculata, B. parviflora* and *A. eucalyptifolia* were the most abundant, followed by *S. alba* which only occurred on this site. Both *R. apiculata* and *B. parviflora* were also dominant in SP3 along with *B. gymnorrhiza.*

The correlations between seed predation and seedling density of each species are shown in Fig. 7.6 and Table 7.5. The seed predation of *A. alba* and *C. decandra* was highest where the seedlings were absent. In contrast, the seed predation of *A. eucalyptifolia* was the highest in SP2 where its seedling density

Table 7.3 Results of correlation analysis between tree dominance (*i.e.*, cover value index) and seed predation in SP1-3, Bintuni Bay, Irian Jaya.
* = $p \leq 0.05$, ** = $p \leq 0.01$

Seed predation	**Tree dominance**							
	A. alba	***A. eucalyptifolia***	***B. gymnorrhiza***	***B. parviflora***	***C. decandra***	***R. apiculata***	***R. mucronata***	***S. alba***
A. alba	-0.391	-0.153	0.051	-0.053	-0.008	0.003	-0.174	-0.041
A. eucalyptifolia	-0.427	0.369	-0.412	-0.623*	-0.279	-0.153	0.229	0.445
B. gymnorrhiza	0.036	-0.131	0.121	-0.009	0.036	0.175	-0.124	-0.100
B. parviflora	-0.729*	0.341	-0.312	-0.752**	-0.299	-0.136	0.328	0.424
C. decandra	-0.589*	0.302	-0.422	-0.529*	-0.249	-0.204	0.330	0.422
R. apiculata	-0.509	0.539*	-0.638*	-0.767**	-0.444	-0.421	0.739**	0.686**

Table 7.4 The seedling density (per 100 m^2) of mangrove species in SP1-3, Bintuni Bay, Irian Jaya on June 1995. Values are means and ranges are given in the parenthesis (n = 5 sub-plots).

Species	Seedling density		
	SP1	SP2	SP3
Avicennia alba	5.7 (0.0 - 31.0)	0.1 (0.0 - 2.0)	0.0 (0.0 - 0.0)
Avicennia eucalyptifolia	0.0 (0.0 - 0.0)	2.5 (0.0 - 10.0)	1.1 (0.0 - 6.0)
Bruguiera gymnorrhiza	2.0 (0.0 - 7.0)	0.1 (0.0 - 2.0)	13.0 (2.0 - 44.0)
Bruguiera parviflora	161.8 (0.0 - 1160.0)	3.0 (0.0 - 18.0)	11.7 (0.0 - 105.0)
Ceriops decandra	2.3 (0.0 - 13.0)	0.5 (0.0 - 6.0)	5.3 (0.0 - 35.0)
Rhizophora apiculata	2.8 (0.0 - 9.0)	4.7 (0.0 - 10.0)	20.7 (0.0 - 78.0)
Rhizophora mucronata	0.2 (0.0 - 4.0)	0.9 (0.0 - 5.0)	1.3 (0.0 - 5.0)
Sonneratia alba	0.0 (0.0 - 0.0)	1.6 (0.0 - 30.0)	0.0 (0.0 - 0.0)
Xylocarpus granatum	3.1 (0.0 - 10.0)	0.1 (0.0 - 2.0)	3.4 (0.0 - 16.0)

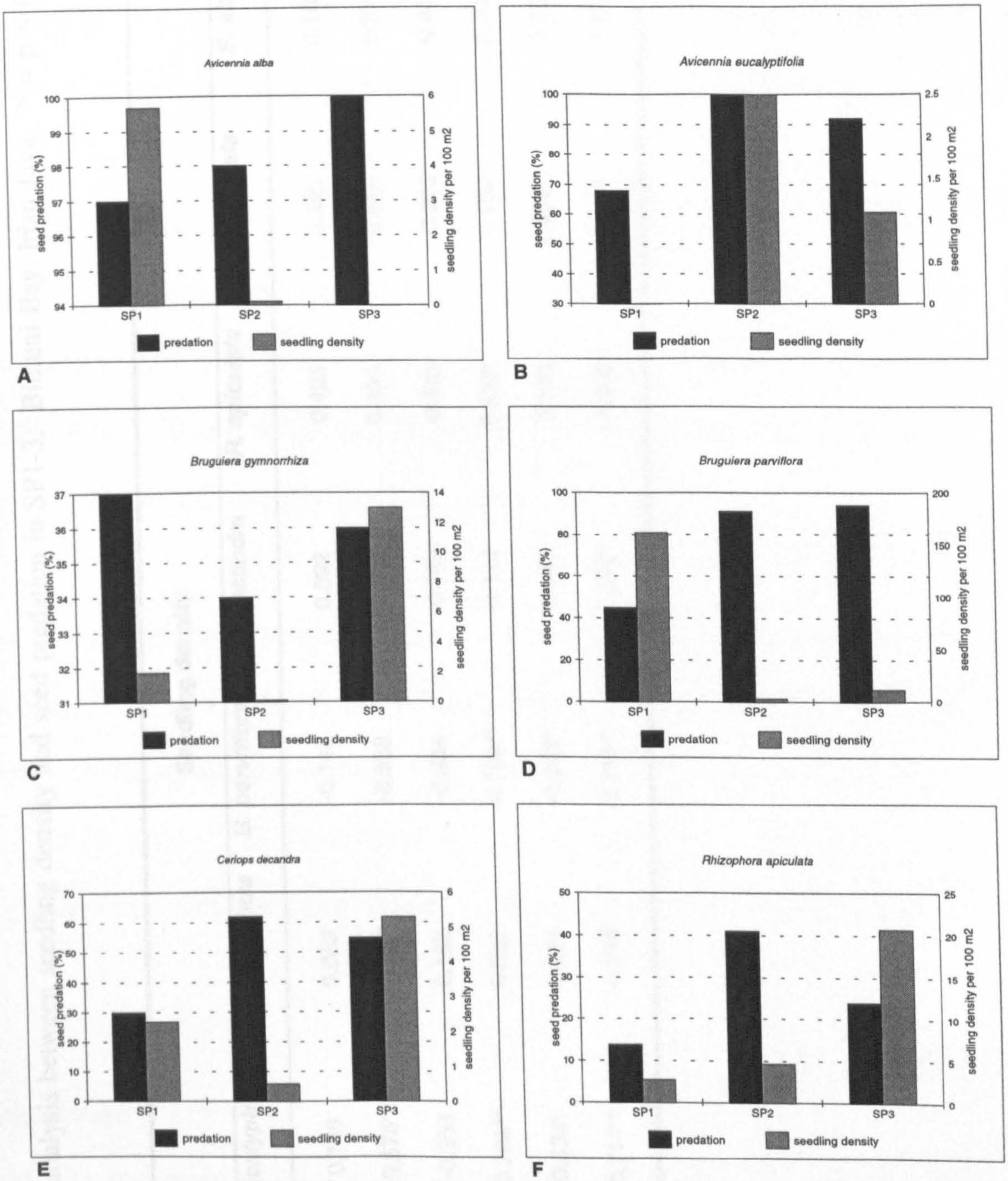


Fig. 7.6. Comparison of seed predation and seedling density in SP1-3, Bintuni Bay, Irian Jaya.

Table 7.5. The results of correlation analysis between seedling density and seed predation in SP1-3, Bintuni Bay, Irian Jaya. * = $p \leq 0.05$, ** = $p \leq 0.01$.

Seed predation	**Seedling density**							
	A. alba	***A. eucalyptifolia***	***B. gymnorrhiza***	***B. parviflora***	***C. decandra***	***R. apiculata***	***R. mucronata***	***S. alba***
A. alba	-0.148	0.149	0.053	-0.143	0.092	0.425	0.355	0.168
A. eucalyptifolia	-0.523*	0.575*	-0.206	-0.559	-0.271	0.393	0.553	0.278
B. gymnorrhiza	-0.084	-0.253	0.182	-0.084	-0.189	-0.065	-0.202	-0.439
B. parviflora	-0.900**	0.788**	0.035	-0.756**	-0.119	0.533*	0.480	0.305
C. decandra	-0.514*	0.534*	-0.221	-0.622*	-0.347	0.225	0.656**	0.230
R. apiculata	-0.729**	0.711**	-0.378	-0.716**	-0.557*	-0.082	0.286	0.310

was highest, and was the lowest in SP1 where its seedlings were absent. The seedling density of *A. alba* and *B. parviflora* was strongly correlated with seed predation of *A. eucalyptifolia, B. parviflora, C. decandra* and *R. apiculata*.

7.4.3.3 Seed density

No seeds of *A. eucalyptifolia* were found, one seed of *A. alba* was found in SP1 and none in SP2 and SP3, and four seeds of *S. alba* were found only in SP2 (Table 7.6). There were significant ($p \leq 0.05$) differences in density between at least two of the sites for all species.

There were no relationships between seed predation and seed density for each species (Fig. 7.7), except for *B. parviflora* which had seed predation strongly negatively correlated with the density of its own seeds and those of some other species (Table 7.7). The seed predation of *R. apiculata*, however, was strongly correlated with the seed density of *B. parviflora, C. decandra* and *S. alba*.

7.5 Discussion

The fact that the seed predation in Bintuni Bay varied and was significantly different among species, sites and time agrees with similar studies elsewhere even though different species and lengths of observation were involved.

In Missionary Bay, Queensland, Australia, Smith (1987a) found an average 75.7% seed predation on five species (*Avicennia marina, Bruguiera exaristata, B. gymnorrhiza, Ceriops tagal* and *Rhizophora stylosa*) in three forest types in

Table 7.6 The natural seed density (per 100 m^2) of mangrove species in SP1-3, Bintuni Bay, Irian Jaya on June 1995. Values are means and ranges are given in the parenthesis (n = 5 sub-plots).

Species	Seed density		
	SP1	SP2	SP3
Avicennia alba	0.0 (0.0 - 1.0)	0.0 (0.0 - 0.0)	0.0 (0.0 - 0.0)
Avicennia eucalyptifolia	0.0 (0.0 - 0.0)	0.0 (0.0 - 0.0)	0.0 (0.0 - 0.0)
Bruguiera gymnorrhiza	0.6 (0.0 - 4.0)	0.5 (0.0 - 5.0)	2.9 (0.0 - 8.0)
Bruguiera parviflora	10.1 (0.0 - 60.0)	0.6 (0.0 - 7.0)	2.0 (0.0 - 17.0)
Ceriops decandra	2.0 (0.0 - 11.0)	0.7 (0.0 - 10.0)	1.1 (0.0 - 8.0)
Rhizophora apiculata	2.5 (0.0 - 11.0)	2.4 (0.0 - 15.0)	7.9 (0.0 - 28.0)
Rhizophora mucronata	2.1 (0.0 - 16.0)	3.0 (0.0 - 15.0)	1.6 (0.0 - 10.0)
Sonneratia alba	0.0 (0.0 - 0.0)	0.6 (0.0 - 4.0)	0.0 (0.0 - 0.0)
Xylocarpus granatum	0.4 (0.0 - 4.0)	0.2 (0.0 - 4.0)	0.2 (0.0 - 6.0)

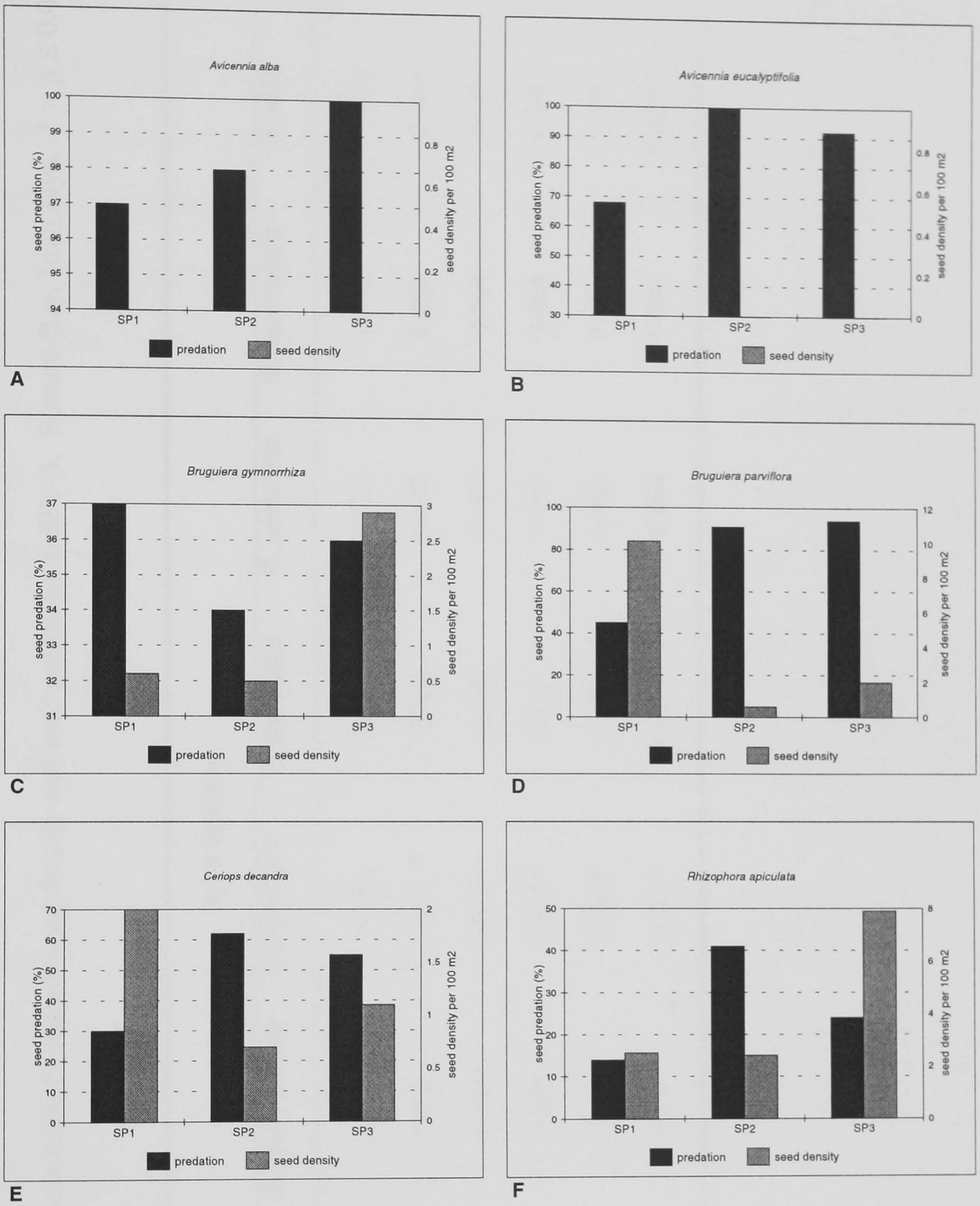


Fig. 7.7. The comparison of seed predation and natural seed density of each species in SP1-3, Bintuni Bay, Irian Jaya.

Table 7.7 The results of correlation analysis between natural seed density and seed predation in SP1-3, Bintuni Bay, Irian Jaya. * = $p \leq 0.05$, ** = $p \leq 0.01$.

Seed predation	**Seed density**						
	A. alba	***B. gymnorrhiza***	***B. parviflora***	***C. decandra***	***R. apiculata***	***R. mucronata***	***S. alba***
A. alba	0.102	0.529	-0.268	0.166	0.217	-0.050	-0.028
A. eucalyptifolia	0.117	0.357	-0.714**	-0.255	0.272	0.280	0.416
B. gymnorrhiza	0.202	-0.288	0.008	-0.225	-0.101	-0.364	0.060
B. parviflora	-0.134	0.323	-0.696**	-0.618*	0.294	-0.064	0.343
C. decandra	-0.224	0.428	-0.589*	0.103	0.409	0.291	0.403
R. apiculata	-0.183	-0.205	-0.571*	-0.523*	-0.040	-0.008	0.670**

an 18-d experiment. McKee (1995b), based on her study in a Belizean mangrove, found the rates of the predation in 9 d were highest for *A. germinans* (60%) and significantly lower for *R. mangle* (18%) and *Laguncularia racemosa* (28%). In Ludmilla Creek, Darwin, Australia, McGuinness (1997) found, averaged over four species (*A. marina, B. exaristata, C. tagal* and *R. stylosa*) and seven forest types, the percentage of propagules eaten by predators in 20 - 22 d was 63.3%. In Bintuni Bay the predation averaged 62.1 % in 36 d and ranged from 14% (*R. apiculata* in SP1) to 100% (*A. alba* in SP3 and *A. eucalyptifolia* in SP2).

The results of Smith et al. (1989) allow direct comparison with Bintuni Bay since the same species were involved. They found that 87.5% of *Avicennia* propagules were consumed where the adults were frequent in the forest, compared with 29.5% where the adult was dominant. In Bintuni Bay the corresponding values were 75 - 77% where the adult was not present (SP2 and SP3), and 50% where the adults were frequent in SP1. For *R. apiculata*, in Malaysia and Australia 24.1% of propagules were consumed in forest where it was rare, and 5.2% where it dominated the canopy. In Bintuni Bay only 1 - 4% of the propagules of *R. apiculata* were consumed in the first 4 d in SP1 and SP3 where the adults were abundant, and 9% in SP2 where the adults were less common. In contrast for *B. gymnorrhiza*, more propagules were consumed in forest where the adults were dominant than where they were less common, as was the case in Bintuni Bay.

7.5.1 Site effect

In general, the mean predation in SP2 (lower intertidal zone) was faster and higher than in SP3 (medium intertidal zone) and in SP1 (higher intertidal zone). In Panama, Smith *et al.* (1989) also found that more propagules of *R. mangle* were consumed in the low intertidal zone.

In a planting experiment of *R. mangle* propagules at different distances from the shoreline in Belize, McKee (1995b) found that many more propagules survived inside the forest compared with those closest to the creek bank. The survival of seedlings increased and evidence of crab damage declined with increasing distance from the shoreline. It should be noted, however, that mangroves in the Old World tropics (Indo-Pacific region) and in the New World tropics (south and central America region) are floristically different.

In contrast to the conditions above, Osborne & Smith (1990) found greater rates of predation in the high intertidal compared with the low intertidal zone for *Aegiceras corniculatum* in Murray River and Missionary Bay, Queensland, Australia. The frequency of tidal inundation, which in turn affects the amount of time available for foraging, was thought to account for differences in predation between low and high intertidal forests. In addition, Smith et al. (1989) reported that in low intertidal forests in Australia where *A. marina* has abundant, the crab fauna was dominated by the genus *Uca*. *Uca* are primarily detritus feeders and have not been reported to eat mangrove propagules (Jones 1984). The crab fauna in higher intertidal forests was dominated by members of the *Grapsidae*, primarily *Sesarma,* which is a well known seed predator.

Predation by other organisms may occur. Smith *et al.* (1989) reported in Florida that sudden consumption of *A. germinans*, coincided with inundation of the plots by tides, implicating a water-borne organism as the major predator in this forest. Fish have been reported to eat *Avicennia* seedlings (Macnae 1969). In other forests in Florida, Smith *et al.* (1989) found that the snails *Melampus coeffeus* and *Cerithidea scalariformis* were the main propagule consumers. These snails were most abundant in low intertidal *A. germinans* forests. Unfortunately no quantification of predation, other than by crabs, was made at Bintuni Bay.

7.5.2 Species effect

Significantly different predation occurred among the six mangrove species. *A. alba, A. eucalyptifolia* and *B. parviflora* were the most predated species, and *C. decandra, R. apiculata* and *B. gymnorrhiza* were the least. This result was similar to those of Smith (1987a), Smith *et al.* (1989), McKee (1995b), and McGuinness (1997) in showing a wide range of species predation.

Smith (1987a) discovered that differences in the nutritive value of the propagules were significantly related to the differences in the amount of predation among species. *A. marina*, the most predated species, had the highest concentrations of simple sugars and the lowest of tannins, fibres, and proteins. In contrast, *Ceriops*, the least palatable of the species, had a high tannin and crude fibre concentration.

Similarly McKee (1995b) found that the nutritive quality was higher, and the content of defensive compounds was lower, in *A. germinans* propagules than in *R. mangle* and *Laguncularia racemosa*, although there were no consistent links with the degree of predation.

Saenger (1982) suggested that *Rhizophora* propagules are covered with a waxy cuticle that was effective in deterring predators. *Avicennia* propagules are covered by a thin fleshy pericarp but it is easily penetrated by predators and is shed after 1 - 2 d in the water.

McKee (1995b), from propagule-cutting experiments, concluded that the size of propagules was related to the high predation of *A. germinans*. She found that when propagules of *R. mangle* were cut into different lengths, the predation varied with size of the propagules. The small size of *A. germinans* probably facilitates burial in crab burrows. Previously, Smith (1987a) based on a principal components analysis of physical and chemical characteristics of five mangrove propagules, believed that size was less important than nutritive quality or defensive compounds.

In addition to the consistent ranking of predation on species in Ludmilla Creek, Darwin, McGuinness (1997) found that the predation was also consistent with forest type. He found that the seed predation was consistently high in the *R.*

stylosa mixed plots; moderate in the *A. marina* plots; and low in the *B. exaristata - C. tagal* plots. He believed that this pattern may result from an interaction between the preference of predators for particular species and the differing background availability of propagules in the plots.

7.5.3 Dominance

7.5.3.1 Tree dominance

Only the predation of *A. alba* clearly supported the dominance-predation hypothesis of Smith (1987a,b) in being highest where adults were absent and lowest where adults were abundant. The results for *B. parviflora, C. decandra,* and *R. apiculata* only partly agreed with the hypothesis.

In contrast, the predation of *A. eucalyptifolia* was the highest where the plants were abundant and least where it was absent. It should be noted, however, that adult *A. eucalyptifolia* were only common in SP2, which was dominated by *Sonneratia alba*.

In Ludmilla Creek, Darwin, McGuinness (1997) found there was no relationship between propagule predation and the abundance of adult conspecifics. Smith *et al.* (1989) suggested that one reason the hypothesis might apply in some places and not others was that the seed predators differed between regions. However McGuinness (1997) argued that the seed predators at Ludmilla Creek were the same as those in North Queensland studied by Smith (1987a) and Smith et al. (1989).

7.5.3.2 Seedling density

The results for *A. alba, C. decandra* and *A. eucalyptifolia* seedling density-predation correlations were similar to the results with the adult trees and confirm that the predators on each site were consistent with their preferences in choosing the propagules. However, this conclusion was still tentative since there was no correlation of natural seed density with seed predation (see the following discussion).

7.5.3.3 Seed density

No conclusion on the relationship between seed predation and natural seed density can be drawn from the results, except for *B. parviflora,* because of the lack of seeds (probably related to fruiting seasonality). However, the predation of *R. apiculata* was strongly correlated with the seed density of other species.

McGuinness (1997) based on his research in Ludmilla Creek, Darwin, concluded that the intensity of predation did not vary as the dominance-predation model (Smith 1987a) predicted. Instead, predation on the propagules of a species appeared to depend on the availability of propagules of other, more highly preferred species. McKee (1995b) noted that the possible reasons for variation in predation rates included abundance of propagules, or availability of other food sources or both. McGuiness (1997) found that predation on *B. exaristata* and *C. tagal* propagules was negatively correlated with the density of naturally occuring *B. exaristata* propagules.

VIII REGENERATION AFTER FELLING

8.1 Introduction

The management of mangrove ecosystems requires a knowledge of their regeneration and species characteristics. Most mangroves regenerate naturally, their species composition is simple, and their dynamics relatively easy to study (Tamai & Iampa 1988).

Mangroves have little capacity for vegetative reproduction and are dependent on seedling recruitment. Consequently, survival of seedlings directly affects species distribution and abundance. All mangrove tree species are dispersed by sea water, and the propagule (fruit, seed or seedling) has some ability to float, even if for a limited time (Tomlinson 1994) (Plate 11).

Establishment of the seedling is often difficult because of the unstable, variable substrates and the tidal influence (Tomlinson 1994). Ball (1988) and McKee (1993a,b) discussed how tidal inundation influences soil redox potential, salinity, pH, and concentrations of nutrients and phytotoxins.

Biotic factors such as seed predation may vary across the intertidal zone and influence mangrove species distribution patterns (Smith 1987a, Smith *et al.* 1989, Mc Kee 1995a). Macnae (1968) and Aksornkoae (1975) had earlier pointed out that light conditions are the main physical factors in the establishment of mangrove trees.

Plate 11 **A - C** All mangrove tree species are dispersed by sea water.

8.2 Methods

All saplings and seedlings on the Regeneration Plots (RP1-6, chapter 2) were measured in June 1994 for stem diameter (at 30 cm above the highest prop-roots for saplings, and just above the hypocotyl for seedlings) and height. Owing to the similarity of the seedlings, most of the species were identified to genera only, except *Bruguiera gymnorrhiza, Bruguiera parviflora, Nypa fruticans* and *Aegiceras corniculatum.* The re-measurement of all seedlings was done after one year, but the seedling survivorship could not be recorded since the plastic tags were broken off by the tide and a more durable material was not available.

8.3 Data analysis

A nested balanced analysis of variance was applied to determine the differences of seedling density between sites, years and species, considering plot as a random factor and site as a fixed factor (Zar 1996). Whenever a significant difference was detected, one-way analyses of variance were applied for further determination. The Tukey test was used for data comparison, and the differences were considered statistically significant at $p \leq 0.05$. The homogeneity of the data was tested and where necessary data were log (n + 1) transformed prior to statistical analyses. The MINITAB release 10.2 (Minitab Inc. 1995) was used for the most of the calculations.

8.4 Results

In total 8857 individu seedlings and saplings of six genera and at least seven species were recorded in both sites in 1994 and 7329 of seven genera and at least eight species in 1995. *Rhizophora* was by far the most common, followed by *Ceriops*, and *Bruguiera gymnorrhiza*. *B. parviflora, Xylocarpus, Nypa fruticans* and *Avicennia* were dense in some plots but absent in others. *Aegiceras corniculatum* was only found as a single individual.

8.4.1 Seedling and sapling density: time, site and species effects

Averaged over all sites, species and years, the density of seedlings and saplings was 26 990 per ha, ranging from 9 480 per ha in RP2 in 1994 to 59 020 per ha in RP5 in 1994 (Table 8.1).

The analysis of variance confirmed that the density was not different between the two years, but there were differences between sites, species and their interactions ($p \leq 0.05$). The year x site interaction factor was significant ($p \leq 0.05$), but year x species was not.

In Site 1 *Rhizophora* with a relative density of more than 90% in all plots was the most common genus for both years. RP1 with mean density of 20 820 per ha was the most dense plot compared with RP2 (9 700) and RP3 (11 520) (Fig. 8.1). In general there was no significant difference in density between the years.

Table 8.1. The seedling and sapling density of each mangrove species at Site 1 (RP1-3) and Site 2 (RP 4-6) in Bintuni Bay, Irian Jaya, in 1994 and 1995. Ranges are given in parentheses (n = 5 sub plots).

	density (per ha)															
	Aegiceras corniculatum		*Avicennia*		*B. gymnorrhiza*		*B. parviflora*		*Ceriops*		*Nypa fruticans*		*Rhizophora*		*Xylocarpus*	
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
RP1	-	-	-	20 (0 - 100)	660 (100 - 2100)	620 (200 - 1800)	20 (0 - 100)	140 (0 - 400)	980 (200 - 2100)	1040 (200 - 2300)	-	120 (0 - 300)	17020 (6900 - 34200)	20780 (9400 - 41300)	80 (0 - 200)	160 (0 - 800)
RP2	-	-	-	20 (0 - 100)	360 (0 - 1400)	280 (0 - 1200)	-	40 (0 - 200)	120 (0 - 400)	80 (0 - 300)	-	20 (0 - 100)	8980 (2400 - 22000)	9480 (4000 - 20400)	20 (0 - 100)	-
RP3	-	-	-	60 (0 - 300)	120 (100 - 200)	40 (0 - 100)	-	60 (0 - 200)	300 (0 - 500)	260 (0 - 700)	-	-	10920 (1800 - 26900)	11120 (700 - 27600)	20 (0 - 100)	140 (0 - 300)
RP4	-	-	980 (0 - 4200)	840 (0 - 3800)	3040 (900 - 5100)	1480 (600 - 2300)	660 (100 - 2600)	880 (100 - 3500)	4680 (500 - 8600)	1820 (400 - 3500)	1420 (200 - 2800)	940 (300 - 2000)	36740 (12400 - 111900)	28160 (8500 - 93400)	1480 (600 - 3400)	1920 (300 - 4900)
RP5	-	20 (0 - 100)	300 (0 - 1000)	160 (0 - 700)	4600 (1300 - 8100)	3960 (1600 - 9800)	460 (100 - 800)	160 (0 - 400)	7660 (2800 - 12400)	3000 (400 - 5500)	1060 (40 - 1900)	400 (100 - 1100)	42480 (3600 - 102400)	32480 (8000 - 74000)	2460 (600 - 4500)	2660 (500 - 4700)
RP6	-	-	120 (0 - 200)	60 (0 - 100)	2280 (700 - 4700)	2180 (1000 - 5200)	480 (100 - 1100)	440 (0 - 900)	4480 (300 - 10200)	1580 (200 - 4400)	620 (100 - 1700)	300 (0 - 800)	19300 (4800 - 36900)	16500 (6200 - 33100)	2240 (800 - 5100)	2340 (1300 - 4600)

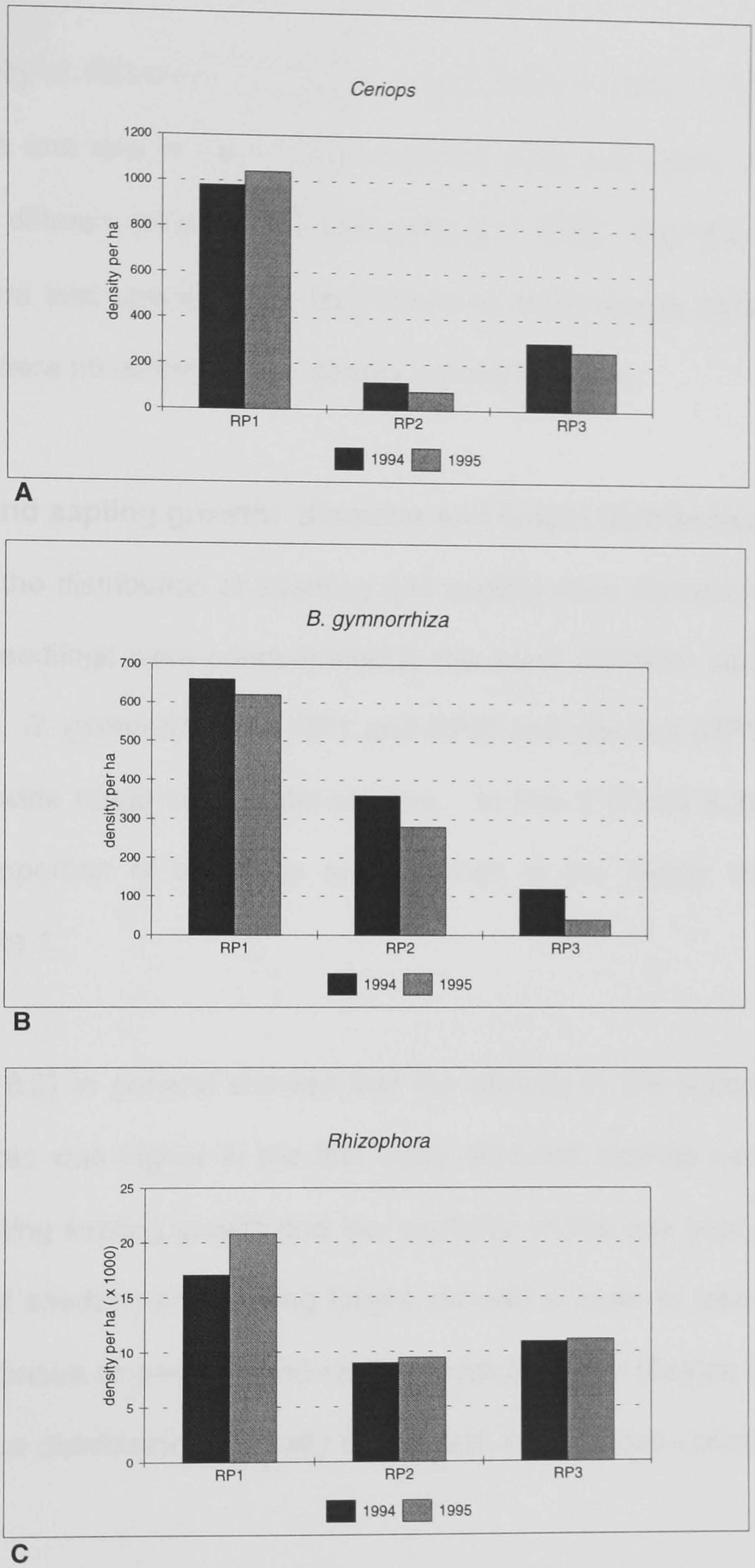


Fig. 8.1. The density of three main seedling and sapling species at Site 1 (RP1-3) in Bintuni Bay, Irian Jaya, in 1994 and 1995.

The relative density of *Rhizophora* was less in Site 2 than in Site 1. The total number of genera and species was similar between plots and years, but the total density was different between the two years ($p \leq 0.05$). Fig. 8.2. shows most of the genera and species were less dense in 1994 except *Xylocarpus* spp., and there were no differences in density among the plots.

8.4.2 Seedling and sapling growth: diameter and height distribution.

Table 8.2 shows the distribution of seedling and sapling stem diameter in Site 1. Most of the seedlings were concentrated in the lower diameter class (< 1 cm). *Rhizophora, B. gymnorrhiza* (in RP1 and RP2) and *Ceriops* (RP1) were represented in a wide range of diameter classes. In Site 2 (Table 8.3) there was a higher proportion of seedlings and saplings in the higher diameter classes than in Site 1.

Rhizophora (Fig. 8.3) in general showed that the density in the second year (1995) in both sites was higher in the last three diameter classes compared with 1994, indicating sapling growth and low mortality in the one year period. The distribution of seedling and sapling height showed a more or less similar trend to the distribution of seedling and sapling stem diameter (Tables 8.4 and 8.5). However, the distribution of density within each height class varied.

Rhizophora height distribution in RP1-3 also changed between the two years, resembling the change in the stem diameter distribution (Fig. 8.4 A-C). In RP4-6 (Fig. 8.4 D-F) the trend was different from RP1-3 and the pattern was

Table 8.2. The distribution of seedling and sapling stem diameter of each mangrove species at Site 1 (RP1-3) in Bintuni Bay, Irian Jaya, in 1994 and 1995. Data are numbers of individuals and ranges are given in parentheses (n = 5 sub plots).

	Seedling diameter (cm)				Sapling diameter (cm)											
	<1		1 - 1.9		2 - 2.9		3 - 3.9		4 - 4.9		> 5		Total	
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
RP1														
Avicennia	-	-	-	20 (0 - 100)	-	-	-	-	-	-	-	-	-	20
B. gymnorrhiza	540 (100 - 1600)	420 (100 - 1200)	80 (0 - 300)	140 (0 - 300)	20 (0 - 100)	20 (0 - 100)	-	20 (0 - 100)	-	20 (0 - 100)	20 (0 - 100)	-	660	620
B. parviflora	-	140 (0 - 400)	20 (0 - 100)	-	-	-	-	-	-	-	-	-	20	140
Ceriops	860 (200 - 1900)	900 (100 - 2100)	60 (0 - 200)	60 (0 - 200)	40 (0 - 100)	60 (0 - 100)	20 (0 - 100)	20 (0 - 100)	-	-	-	-	980	1040
Nypa fruticans	-	100 (0 - 300)	-	20 (0 - 100)	-	-	-	-	-	-	-	-	0	120
Rhizophora	8100 (2600 - 17700)	10760 (5000 - 21700)	4240 (2100 - 6700)	3600 (1200 - 7600)	2820 (1800 - 4000)	3600 (1300 - 7100)	1660 (300 - 5800)	1980 (1100 - 3400)	200 (0 - 700)	600 (100 - 1100)	-	240 (0 - 400)	17020	20780
Xylocarpus	80 (0 - 200)	120 (0 - 600)	-	40 (0 - 200)	-	-	-	-	-	-	-	-	80	160
												Total	18760	22880
RP2														
Avicennia	-	20 (0 - 100)	-	-	-	-	-	-	-	-	-	-	0	20
B. gymnorrhiza	240 (0 - 1100)	220 (0 - 1000)	40 (0 - 100)	-	-	-	40 (0 - 100)	-	-	20 (0 - 100)	40 (0 - 200)	40 (0 - 200)	360	280
B. parviflora	-	40 (0 - 200)	-	-	-	-	-	-	-	-	-	-	0	40
Ceriops	120 (0 - 400)	80 (0 - 300)	-	-	-	-	-	-	-	-	-	-	120	80
Nypa fruticans	-	20 (0 - 100)	-	-	-	-	-	-	-	-	-	-	0	20
Rhizophora	2260 (800 - 5500)	2640 (600 - 5300)	2860 (800 - 7400)	1960 (700 - 5500)	3440 (800 - 8200)	2280 (800 - 5400)	380 (0 - 800)	1740 (600 - 3300)	40 (0 - 100)	660 (400 - 1400)	-	200 (0 - 500)	8980	9480
Xylocarpus	-	-	20 (0 - 100)	-	-	-	-	-	-	-	-	-	20	0
												Total	9480	9920
RP3														
Avicennia	-	60 (0 - 300)	-	-	-	-	-	-	-	-	-	-	0	60
B. gymnorrhiza	100 (0 - 200)	20 (0 - 100)	20 (0 - 100)	-	-	20 (0 - 100)	-	-	-	-	-	-	120	40
B. parviflora	-	60 (0 - 200)	-	-	-	-	-	-	-	-	-	-	0	60
Ceriops	300 (0 - 500)	240 (0 - 700)	-	20 (0 - 100)	-	-	-	-	-	-	-	-	300	260
Rhizophora	3940 (900 - 8400)	3600 (500 - 10700)	4220 (500 - 11500)	3140 (100 - 7800)	2540 (300 - 6500)	2680 (100 - 5800)	200 (0 - 400)	1280 (0 - 2800)	20 (0 - 100)	380 (0 - 600)	-	40 (0 - 100)	10920	11120
Xylocarpus	20 (0 - 100)	120 (0 - 300)	-	20 (0 - 100)	-	-	-	-	-	-	-	-	20	140
												Total	11360	11680

Table 8.3. The distribution of seedling and sapling stem diameter of each mangrove species at Site 2 (RP4-6) in Bintuni Bay, Irian Jaya, in 1994 and 1995. Data are number of individuals and ranges are given in parentheses (n = 5 sub plots).

	Seedling diameter (cm)				Sapling diameter (cm)									
	<1		1 - 1.9		2 - 2.9		3 - 3.9		4 - 4.9		> 5		Total	
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
RP4														
Avicennia	740 (0 - 3300)	460 (0 - 2300)	160 (0 - 800)	180 (0 - 700)	40 (0 - 100)	140 (0 - 700)	-	40 (0 - 100)	20 (0 - 100)	-	20 (0 - 100)	20 (0 - 100)	980	840
B. gymnorrhiza	2600 (800 - 4900)	1060 (200 - 1900)	300 (0 - 1000)	260 (0 - 900)	80 (0 - 100)	120 (0 - 300)	60 (0 - 200)	20 (0 - 100)	-	20 (0 - 100)	-	-	3040	1480
B. parviflora	540 (0 - 2100)	440 (0 - 1700)	100 (0 - 500)	340 (0 - 1400)	-	80 (0 - 400)	20 (0 - 100)	-	-	-	-	20 (0 - 100)	660	880
Ceriops	4240 (500 - 7700)	1240 (300 - 2100)	380 (0 - 1300)	440 (100 - 1100)	20 (0 - 100)	100 (0 - 400)	40 (0 - 200)	-	-	20 (0 - 100)	-	20 (0 - 100)	4680	1820
Nypa fruticans	380 (0 - 800)	300 (0 - 600)	240 (0 - 500)	300 (0 - 1300)	280 (0 - 700)	80 (0 - 300)	200 (0 - 600)	80 (0 - 200)	40 (0 - 200)	40 (0 - 200)	280 (0 - 1000)	140 (0 - 700)	1420	940
Rhizophora	18860 (2000 - 65200)	11140 (100 - 416)	9440 (300 - 32500)	7280 (1300 - 30200)	5820 (600 - 13000)	4600 (200 - 14900)	1560 (300 - 3100)	2860 (400 - 5600)	620 (0 - 1700)	980 (300 - 2100)	440 (0 - 1500)	1300 (300 - 3300)	36740	28160
Xylocarpus	1360 (600 - 3200)	1820 (300 - 4700)	100 (0 - 300)	80 (0 - 200)	20 (0 - 100)	-	-	-	-	-	-	20 (0 - 100)	1480	1920
												Total	49000	36040
RP5														
Aegiceras corniculatum	-	-	-	-	-	20 (0 - 100)	-	-	-	-	-	-	0	20
Avicennia	300 (0 - 1000)	140 (0 - 600)	-	20 (0 - 100)	-	-	-	-	-	-	-	-	300	160
B. gymnorrhiza	4460 (1300 - 7700)	3640 (1500 - 8800)	100 (0 - 300)	160 (0 - 700)	20 (0 - 100)	40 (0 - 100)	-	80 (0 - 100)	-	20 (0 - 100)	20 (0 - 100)	20 (0 - 100)	4600	3960
B. parviflora	440 (100 - 700)	140 (0 - 300)	20 (0 - 100)	20 (0 - 100)	-	-	-	-	-	-	-	-	460	160
Ceriops	7140 (1600 - 12400)	2700 (400 - 4500)	380 (0 - 400)	160 (0 - 500)	60 (0 - 100)	80 (0 - 300)	20 (0 - 100)	20 (0 - 100)	40 (0 - 100)	20 (0 - 100)	20 (0 - 100)	20 (0 - 100)	7660	3000
Nypa fruticans	660 (200 - 1400)	200 (0 - 700)	240 (100 - 400)	180 (0 - 400)	60 (0 - 200)	-	40 (0 - 200)	20 (0 - 100)	40 (0 - 100)	-	20 (0 - 100)	-	1060	400
Rhizophora	26540 (2000 - 68600)	13040 (5600 - 27900)	13400 (700 - 31100)	11160 (1100 - 316)	1880 (200 - 3400)	5440 (300 - 11600)	360 (100 - 1200)	1840 (400 - 3100)	160 (0 - 800)	540 (0 - 1400)	140 (0 - 400)	460 (0 - 1000)	42480	32480
Xylocarpus	2180 (300 - 4300)	2380 (100 - 4500)	240 (100 - 400)	180 (0 - 400)	20 (0 - 100)	80 (0 - 200)	-	20 (0 - 100)	-	-	20 (0 - 100)	-	2460	2660
												Total	59020	42840
RP6														
Avicennia	100 (0 - 200)	40 (0 - 100)	20 (0 - 100)	20 (0 - 100)	-	-	-	-	-	-	-	-	120	60
B. gymnorrhiza	1900 (600 - 3600)	1640 (600 - 3900)	160 (0 - 600)	280 (0 - 800)	140 (0 - 300)	100 (0 - 300)	40 (0 - 100)	120 (0 - 300)	40 (0 - 100)	40 (0 - 100)	-	-	2280	2180
B. parviflora	320 (0 - 700)	240 (0 - 400)	80 (0 - 200)	60 (0 - 100)	60 (0 - 200)	-	20 (0 - 100)	120 (0 - 300)	-	20 (0 - 100)	-	-	480	440
Ceriops	4220 (200 - 10100)	1320 (100 - 3800)	160 (0 - 600)	160 (0 - 400)	80 (0 - 300)	60 (0 - 200)	-	20 (0 - 100)	-	-	20 (0 - 100)	20 (0 - 100)	4480	1580
Nypa fruticans	320 (0 - 700)	280 (0 - 800)	140 (0 - 400)	20 (0 - 100)	140 (0 - 600)	-	-	-	-	-	20 (0 - 100)	-	620	300
Rhizophora	6700 (700 - 19700)	4420 (1900 - 9700)	5340 (0 - 14500)	4060 (200 - 11000)	4840 (500 - 12500)	3220 (0 - 9300)	1600 (800 - 2300)	2360 (200 - 5800)	560 (300 - 1000)	1260 (400 - 2300)	260 (100 - 900)	1180 (600 - 2000)	19300	16500
Xylocarpus	1960 (800 - 4600)	2020 (1100 - 4100)	260 (0 - 600)	240 (100 - 600)	20 (0 - 100)	40 (0 - 100)	-	20 (0 - 100)	-	20 (0 - 100)	-	-	2240	2340
												Total	29520	23400

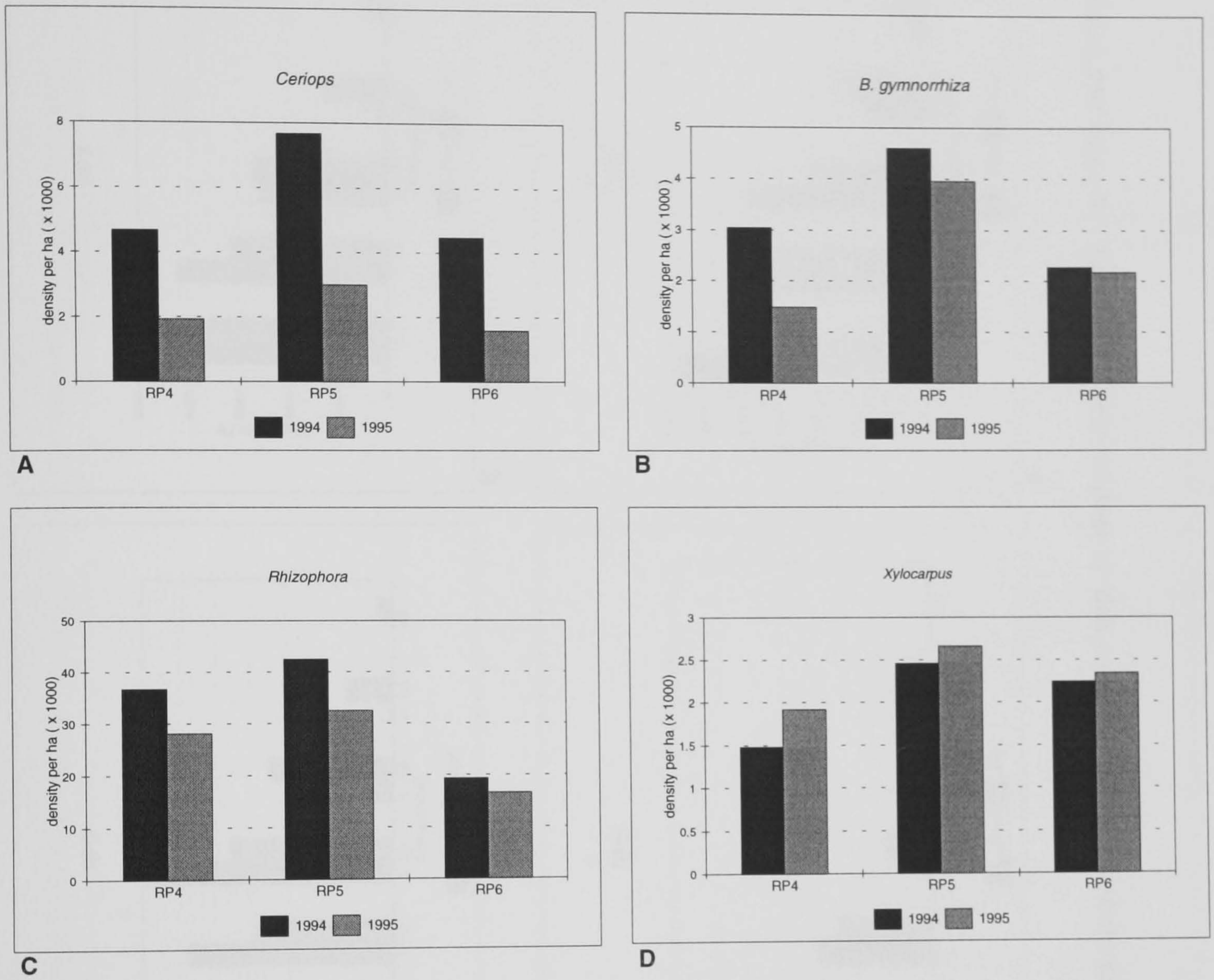


Fig. 8.2. The density distribution of four main seedling and sapling species at Site 2 (RP 4-6) in Bintuni Bay, Irian Jaya, in 1994 and 1995.

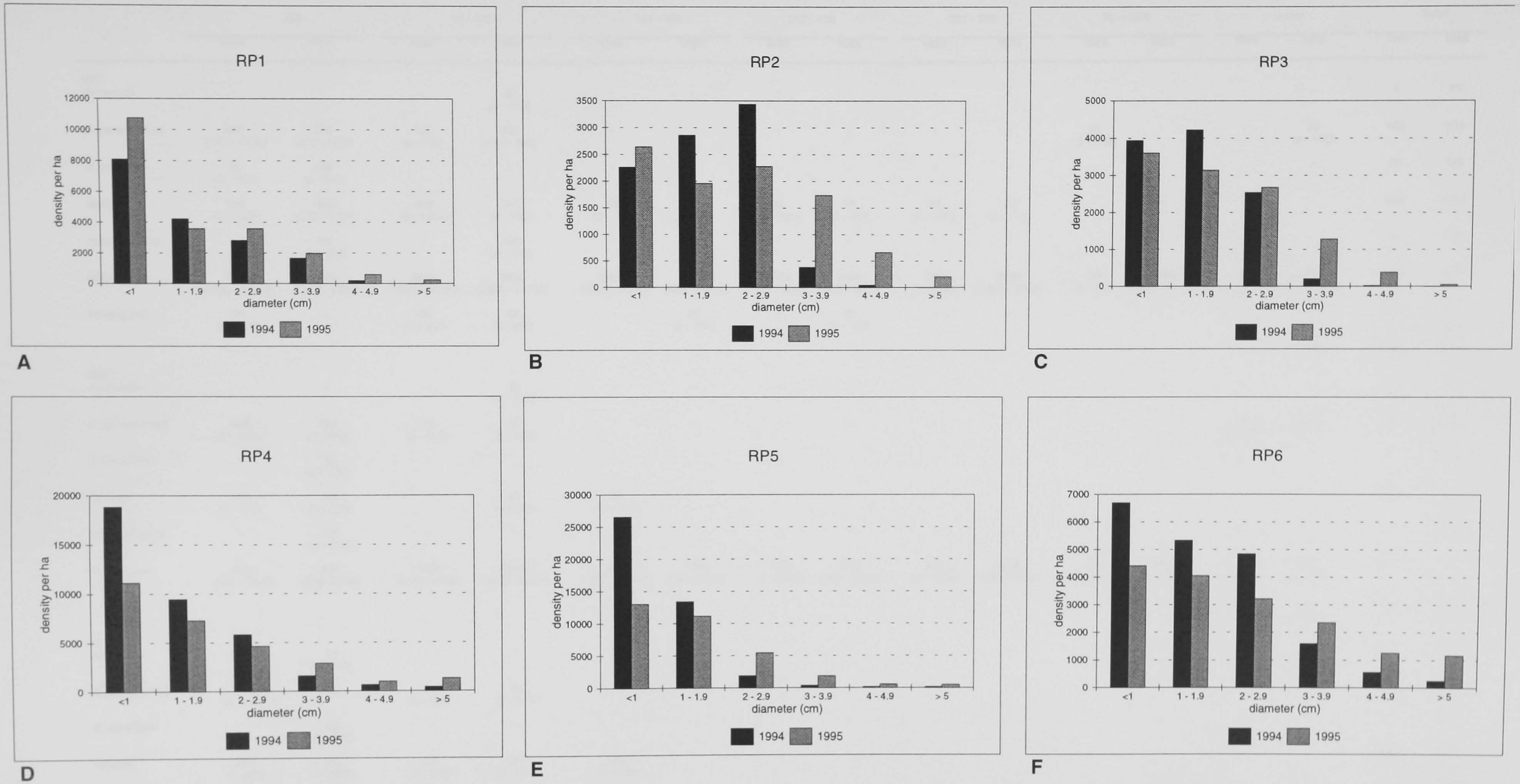


Fig. 8.3. The distribution of seedling and sapling stem diameter of *Rhizophora* spp. in Bintuni Bay, Irian Jaya, in 1994 and 1995.

Table 8.4. The distribution of seedling and sapling height of each mangrove species at Site 1 (RP1-3) in Bintuni Bay, Irian Jaya, in 1994 and 1995. Data are number of individuals and ranges are given in parentheses (n = 5 sub plots).

	Height (cm)																	
	<50		50 - 100		101 - 150		151 - 200		201 - 250		251 - 300		> 300		Total	
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
RP1																
Avicennia	-	-	-	20 (0 - 100)	-	-	-	-	-	-	-	-	-	-	0	20
B. gymnorrhiza	480 (100 - 1300)	320 (100 - 900)	160 (0 - 700)	280 (100 - 800)	-	-	-	-	-	-	20 (0 - 100)	-	-	20 (0 - 100)	660	620
B. parviflora	20 (0 - 100)	140 (0 - 400)	-	-	-	-	-	-	-	-	-	-	-	-	20	140
Ceriops	600 (0 - 1900)	660 (200 - 1300)	320 (0 - 1400)	300 (0 - 900)	20 (0 - 100)	40 (0 - 200)	20 (0 - 100)	20 (0 - 100)	20 (0 - 100)	20 (0 - 100)	-	-	-	-	980	1040
Nypa fruticans	-	20 (0 - 100)	-	100 (0 - 300)	-	-	-	-	-	-	-	-	-	-	0	120
Rhizophora	7080 (2500 - 13700)	6060 (3500 - 8700)	4860 (2900 - 7100)	5800 (2200 - 14700)	2540 (1000 - 5300)	1280 (400 - 2000)	1760 (0 - 5300)	1480 (700 - 1900)	660 (0 - 2600)	2320 (1200 - 4100)	80 (0 - 300)	1640 (300 - 3600)	40 (0 - 100)	2200 (200 - 7200)	17020	20780
Xylocarpus	20 (0 - 100)	-	60 (0 - 200)	80 (0 - 400)	-	60 (0 - 300)	-	20 (0 - 100)	-	-	-	-	-	-	80	160
														Total	18760	22880
RP2																
Avicennia	-	-	-	20 (0 - 100)	-	-	-	-	-	-	-	-	-	-	0	20
B. gymnorrhiza	240 (0 - 1200)	160 (0 - 700)	80 (0 - 200)	60 (0 - 300)	-	-	-	-	-	-	-	-	40 (0 - 100)	60 (-)	360	280
B. parviflora	-	40 (0 - 200)	-	-	-	-	-	-	-	-	-	-	-	-	0	40
Ceriops	120 (0 - 400)	40 (0 - 100)	-	40 (0 - 200)	20 (0 - 100)	-	-	-	-	-	-	-	-	-	140	80
Nypa fruticans	-	20 (0 - 100)	-	-	-	-	-	-	-	-	-	-	-	-	0	20
Rhizophora	1560 (400 - 3900)	940 (200 - 2200)	3380 (1100 - 8400)	2740 (1200 - 5900)	2400 (800 - 5800)	1380 (400 - 3400)	1180 (0 - 2700)	940 (400 - 2000)	440 (0 - 1200)	2080 (700 - 4700)	20 (0 - 100)	880 (200 - 2000)	-	520 (0 - 1200)	8980	9480
														Total	9480	9920
RP3																
Avicennia	-	60 (0 - 300)	-	-	-	-	-	-	-	-	-	-	-	-	0	60
B. gymnorrhiza	100 (0 - 200)	-	20 (0 - 100)	40 (0 - 100)	-	-	-	-	-	-	-	-	-	-	120	40
B. parviflora	-	60 (0 - 200)	-	-	-	-	-	-	-	-	-	-	-	-	0	60
Ceriops	260 (0 - 500)	160 (0 - 600)	20 (0 - 100)	100 (0 - 400)	20 (0 - 100)	-	-	-	-	-	-	-	-	-	300	260
Rhizophora	3860 (1000 - 5800)	1640 (300 - 3600)	3860 (800 - 10000)	4300 (300 - 11600)	1720 (0 - 5000)	1720 (100 - 4100)	1060 (0 - 4000)	1460 (0 - 3500)	260 (0 - 1300)	1100 (0 - 2100)	140 (0 - 700)	620 (0 - 1600)	20 (0 - 100)	280 (0 - 1200)	10920	11120
Xylocarpus	-	-	-	120 (0 - 300)	20 (0 - 100)	20 (0 - 100)	-	-	-	-	-	-	-	-	20	140
														Total	11360	11680

Table 8.5. The distribution of seedling and sapling height of each mangrove species at Site 2 (RP4-6) in Bintuni Bay, Irian Jaya, in 1994 and 1995. Data are number of individuals and ranges are given in parentheses (n = 5 sub plots).

	Height (cm)															
	<50		50 - 100		101 - 150		151 - 200		201 - 250		251 - 300		> 300		Total	
	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995	1994	1995
RP4																
Avicennia	500 (0 - 2200)	320 (0 - 1600)	280 (0 - 1300)	220 (0 - 1100)	100 (0 - 500)	40 (0 - 100)	40 (0 - 100)	120 (0 - 500)	20 (0 - 100)	60 (0 - 300)	-	-	40 (0 - 200)	80 (0 - 200)	980	840
B. gymnorrhiza	1640 (600 - 3700)	380 (0 - 1100)	840 (100 - 1700)	600 (100 - 1100)	240 (0 - 900)	100 (0 - 200)	120 (0 - 400)	120 (0 - 300)	80 (0 - 300)	60 (0 - 100)	80 (0 - 400)	80 (0 - 300)	40 (0 - 100)	140 (0 - 500)	3040	1480
B. parviflora	260 (0 - 900)	240 (0 - 1000)	180 (0 - 800)	140 (0 - 600)	100 (0 - 500)	120 (0 - 400)	40 (0 - 200)	100 (0 - 400)	40 (0 - 100)	60 (0 - 200)	20 (0 - 100)	-	20 (0 - 100)	220 (0 - 900)	660	880
Ceriops	3740 (0 - 7700)	820 (0 - 1800)	560 (0 - 2000)	580 (0 - 1700)	320 (0 - 900)	260 (0 - 900)	60 (0 - 300)	120 (0 - 400)	-	80 (0 - 200)	-	-	-	-	4680	1860
Nypa	420 (0 - 1000)	80 (0 - 200)	300 (0 - 1100)	260 (0 - 500)	240 (0 - 900)	60 (0 - 300)	100 (0 - 300)	160 (0 - 700)	100 (0 - 500)	20 (0 - 100)	40 (0 - 200)	80 (0 - 300)	220 (0 - 800)	300 (0 - 11)	1420	960
Rhizophora	12380 (900 - 37400)	3120 (0 - 6900)	5480 (100 - 25300)	7320 (200 - 31500)	3040 (700 - 12000)	1400 (0 - 5700)	2220 (0 - 8500)	1620 (0 - 7100)	3460 (300 - 12400)	1080 (0 - 5000)	3200 (100 - 10500)	1140 (0 - 5400)	6960 (500 - 17600)	12480 (1600 - 31700)	36740	28160
Xylocarpus	380 (0 - 1300)	40 (0 - 200)	800 (200 - 1800)	1260 (0 - 3700)	280 (0 - 700)	520 (100 - 1200)	20 (0 - 100)	40 (0 - 200)	-	-	-	-	-	-	1480	1860
														Total	49000	36040
RP5																
Aegiceras	-	-	-	-	-	-	-	20 (0 - 100)	-	-	-	-	-	-	0	20
Avicennia	200 (0 - 700)	-	100 (0 - 300)	100 (0 - 500)	-	40 (0 - 100)	-	-	-	-	-	-	-	20 (0 - 100)	300	160
B. gymnorrhiza	4060 (1100 - 7600)	2320 (500 - 7000)	460 (200 - 1200)	1440 (700 - 2300)	40 (0 - 200)	40 (0 - 100)	-	100 (0 - 400)	20 (0 - 100)	20 (0 - 100)	-	-	20 (0 - 100)	40 (0 - 100)	4600	3960
B. parviflora	440 (100 - 700)	120 (0 - 300)	20 (0 - 100)	20 (0 - 100)	-	-	-	-	-	20 (0 - 100)	-	-	-	-	460	160
Ceriops	6500 (1200 - 11000)	1540 (100 - 3800)	620 (400 - 900)	960 (200 - 1900)	320 (0 - 600)	360 (100 - 600)	80 (0 - 200)	80 (0 - 200)	80 (0 - 200)	20 (0 - 100)	20 (0 - 100)	-	40 (0 - 200)	40 (0 - 200)	7660	3000
Nypa	480 (100 - 1000)	40 (0 - 100)	380 (100 - 700)	180 (0 - 600)	180 (0 - 400)	140 (0 - 500)	20 (0 - 100)	-	-	40 (0 - 100)	-	-	-	-	1060	400
Rhizophora	16160 (1000 - 38100)	3220 (400 - 5400)	6880 (800 - 19400)	6420 (3000 - 14300)	4980 (100 - 15100)	2440 (800 - 5000)	4300 (0 - 11500)	2580 (100 - 7500)	4820 (300 - 10400)	2040 (200 - 5400)	3700 (300 - 8700)	2840 (200 - 7200)	1640 (0 - 5200)	12940 (30100 -)	42480	32480
Xylocarpus	140 (0 - 300)	80 (0 - 200)	1860 (300 - 4100)	1540 (100 - 3100)	420 (100 - 1000)	800 (100 - 1400)	20 (0 - 100)	140 (0 - 400)	20 (0 - 100)	20 (0 - 100)	-	60 (0 - 200)	-	20 (0 - 100)	2460	2660
														Total	59020	42840
RP6																
Avicennia	80 (0 - 200)	20 (0 - 100)	20 (0 - 100)	-	-	20 (0 - 100)	20 (0 - 100)	20 (0 - 100)	-	-	-	-	-	-	120	60
B. gymnorrhiza	1460 (600 - 2500)	1100 (200 - 2000)	420 (0 - 1300)	580 (0 - 1900)	80 (0 - 200)	140 (0 - 400)	160 (0 - 500)	140 (0 - 500)	100 (0 - 500)	60 (0 - 200)	60 (0 - 200)	20 (0 - 100)	-	140 (0 - 400)	2280	2180
B. parviflora	340 (100 - 700)	240 (0 - 400)	-	20 (0 - 100)	-	20 (0 - 100)	20 (0 - 100)	20 (0 - 100)	20 (0 - 100)	-	40 (0 - 200)	-	60 (0 - 200)	140 (0 - 400)	480	440
Ceriops	3760 (100 - 9400)	680 (0 - 1700)	380 (0 - 1300)	520 (0 - 1700)	280 (0 - 900)	220 (0 - 600)	40 (0 - 100)	100 (0 - 300)	-	40 (0 - 200)	-	-	20 (0 - 100)	20 (0 - 100)	4480	1580
Nypa	380 (0 - 1000)	160 (0 - 800)	140 (0 - 500)	80 (0 - 400)	60 (0 - 200)	40 (0 - 100)	40 (0 - 100)	20 (0 - 100)	-	-	-	-	-	-	620	300
Rhizophora	4660 (700 - 15500)	1860 (200 - 4000)	1480 (0 - 4400)	1480 (200 - 4600)	1580 (0 - 3900)	760 (100 - 2100)	1180 (100 - 2600)	1300 (0 - 2900)	2000 (200 - 5100)	680 (100 - 1900)	1480 (400 - 4100)	1340 (0 - 3900)	6920 (500 - 18700)	9080 (2000 - 21700)	19300	16500
Xylocarpus	340 (0 - 1100)	20 (0 - 100)	1400 (500 - 3200)	1400 (600 - 3100)	400 (100 - 900)	700 (400 - 900)	100 (0 - 300)	120 (0 - 300)	-	40 (0 - 200)	-	-	-	60 (0 - 200)	2240	2340
														Total	29520	23400

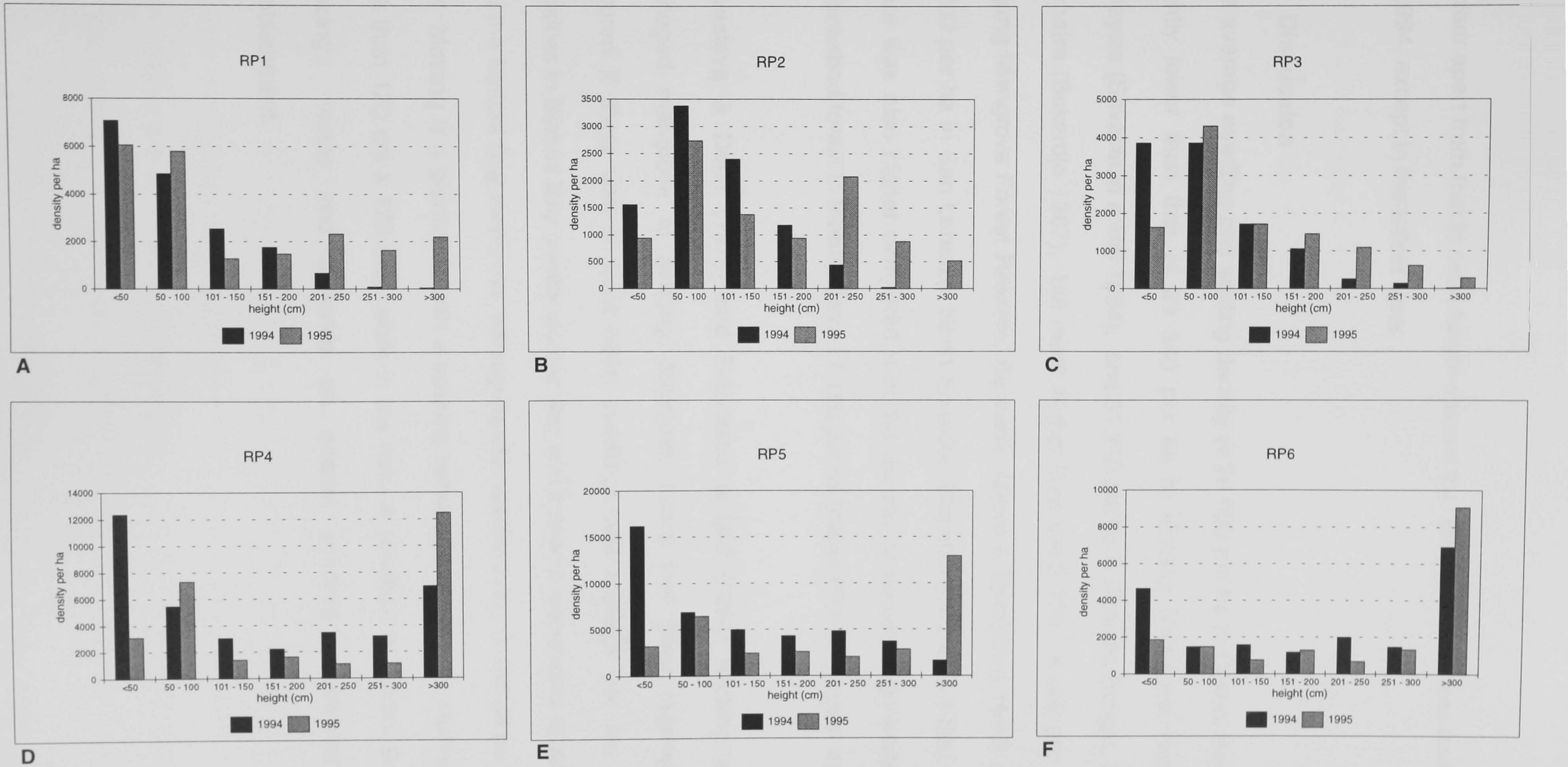


Fig. 8.4. The distribution of seedling and sapling height of *Rhizophora* spp. in Bintuni Bay, Irian Jaya, in 1994 and 1995.

unclear apart from that in most height classes the density in 1995 was less than in 1994, except in the tallest class .

8.5 Discussion

The average seedling and sapling density of 26 990 per ha in Bintuni Bay was slightly lower than that of 29 340 per ha in Matang Mangrove Reserve, Malaysia (Srivastava & Bal 1984), and 31 210 per ha in Tanjung Bungin, South Sumatra (Sukardjo 1987), but much higher than the 2 700 - 4 400 per ha in Rejang Mangrove Forest Reserve, Sarawak (Jawa & Srivastava 1989) or the 8 700 per ha in San Lorenzo, North Ecuador (Blanchard & Prado 1995). The value was also higher compared with the density of natural regeneration of undisturbed forest in Bintuni Bay, 17 180 per ha (mean FP1-3, chapter 4).

Srivastava & Daud (1978) and Srivastava & Ball (1984) working in the managed mangrove at Matang, Malaysia, found that good regeneration occured if there was at least 6810 seedlings and saplings per ha. The densities in Bintuni Bay greatly exceed this and it seems reasonable to assume that the Bintuni Bay mangrove will regenerate satisfactorily. It should be noted that Matang is a plantation with a spacing between seedlings or saplings not less than 120 cm x 120 cm, while in the natural condition in Bintuni Bay the spacing varies and depends on natural seedling recruitment and establishment.

8.5.1 Seedling and sapling density: time, site and species effects

The density of *Rhizophora* increased in Site 1 and decreased in Site 2 between the first and second years of observations. The space availability was perhaps the main reason for this change. Site 1 is less dense, with many unoccupied areas where undecomposed debris and post-logging slash have accumulated (Plate 12A). Similar accumulations have been observed in Matang (Noakes 1951) and Sarawak (Jawa & Srivastava 1989). In the second year, as some of the debris and slash decomposed, there was more chance of seed establishment. In Matang, Srivastava & Bal (1984) discovered that seedling density after a second thinning was higher in older forest, and Jawa & Srivastava (1989) also found that seedling density in nine-year old plots after a clear cut in Sarawak was much higher than in six-year old plots.

In Site 2, however, most of the microsites were occupied in 1994 (Plate 12B). In RP5, for example, the total density was 59 020 per ha, almost 10 times the 'ideal' density for regeneration proposed by Srivastava & Daud (1978) and Srivastava & Bal (1984). Hence, competition for space, light and nutrients were assumed to be the cause of the decreasing *Rhizophora* density in 1995.

Site 2 had a much higher seedling and sapling density than Site 1 in both years, even though Site 1 had been planted (see chapter 2). This may have been because of edaphic differences (chapter 3). In the absence of more detailed investigation of species response to soil factors, however, it is impossible to say how far the chemical differences account for the differences in regeneration characteristics. Some studies have revealed that initial

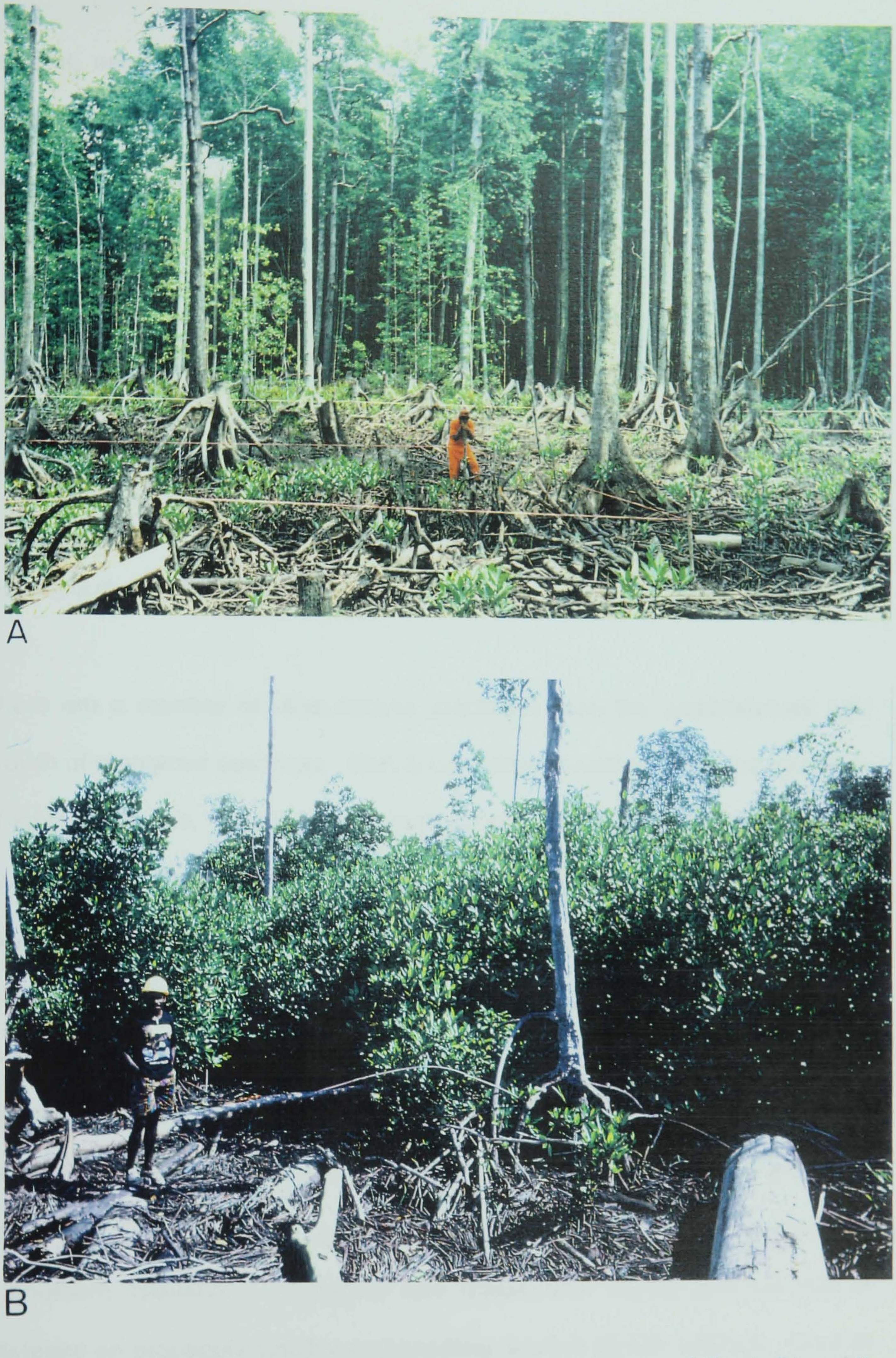


Plate 12 Typical mangrove regeneration seven year after clear felling in Bintuni Bay. **A** Site 1 (Amutu Besar Island), **B** Site 2 (Amutu Kecil Island).

seedling establishment is not dependent on soil conditions. Soil properties appear to influence the growth of saplings or mature trees of mangroves more than that of seedlings (Tamai *et al.* 1986), possibly because mangrove seedlings have large resources which are adequate for their early growth.

Site aspect may also have great influence on seedling recruitment and establishment. Site 2 (Fig. 2.9) is more protected against waves than Site 1 which is facing the open bay. Clarke & Myerscough (1993) also suggested that protection from waves resulted in higher establishment of *Avicennia marina* in a plot in southeastern Australia.

There are a number of other factors which influence the establishment and growth of mangrove seedlings. Chai & Lai (1984) considered that the presence of lobster mounds, invasion of *Acrosticum aureum* weeds, frequency of tidal inundation and felling intensities were important in Sarawak. In a *Rhizophora mangle* strip-clearcut forest in northwest Ecuador, Blanchard & Prado (1995) found that quality of seed trees, distance from seed trees, and site elevation were among the factors with great influence on regeneration, while interstitial soil salinity, litter cover and *Acrosticum aereum* density had only little effect. Tamai & Iampa (1988) reported that light conditions also affected the growth of young trees (> 1 year old) to a greater degree than that of first year seedlings in southern Thailand. Propagule size (Rabinowitz 1978a) and the role of predators on propagule viability and seedling survival (Smith 1987a,b; Onuf *et al.* 1977 ; Robertson *et al.* 1990) were also mentioned as important for mangrove seedling establishment and regeneration.

Clarke & Allaway (1993) concluded there was no restriction for the establishment of propagules of *Avicennia marina* within mangrove stands other than the supply of propagules and tidal or wave action. They discovered that most of the *Avicennia marina* sites within intertidal limits in southeastern Australia are suitable for seedling establishment. In contrast, recruitment to the sapling stage appeared to be restricted by light and sediment resources.

In Bintuni Bay, *Rhizophora*, mostly *Rhizophora apiculata*, was the most dominant seedling and sapling in both sites and in both years, followed by *Ceriops decandra* and *Bruguiera gymnorrhiza*. This is a common condition in Indo-Pacific mangrove forests even though the proportion of the species may vary. In Sarawak, Jawa & Srivastava (1989) reported that *Rhizophora apiculata* was the most dominant species (83.56%) of the seedling crop in six-years-old forest after a clear cut, followed by *Bruguiera parviflora* (9.65%) and *Bruguiera gymnorrhiza* (4.5%). Similarly in Matang, *Rhizophora apiculata* accounted for 88.9% of the seedlings, and *Bruguiera parviflora* was the only associate (Srivastava & Bal 1984).

8.5.2 Seedling and sapling growth: diameter and height distribution.

Most seedlings and saplings in Sites 1-2 were concentrated in the lowest diameter and height classes, similar to the results from Sarawak (Jawa & Srivastava 1989) and Matang (Srivastava & Bal 1984). This indicates that seedling recruitment and establishment in both Sites was high. Macnae (1968) stated that mangroves normally have a light requirement for their growth, and *Rhizophora* like most other mangrove species is a light demander (Liew *et al.* 1975). As Site 1 and Site 2 were open areas 7 years after forest clearcut, the light intensity must be much higher than under an undisturbed forest canopy. This may explain why seedling density is much higher than in the floristic plots (FP1-3) (Plate 13).

Plate 13 Regeneration in undisturbed mangrove in Bintuni Bay: **A** Under canopy of mature *Rhizophora apiculata*, **B** and **C** *Bruguiera parviflora* and *Rhizophora mucronata* on the river banks.

IX CONCLUSIONS

The different lines of enquiry have given insight into the some aspects of the structure and function of the Bintuni Bay ecosystem. The key points which have emerged and which have fulfilled the main aims of the thesis are given in the following paragraphs.

- The Bintuni Bay mangrove belongs to one of the largest single stands of mangroves in the world (Spalding *et al.* 1997) which is a result of the physical condition of the Bay. Sheltered from the excessive wave action of the open sea, the Bay is surrounded by a dendritic network of rivers which supply fresh water, organic materials and silt from the surrounding area, and has a high annual rainfall. The salinity of the water in Bintuni Bay is about 75% of that of the open ocean.

- The mixed semi-diurnal tide, with two high and two low water levels per day, and the tidal amplitude of up to 5.6 m encourages water movement in the Bay which in turn speeds up nutrient transport, and promotes a better soil condition, and regulates seed distribution.

- The soils in Bintuni Bay are *Potential Acid Sulphate soils* with a distinctly low pH, probably due to the production of sulphuric acid by oxidation when the soils are dried.

- There are 30 vascular plant mangrove species (of all life forms) found in Bintuni Bay of which the trees *Rhizophora apiculata*, *Bruguiera gymnorrhiza* and *Ceriops decandra* are the most common. Like all mangroves, Bintuni Bay has a distinctive character of low species diversity. Mangrove zonation is clearly shown in Bintuni Bay, although its precise causes are not known.
- Sapling and seedling composition were more or less similar to the adult tree composition, except there was a lack of *Avicennia eucalyptifolia* and

Sonneratia alba in the juvenile categories which reflects their light-demanding physiology. *Rhizophora apiculata* was the commonest seedling species, but it was sometimes less common than *Ceriops decandra* or other species in the sapling stage.

- The mangroves in Bintuni Bay seem to regenerate successfully, at least in the first 7 years after clear felling in the sample Sites 1 and 2.

- The Bintuni Bay mangroves are among the more productive ecosystems in terms of small litterfall. The litterfall is markedly seasonal and partially follows the seasonality of the rainfall. The litterfall loss rate is high due to the removal of litter by sea water and perhaps also by crabs.

- The litterfall mineral element concentrations fluctuated during the year but patterns were unclear. Nitrogen had the biggest amounts returned to the ecosystem through small litterfall, followed by calcium, sodium, magnesium, potassium, and phosphorus.

- A litter bag experiment showed that leaf decomposition rates were ranked: *Sonneratia alba* > *Avicennia eucalyptifolia* > *Rhizophora apiculata* > *Bruguiera gymnorrhiza* > *Bruguiera parviflora*. It is suggested that site exposure to sea water and leaf chemistry were the causes of the differences in decomposition rates between species. Except for *B. parviflora*, the decomposition rates were faster in the first 4 - 12 weeks, and then slowed until week 22 (the end of the experiment). A single exponential decay model (Olson 1963, Wieder & Lang 1982, Ezcurra & Becerra 1987) described the decomposition rate of all the species well.

- The mean leaf area loss to herbivory in Bintuni Bay, averaged over species, plant height and leaf age was only 3.9%. It was different among sites, species, plant height and leaf age, with clear patterns associated with the last three variables. There was an indication that *Rhizophora* and *Bruguiera* may have different herbivores and different defence strategies against herbivory.

- Seed predation clearly affected the viability of mangrove seeds in Bintuni Bay. Predation was faster in the lower intertidal zone than in the medium and higher intertidal zones. *Avicennia alba, A. eucalyptifolia*, and *B. parviflora* were the most predated species. Only the predation of *A. alba* clearly supported the dominance-predation hypothesis of Smith (1987a,b).

Future work on the mangroves should build on this preliminary study in the following ways:

- Soil - plant relationships. A more detailed study of the relationship between soil and vegetation should be done in Bintuni Bay, especially experimental work on those soil properties which change after forest clearing and their effect on seedling establishment.

- Logging and litterfall production. Detailed studies should be initiated to monitor the effect of the sudden reduction and long term depletion of litterfall which is caused by logging activities. The effect of the loss of this source of nutrients for marine animals may be substantial and should be quantified.

- Logging and regeneration. Experiments should be made to test the efficacy of different logging methods and artificial vs natural regeneration. The influence on crabs of these treatments should be investigated since changes in their populations may influence regeneration.

- Future work should be directed at effectively managing the mangroves.

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