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**ZONATION, LEAF PHENOLOGY AND LITTER
DYNAMICS OF MANGROVE FOREST
AT PUDUVYPPU**

By

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THESIS

**Submitted in partial fulfilment of the
requirement for the degree of**

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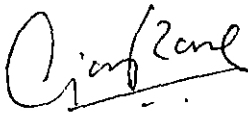
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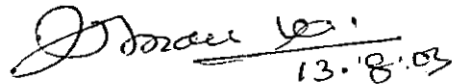
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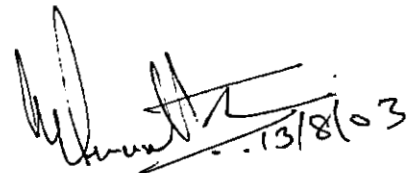
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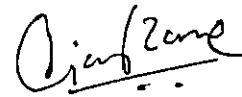
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Ajay Dattaram Rane

*Dedicated to my loving parents
and brothers*

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Introduction

INTRODUCTION

Mangroves are coastal vegetations found in the intertidal zones of river deltas and backwater areas in the tropics (Rodriguez, 1987). Distribution of mangroves is mainly governed by topography, tidal height, substrate characteristics and salinity. In India, mangroves are present both on the western and eastern coastlines, besides the Andaman islands, covering an area of about 3997 km². Kerala despite having a humid tropical climate and located on the western coast of the Indian peninsula has only vestiges of mangroves. Basha (1992) estimated the mangrove cover of Kerala as 1671 ha.

The ecological, environmental and socio-economic benefits of mangroves are enormous. They support diverse kinds of macro and microorganisms. Indian mangroves are reported to contain 105 species of fish, 20 shellfish species and 229 crustacean species (Jagtap *et al.*, 1993). The royal Bengal tiger is sited in the Sunderban mangroves. Different monkey species, otters, deer, fishing cats, snakes and wild pigs also inhabit these forests. According to Mukherjee (1975), 117 species of migratory and restricted birds are seen in these forests.

Traditionally, the mangroves have been exploited for their wood for minor construction, fuelwood, stakes and for non-wood forest products (NWFP) like fodder, tannins, fruits and medicinal products. In addition, they are used for integrated paddy-prawn farming, aquaculture and salt production. Above all, mangroves are valuable for shoreline protection and stabilization. In spite of this some people consider mangroves as mere wastelands. As a result, anthropogenic depletion of this valuable resource abounds in most part of the world. Kerala is perhaps no exception to this general rule and vast stretches of mangroves over different parts of the state have been cleared already for various purposes, including construction of Cochin port (Blasco, 1975).

There is, however, a growing concern about the destruction of mangroves in view of their potential for sea-shore protection. The projected rise in sea levels especially in the aftermath of global warming may provide additional justification for mangrove conservation. While mangrove destruction in Kerala during the recent past proceeded at an unprecedented rate, new mangrove formations have established on newly formed sites. For instance, on account of sedimentation by

inflowing rivers and dredging activities in the Cochin bar mouth, there has been intense land building activity at Puduvypu, near Kochi (Nameer *et al.*, 1992; Kumar and Kumar, 1997). Many mangrove species have colonized this site and a knowledge on the structural and functional attributes of this ecosystem is needed for restoration and rehabilitation activities.

The occurrence of mangrove species in distinct monospecific zones is one of the most discussed themes in mangrove ecology. Although distinct zonation patterns were observed in various mangrove formations of our country (Selvam *et al.*, 1991; Watter, 1991; Singh, 1996; Ellison *et al.*, 2000), two previous studies at Puduvypu did not reveal any clear trend in this respect (Nameer *et al.*, 1992; Kumar and Kumar, 1997). Since the field work for the last study at this site was carried out in 1993 (Kumar and Kumar, 1997), it is expected that over a period of time (> 8 years) floristic attributes and zonation patterns may change. This in turn, prompted the present attempt to characterize floristics and zonation pattern.

Mangrove zonation is more often manifested as a mosaic that varies with the complex of physical, chemical and biological interaction occurring in a particular area (Rodriguez, 1987). Field investigations and comparative studies suggest that zonation corresponds to gradients of electro-chemical properties, regional geomorphology and tidal frequency (Chen and Twilley, 1998). Therefore, an attempt to elucidate the interdependence of edaphic and floristic attributes of the mangrove forests at Puduvypu also was made.

Mangrove forests have been recognized as extremely productive ecosystems (Lugo *et al.*, 1990). Litter production is important in maintaining estuarine productivity, as it exports considerable quantities of organic matter and nutrients to the soil and water nutrient pools (Bunt 1982). Nevertheless, species and site characteristics (climatic, edaphic and tidal characteristics) co-determine the magnitude of litterfall (Hardiwinoto *et al.*, 1989), about which little information exist in the context of the peninsular Indian mangrove formation.

Likewise, litter decay represents a significant mechanism for nutrient release in the coastal ecosystem with positive impacts on fisheries and aquaculture (Rajendran and Kathiresan, 1999). Leaf litter decay in mangrove system is mainly governed by tidal inundation (Robertson *et al.*, 1992) and the bio-chemical quality of litter (Furniss and Ferrar, 1982). Since this aspect has been overlooked in the

peninsular Indian context, an experiment on decomposition dynamics of six important species was planned. Specific objectives are as follows:

1. To investigate the zonation pattern and regeneration status of Pudukkottai mangroves in relation to soil electro-chemical properties along an ocean-to-land- interior gradient.
2. To study the phenological attributes of important mangrove species in this forest
3. To estimate the quantum of mangrove litterfall and analyze the decomposition dynamics of predominant mangrove species at Pudukkottai.

Review of Literature

2. REVIEW OF LITERATURE

Mangroves are unique plant communities growing in the intertidal silted up deltaic regions, estuarine mouths, sheltered shallow coasts, edges of the islands; backwaters and saline mud flats in the tropical and subtropical regions of the world. These ecosystems are mostly restricted on the shelter shore lines covered with soft intertidal sediments with frequently inundating intertidal or brackish water. Mangrove species are very much distinct from other plant species with respect to their morphological, anatomical, physiological, seeds and seedlings developmental, physiognomical adaptations and succession mechanisms.

The term mangrove has been derived from Portuguese word "Mangue" means the community of mangrove trees and English word "Grove" meaning trees or bushes. The term mangrove has been used to refer either to constituent plants of tropical intertidal forest communities or the community itself. (Tomlinson, 1986). Mac Nae (1968) proposed "mangal" as a term for the community, leaving "mangrove" for the constituent plant species, and this usage is increasingly adapted.

2.1 Distribution of mangroves

The major mangroves ecosystems are distributed both in the old world tropics and in the new world tropics. These are extended mainly within the tropics and subtropics between latitude $32^{\circ}00'$ N and $33^{\circ}00'$ S and longitude 30° W and 165° E (Mañintosh, 1984). In the new world, the mangroves are distributed in North America at Louisiana, Pacific coast of north-west Mexico, Bermuda islands and Pacific coasts of South America (Mañintosh, 1984). The sporadic mangals have also been reported by different workers from the west coast of Africa and east coast of South America, *i.e.* on Atlantic Ocean. These ecosystems are usually found in the littoral zones with a high amount of rainfall, they are also found in the semiarid and arid regions of Middle East and West Africa (Chapman, 1976). These ecosystems have also extended in the warm temperate regions like Ryukyn Islands of Japan and Auckland of New Zealand.

The total mangrove area of the world has been assessed to be approximately 16,670,000 ha (16 million ha), with 7,487,000 ha in tropical Asia, 5,781,000 ha in tropical America and 3,402,000 ha in tropical Africa (Saenger *et*

al., 1987). Finlayson and Moser (1991) highlighted the total world mangrove area as 14 million ha. Among these, the Indo-West Pacific tropical zones and the tropical Australia have the most dominant mangroves.

In the Indian sub-continent, the mangroves are distributed within the intertidal or tidal, supra tidal or sub-tidal deltaic zones of both east coast facing the bay of Bengal and west coast facing the Arabian sea. Besides these coastal intertidal zones, the mangroves are also spread over Bay and Lakshadweep islands. In India, most of the mangroves are restricted in the deltaic regions, within the major Indian estuaries, *viz.*, the *Hoogly* river (West Bengal), the Mahanadi river (Orissa), Krishna and Godavari rivers (Andhra Pradesh), the Cauvery river (Tamil Nadu) and the Tapti-Narmada, the Runn of Kutch (Gujarat). Seventy per cent of these deltaic areas are in the east coast. Besides these deltaic mangals, they are also spread over in several intertidal flat coastal zones, edges of gullies or canals (Untawale and Jagtap, 1992).

Sunderban (64 % of Indian mangrove) is the largest prograding delta in this planet formed at the estuarine phase of the Ganga-Brahmaputra river system. This is the only mangrove tiger land on globe, with an area of 1434.4 km²; Sunderban has been declared as the world heritage site by the IUCN (Sanyal, 1999). Total area under mangrove was estimated differently by different authors as 681 976 ha (Sidhu, 1963), 549 950 ha (Khan, 1959) and 356 500 ha (Blasco, 1977) which were approximations. The government of India through a satellitic survey projected an area of 3997 km² under mangroves, constituting 7 per cent of the world's mangroves extending along the 5700 km coastline.

Kerala has 590 km long narrow coastline constituted by long stretches of backwaters which consist of a series of lagoons running parallel to the sea and separated from it by land strips of varying width from a few hundred meters to several kilometers. Kerala possesses very small patches of mangroves, distributed in a highly separated and discontinuous manner. These thin patches of mangroves are at Veli estuary, Quilon, Kumarakam, Kannamali (Cochin), Chetwai, Nadakkavu (Calicut), Edakkad, Pippinisseri, Kungimangalam and Chittari (Ramachandran *et al.*, 1986).

The earliest mention about the mangroves of Kerala was made by Bordillon (1908) who reported *Bruguiera cylindrica* and two species of *Rhizophora* being

very common in Quilon region. Troup (1921), Erlanson (1936), Mudaliar and Kamath (1954), Thomas (1962), Ernakulam District Gazetteer (1965), Cannanore District Gazetteer (1972), Rao and Sasthry (1974), Kottayam District Gazetteer (1975), Blasco (1975), Kurien (1980), Ramachandran *et al.* (1986), Basha (1991) and Nameer *et al.* (1992) have made mentions of mangroves in Kerala. It is said that Kerala coasts once supported about 700 km² of mangrove forests but, due to massive destruction it is left with scattered patches of only 17 km² now (Ramachandran *et al.*, 1986). Basha (1992) reported an area of 1671 ha under mangrove in Kerala, out of which, 1470 ha (88 %) are with private land holders and only about 200 ha area in government or Quasi-government ownership. Kannur district has the maximum area of mangroves (755 ha) followed by Kozhikode (293 ha) and Ernakulam (260 ha). Puthuvypu in Ernakulam district can be regarded as the largest single patch of mangrove in Kerala which has an area of approximately 101 ha (Basha, 1991).

As distribution is considered the Indian sub-continent is blessed with a rich diversity of mangroves and Kerala in particular has some fine patches of mangroves.

2.2 Flora of mangroves

Mangrove forests are characterized by low floristic diversity. The number of mangrove species has been reported differently by various authors. Chapman (1970) reported 90 species of mangroves in the world out of which the Indo-West Pacific region has 63 species, while 16 species each in the Pacific and Atlantic coast of America and 11 in the African coast. Saenger *et al.* (1983) have reported the world mangroves consisting of 79 species, under 31 genera out of these the tree species are 66 (22 genera), shrubs 10 (6 genera), palm 3 (3 genera), fern 3 (1 genus) and 4 other shrub and trees. Tomlinson (1986) reported 40 true mangrove species from the old world tropics and eight species from the new world tropics. Among these, the Indo-West-Pacific tropical zones and the tropical Australia have the most dominant mangroves and are important in respect of species diversity, richness, abundance and unique succession features (Sanyal, 1999).

Auberville (1970) and Blasco (1975) have subdivided the mangroves into swampy mangroves and tidal mangroves. Untawale (1986) has reported 59 species

of mangroves under 41 genera and 21 families, out of these 34 species belong to the west coast, 47 on the east coast and 48 species in the inland group.

According to a survey conducted by Thomas (1962) along the mangroves of Kerala, 25 species of mangroves were present in the Veli region. Nair *et al.* (1987) reported 11 species of mangroves from the Veli region. Ramachandran *et al.* (1986) reported 27 species of mangroves and mangrove associates from the banks of different estuaries and backwaters. Kumarakom mangroves with a small mangrove area has 15 species of mangroves and mangrove associates. Basha (1991) reported that the Puthuvypu mangrove consists primarily of *Avicennia sp.* with scattered population of *Rhizophora sp.* and *Bruguiera sp.* Though there are variations in the estimates put forth by various authorities, we can conclude that these ecosystems are less diversified compared to other terrestrial ecosystems.

2.2.1 Classification of mangroves

Mangrove plants are classified according to their morphological characteristic and distribution within a habitat. Tomlinson (1986) by critically analyzing these mangroves on the basis of their composition classified them as, (a) the major elements of mangal (b) minor elements of mangal (c) mangrove associates including the coastal species like black mangal, salt marsh flora, wet coastal communities, beach or coastal communities, low land swamps and swamp forests. The major elements of mangroves include the genera *Rhizophora* (8 sp.), *Bruguiera* (6 sp.), *Ceriops* (2 sp.), *Kandelia* (1 sp.), *Avicennia* (8 sp.), *Sonneratia* *etc.* The 20 minor elements of mangals or mangrove of cosmopolitan distribution under 11 genera *i.e.* *Comptostemon* (2 sp.), *Excoecaria* (2 sp.), *Pemphis* (1 sp.), *Xylocarpus* (2 sp.), *Aegiceras* (2 sp.), *Osbornia* (1 sp.), *Pelliciera* *etc.* The third category, the mangal associates consists of nearly 60 cosmopolitan species under 46 genera, important among them are *Acanthus* (3 sp.), *Cerbera* (3 sp.), *Barringtonia* (2 sp.), *Derris* (4 sp.), *Thespesia* (2 sp.), *Phoenix* (1 sp.), *etc.* (Tomlinson, 1986). Naskar and Mandal (1999) reported 28 families of true mangroves and 17 families of back mangrove species. The most important among them are *Rhizophoraceae*, *Avicenniaceae*, *Sonneratiaceae*, *Acanthaceae* and *Sterculiaceae* among the true mangrove and *Malvaceae*, *Pandanaceae* and *Barringtoniaceae* among the back mangroves.

Curties (1933) has classified the littoral and swamp forests into four types viz., salt water forests, mangrove forests, moderate salt water forest and fresh water forest. Champion and Seth (1968) classified the forests into five types viz., mangrove scrub (4B/TS), mangrove forests (4B/TS2), salt water mixed forest (4B/TS3), brackish water mixed forest (4B/TS4) and palm swamp (4B/TS5). They only classified the Indo-Burman mangroves and not the west coast mangroves. However, Thotharthri (1981) identified the west coast swamps as 4B/TS2 having species almost similar with those seen in Sunderbans and Andaman.

Though these mangroves are characterized by low species diversity, no detailed studies have been conducted on the vegetation type and association of species resulting in a lot of contrasting and speculative reports on the number of species and genera.

2.3 Zonation

Zonation is the most peculiar character of the mangrove vegetation. Zonation is the existence of more or less distinct zones, each dominated by different mangrove species and is usually evident in well developed mangroves. Mangrove zonation is more often manifested as a mosaic that varies with the complex of physical, chemical and biological interactions, occurring in a particular area. Zonation has been thought of as an expression of successional process that occurs as coastlines extend seaward due to land building by mangroves, and as an expression of the different physiological requirements of different species, as a function of propagule size, or as the result of the geographical variations that continually reshape the coastline (Rodriguez, 1987).

Many studies show that the zonation concept prevail in the mangroves. In Florida, the red mangrove, *Rhizophora mangle* L. usually occurs lower in the intertidal zone than the black mangroves, *Avicennia germinans* (L.) which may be found in more inland sites where tidal inundation is less frequent (Davis, 1940). Three zones of mangrove vegetation were reported at Bombay (Watter, 1991). The first zone is of tree forms like *Sonneratia apetalla* and *Avicennia officinalis*, second zone comprises, *Avicennia alba* and *Rhizophora mucronata*, whereas, *Acanthus ilicifolius*, *Ceriops tagal* and *Aegicerus corniculatum* formed the third zone. Singh (1996) divided the Kutch mangroves into 3 settings of zonation based on various factors. He found that the four species of *Avicennia* were found in the

first too setting, whereas, successional stages of other seven species and marsh vegetation in the third setting with distinct demarcation. Chen and Twilley (1998) developed a gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resources. They found that the decrease in nutrient availability from marine to mesohaline sites modelled basal area of *Avicennia germinans* and *Laguncularia racemosa*.

However, Khotmire and Bhosale (1985) did not find any distinct zonation patterns in Deogad estuary of Maharashtra as stated by earlier workers. The estuary was dominated by *Sonneratia alba* and *Rhizophora mucronata* while *Excoecaria agallocha*, *Avicennia officinalis* and *Ceriops tagal* were found in most places. Mangrove zonation studied in Mobbs Bay, Australia (Youssef *et al.*, 1999) revealed that various soil variables didn't explain the zonation pattern of mangroves. A similar study in Bangladesh Sunderbans showed that the canonical correspondence analysis relating edaphic variables to species distributions accounted for only 24 per cent of the variance in species composition (Ellison *et al.*, 2000).

2.3.1 Factors affecting zonation

Distribution of species in different zones is governed by various factors such as level of maximum tides, hydrodynamic stress, crown exposure, tidal current, salinity, pH, sediment flux, oxygen in water, form and abundance of a range of anions and cations, interspecific competition and successional factors (Singh, 1996). Usually a gradient in the soil and water environment results in zonation (Cintron *et al.*, 1978). Many workers have predicted zonation patterns on various attributes like, on the basis of the submersion pattern of the forest (Karim and Mukharjee, 1993), stress factor of physical and chemical factors of the soil (Sengupta and Chaudhuri, 1993), sediment accumulation (Thom, 1982; Singh, 1996), soil salinity (Selvam *et al.*, 1991; Sengupta and Chaudhuri, 1993; Ukpong and Areola, 1995; Singh, 1996; Ellison *et al.*, 2000), soil nutrient gradient (Selvam *et al.*, 1991; Chen and Twilley, 1998; Ukpong, 2000), biotic interactions (consumption of propagules and interspecific competition) (Bull, 1980; Smith, 1987), tidal inundation (Watson, 1928; Davis, 1940; Chapman, 1944; Rodriguez, 1987) and soil redox potential and interstitial water sulphide concentration (Mckee, 1993).

2.3.1.1 Salinity gradient

This is the most important among all the factors, which determine the zonation pattern. Soil salinity is usually determined by the stage of soil formation and the extent of inundation (Sengupta and Chaudhuri, 1993). Mangroves respond physiologically to these gradients so that each mangrove species has a preferred area within a shore. It has been seen that the mangrove species differ in their degree of salt tolerance (Bhosale, 1983). In case of *Avicennia marina*, the optimum soil salinity ranges from 3.5 to 17.5 x 10⁻³ (Clough, 1984) and 80 to 90 x 10⁻³ (Mac Nae, 1968). This salinity tolerance may be related to interspecific competition as we can see in *Rhizophora mangle* which does well in fresh water, in the absence of competitors (Rodriguez, 1987). Ukpong and Areola (1995) correlated the zonation pattern with that of the salinity gradient and observed that the soil salinity gradient was negatively correlated with vegetation competition and adaption gradients ($r = -0.38$, $r = -0.35$). The highest salinity levels were associated with true mangroves (*Avicennia africana* and *Rhizophora sp.*), which dominated the lower estuaries, whereas the high, intermediate and low values overlapped among the beach ridge stran species (*Ipomoea sp.* and *Cyperus articulatus*). The metabolic basis of zonation has also been demonstrated in which the respiration is positively correlated with interstitial soil salinities (Carter *et al.*, 1973). Gunasekaran *et al.* (1992) concluded that salinity was one of the important factors in dividing the forest into three zones with different species, which ranged from 1.65 to 7.10 mmhos cm⁻¹.

2.3.1.2 Sedimentation

Primary dunes are formed in the mangrove forest, due to sedimentation, leading to the differences in elevation resulting in differences in inundation frequency. Sedimentation along with variation in geomorphological settings results in spatial patterns of mangrove forests (Thom, 1982). The variation in inundation frequency gives rise to vertical zonation of salt marsh vegetation (Gray, 1992). Sedimentation indirectly affects salinity by altering the extent of inundation (Sengupta and Chaudhuri, 1993). Sedimentation usually decreases inundation frequency and increases nutrient (especially N) availability (Olf *et al.*, 1997). It was observed in the Gulf of Kutch (Singh, 1996) that the mangrove community

changes because the plants induced sediment accumulation resulting in variation in soil salinity and input of nutrients in an area.

2.3.1.3 Soil nutrients

Spatial variations of soil nutrient resources along a tidal flooding gradient have been demonstrated in many mangrove forests (Boto and Wellington, 1984; Mckee, 1995). The resource ratio hypothesis of plant succession predicts that spatial heterogeneity of resources favours different plant species in different locations (Tilman, 1982). Sengupta and Chaudhuri (1993) reported that nitrogen content in the soil varied along the gradient with lowest in formative mangrove swamp soil and highest in agriculture cropped soil. Usually soil salinity and nutrient availability are inversely linked with each other. Chen and Twilley (1998) observed that the response curves for each species along gradient of soil nutrients resources and salinity illustrated their relative competitive balance over time. It was found that some species like *Laguncularia racemosa* dominated in fertile soils with low salinity and *Avicennia germinans* in soils with less nutrient content and high salinity with *Rhizophora mangle* in soils with low fertility and low salinity (Chen and Twilley, 1998).

2.3.1.4 Sulphate and Redox Potential

Seawater provides an ample supply of sulphate for reduction by sulphate reducing bacteria (e.g. *Desulfovibria*) and the concentration of sulphide may exceed 1mM in mangrove soils (Carlson *et al.*, 1983; Mckee *et al.*, 1988). The growth of mangroves may be influenced not only by a species capacity to maintain aerobic metabolism in its roots, but also its sensitivity to soil phytotoxins, particularly H₂S (Mckee, 1993). Mckee (1993) found that the distribution of two dominant species in a neotropical forest were associated with spatial variation in soil redox potentials (Eh) and interstitial water sulphide concentration. It was observed that the changes in Eh and sulphide concentration were strongly associated with changes in occurrences of *Avicennia germinans* and *Rhizophora mangle*. *Rhizophora mangle* alone or in combination with *Avicennia germinans* were characterized by moderately reducing soils (Eh = 100-300 mv) with low sulphide concentrations ($\leq 0.3 \mu\text{m}$), where as a zone dominated by *Avicennia germinans* had strongly reducing soils (Eh $\leq -100 \text{ mu}$) with high sulphide (2-4 mm).

Among all the above mentioned factors the salinity gradient and sedimentation decides the zonation pattern to a greater extent. It is also observed that in some cases there may not be a true picture of zonation patterns along the gradient because other factors come into play.

2.3.2 Succession

The notions that zonation is a spatial expression of plant succession and that mangrove vegetation is not a climax forest but rather a number of seral communities arranged in fairly definite zone (Davis, 1940). According to Davis scheme, the shoreline is extending in a seaward direction due to the land building role of mangroves in a continuous process of accretion and succession and is only interrupted by natural destructive forces. But this succession paradigm is questioned, (Snedaker, 1982) especially the land building concept. The succession stages determine the age of the soil formation, which in turn determines the availability of nutrients and other elements. Usually the relationship between the stage of soil formation and plant succession with availability of these nutrients are exactly reverse (Sengupta and Chaudhuri, 1993). Nitrogen and organic matter content of soil increased directly with stages of successions while phosphorus content decreased. Singh (1996) divided the Kutch mangroves into four successional settings, each with different species composition depending upon soil physico-chemical factors. Sengupta and Chaudhuri (1993) also divided the Sunderban mangroves into four ecosuccessional stages depending upon soil physico-chemical factors.

2.3.3 Regeneration

Natural regeneration in mangrove varies from place to place and from species to species. It also depends on various factors *viz.*, production of abundant propagules/seeds, favourable site conditions for germination-cum-establishment, degree of biotic interference and other abiotic factors (Kumar, 1999). Natural regeneration in mangrove forest occurs in the form of plants of varying heights, which increase with age. A mangrove plant above 90 cm height can be considered as well established regeneration plant (Kumar, 1998). Usually the propagules density is high during June and decreasing there after (Soares *et al.*, 1987).

2.4 Leaf phenology

In tropical forestry, various factors regulate leaf phenology at the individual population and community levels (Osada *et al.*, 2002). Physiological factors of trees are considered the most important in determining leaf phenology. In forests that experience a severe dry season, water stress is the primary factor (Reich and Borchert, 1984; Wright, 1991; Borchert, 1994) whereas in rainforests without a severe dry season, seasonality of irradiance is considered most important, because plants that produce new leaves at the seasonal peak of irradiance will be adaptive (Van Shaik *et al.*, 1993; Reich, 1995; Wright, 1996). This hypothesis has been confirmed as a community level trend (Wright and Van Shaik, 1994) but not as a species-specific response.

A number of works in this respect have discussed aspects of seasonal growth and productivity of mangroves from community level to species level. Many have related leaf phenology to some components of climate, such as rainfall, temperatures, radiations, and wind speed (Gill and Tomlinson, 1971; Duke *et al.*, 1984; Saenger and Monerley, 1985; Wium-Andersen, 1991) or to some presumed endogenous gradients (Gill and Tomlinson, 1969; Gill and Tomlinson, 1971; Duke, 1990). Detailed site-specific phenological studies have been documented for the members of the family *Avicenniaceae* for instance the genera *Avicennia* (Wium-Andersen and Christensen, 1970; Lopez-Portillo and Ezcurra, 1985; Duke, 1990), *Rhizophoraceae* for instances the genera *Bruguiera* (Steinke and Charles, 1984), *Rhizophora* (Gill and Tomlinson, 1971; Wium-Andersen, 1991) and *Ceriops* (Slim *et al.*, 1996).

2.4.1 Climate and phenology

In many tropical deciduous forests, the major phenological events occur parallel with the season, with leaf shedding during early dry season and emergence of new shoots on the onset of the wet season (Frankie *et al.*, 1974). Seasonal water stress is thus likely to determine the timing of phenological events in the dry forest (Murphy and Lugo, 1986). Water is commonly considered the most important environmental factor affecting growth and distribution of trees (Hinckley *et al.*, 1991). It has long been recognized that seasonal changes in the physiogamy of tropical forests are caused primarily by seasonal variation in rainfall (Schimper, 1890), which in conjunction with soil moisture availability is the principal

determinant of tree water status (Doley, 1981). Detailed analyses of the interrelation between environmental conditions, water status and phenology of the tropical deciduous trees have been documented (Borchert, 1980; Reich and Borchert, 1982). It is usually observed that the leaf fall occurs around the year, but more pronounced during dry periods and shoots grow constantly, but the growth is more active during the wet season (Fournier and Fournier, 1986; Porras, 1991).

Gwada *et al.* (2000) while working with the *Kandelia candel* (L.) Druce through canonical correlation analysis found that about 70 per cent of the seasonal variation in leaf production was explained by variations in temperature, humidity and day length. A study made by Sarkar *et al.* (1987) in the mangroves of Sunderbans observed that phenological features were mostly controlled by the salinity and day length and that the different mangrove species had little variations in their phenological patterns.

Leaf phenology is very important in the context of litter dynamics of the forest which are in turn decided by the climatic and physiological parameters.

2.5 Litterfall

The fall and decomposition of litter usually represents a major pathway for matter and energy flow in terrestrial ecosystems. For instance, Bray (1964) estimated that at least 90 per cent of the canopy leaves in temperate forests escaped consumption on the tree, eventually contributing their organic matter and nutrients to the litter store on the forest floor (Barbara and Ariel, 1990). Litterfall and decomposition are two primary mechanisms by which the forest ecosystem's nutrient pool is maintained. The litter on the forest floor acts as an input-output system for nutrients (Das and Ramakrishnan, 1985). The rate of litterfall and decay regulate energy flow, primary productivity and nutrient cycling in forested ecosystem (Waring and Schlesinger, 1985). It is particularly important in the nutrient budget of tropical forest ecosystems with nutrient poor soils where vegetation depends on the recycling of nutrients contained in the plant detritus (Prichett and Fisher, 1987). Mangroves can be considered as open systems that are important in providing energy and matter to estuarine and coastal system (Lugo and Snedaker, 1974) through litterfall and decomposition.

Litter production and decomposition have been widely studied during the last half-century, with most studies focusing on the role of litter on the carbon

balance (e.g. Odum, 1960; Olson, 1963; Golley, 1965;) and the cycling of nutrients (e.g. Furniss and Ferrar, 1982; Boerner, 1983; Holland and Coleman, 1987). More recently, many researchers have investigated the effects of litter on particular population (e.g. Schlatterer and Tisdale, 1969; Warner, 1975; Cheplick and Quinn, 1987; Hamrick and Lee, 1987) and the effects of litter on community structure and dynamics (e.g. Sydes and Grime, 1981a; Sydes and Grime, 1981b; Beatty and Sholes, 1988; Carson and Peterson, 1990). Few attempts have been made to understand the mechanisms underlying the effects of litter on plant populations and communities (Facelli and Pickett, 1991).

2.5.1 Factors influencing litterfall

Litter production depends primarily on the productivity of the plant community at a site. Usually similar factors determine litter production and primary productivity (Bray and Gorham, 1964). In the earlier studies, the main emphasis was placed on fluctuations and composition of litterfall (Chandler, 1943) as well as distribution (Kirkridge, 1948).

Stress in recent studies, however, has been on ecosystem analysis with litterfall playing a central part, particularly on nutrient cycling in forest. Many authors reported that species composition, basal area, age, structure (Stohlgren, 1988), altitude (Reiners and Long, 1987), latitude (Bray and Gorham, 1964) and season (Luizao and Schubart, 1987) are factors that strongly influence the litterfall dynamics in natural forests.

2.5.1.1 Location

Most of these studies had either natural forest ecosystems or homogenous stands in the temperate regions as their principal focus with relatively little attention paid to the tropics (Kumar, 2001). Tropics are characterized by higher rates of litterfall and rapid organic matter turnover than the temperate regions, both in natural forests as well as the managed land use systems. Bray and Gorham's (1964) inverse relationship between total detritus production and latitude of the region substantiate this. Annual litter production in warm temperate forests range from 5-7 t ha⁻¹ yr⁻¹ but can be as high as 18 t ha⁻¹ yr⁻¹ (Bray and Gorham, 1964).

William and Gray (1974) reported a litter production rate of about 5.5 to 15.3 Mg ha⁻¹ yr⁻¹ for equatorial forest, which was substantially greater than that of temperate ecosystems. (e.g. cool temperate forest type showed litterfall values 4.5

to 6.4 Mg ha⁻¹ yr⁻¹, Stohlgren, 1988). Mean annual litterfall for the evergreen forest formation of Attappadi in Western ghats (8.5 Mg ha⁻¹ yr⁻¹, Pascal, 1988) however, was lower than that of the deciduous forest formation in the same locality. Annual litterfall ranged from 12.2 to 14.4 Mg ha⁻¹ yr⁻¹ for the tropical moist deciduous forests in the western ghats of Kerala (Kumar and Deepu, 1992).

Productivity in freshwater and saltwater-forested wetland is generally higher under flowing conditions and decreases when stagnant condition occur (Lugo *et al.*, 1990). In particular soil salinity can have large effect on productivity. There are only a few studies on mangroves to quantify litterfall. A study in mangrove forests of *Rhizophora mangle* in Florida, the litterfall ranged from 5.00 t ha⁻¹ yr⁻¹ (Golley *et al.*, 1962) to 9.00 t ha⁻¹ yr⁻¹ of dry weight (Heald and Odum, 1970). Leaf litter production was measured in *Rhizophora* dominated mangrove forests of Rawa Timur (Java); a very low annual litter production of 3.713 t ha⁻¹ yr⁻¹ was recorded (Anwar, 1987). A similar low values of litter production of 4.9 t ha⁻¹ yr⁻¹ of dry weight was observed in a mixed stand of *Rhizophora apiculata* and *Rhizophora mucronata* forest of Muara Agke-Jakarta, Indonesia (Sukardjo, 1984). Litter production studies by Hardiwinoto *et al.* (1989) in three mangrove communities of Okinawa island of Japan revealed that annual litter production was 8.72, 10.74 and 7.73 t ha⁻¹ yr⁻¹ respectively in *Kandelia candel*, *Kandelia candel* and *Bruguiera gymnorrhiza* mixed stand and *Bruguiera gymnorrhiza* stand. Litterfall was quantified in mixed forest of mangrove at Siar beach of Sarawak (Othman, 1989) with *Rhizophora mucronata* as a dominant species and co-dominated by *Rhizophora apiculata* with *Bruguiera gymnorrhiza*, *Bruguiera parviflora*, *Bruguiera cylindrica*, *Avicennia alba*, *Lumnitzera sp.*, *Nypa fruticans* and *Oncosperma sp.* as associates. The annual litterfall was 5.72 t ha⁻¹ yr⁻¹ and of this 4.49 t ha⁻¹ yr⁻¹ (78.5 %) was leaf litter.

A study by Dagar and Sharma (1991) in the mangrove forests of Andamans, quantified an annual litter of 8.08 to 10.30 Mg ha⁻¹ yr⁻¹ for *Rhizophora apiculata* at different sites. A study conducted by Sukardjo and Yamada (1992) in the *Rhizophora mucronata* plantation of central Java, Indonesia revealed that the litter production varied from 7.058 to 10.395 t ha⁻¹ yr⁻¹ of dry weight. Sengupta and Chaudhuri (1993) quantified annual litterfall ranging from 5.11 to 7.09 Mg ha⁻¹ yr⁻¹

at different sites of Andaman mangroves. Leaves contributed 68.1% to 73.3% of total litterfall and twigs contributed very little:

2.5.1.2 Season

Litter production exhibits definite seasonal patterns, which vary with latitude and vegetation type (Bray and Gorham, 1964). In equatorial rain forests, litter production is even throughout the year, while in temperate evergreen forests there are peaks related to leaf production and litterfall. In xerophytic woodlands, the peak of litter production may be either at the beginning or near the end of the dry period, depending on the foliar strategies of the dominant populations (Hopkins, 1996).

In some cases peak fall, however, coincided with the peak rainfall events e.g. In the Puerto Rican plantations (Lugo, 1992) and in the *Rhizophora mucronata* plantations of central Java, Indonesia (Sukardjo and Yamada, 1992) litterfall was highest in rainy season. Since water stress triggers *de novo* synthesis of abscissic acid in the foliage of plants and results in leaf senescence. Annual/seasonal drought (Cintron and Lugo, 1990), hot winds or other adverse environmental factors such as changes in soil salinity (Twilley *et al.*, 1986) causes leaf fall.

2.5.1.3 Site characteristics

Soil fertility and soil water retention determines litterfall in the same climatic range (Facelli and Pickett, 1991). Litterfall rates were measured for Mahogany plantation established in three types of forest namely subtropical dry forest, cloud canopy deciduous forest and scrub forest in Guanica, Puerto Rico by Cintron and Lugo (1990). They found that in space, mean annual litterfall reflected the change of forest physiogamy from scrub to tall deciduous due to small scale edaphic variations within the forest, which affect the water holding capacity of the soil. Twilley *et al.* (1986) found that annual litterfall was inversely related to average soil salinity in the mangrove forests of southern Florida. A study carried out by Eusse and Aide (1999) in the wetlands of Puerto Rico, involving *Pterocarpus officinalis* and *Laguncularia racemosa* revealed that the litter production in the species varied along the salinity gradient. The leaf fall for *Pterocarpus officinalis* was $4.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in low salinity sites and $1.8 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ in high salinity site, but total stand litterfall was greatest in the area of high salinity due to the contribution of *Laguncularia racemosa*.

Litter production in mangroves and swamps is also influenced by the water turnover within the forest (Pool *et al.*, 1977). Tides are energy subsidies to the net primary production of inter tidal wetlands (Odum, 1960). Wharton and Brinson (1979) suggested that water movement provide not only a source of silt and clay but also a supply of nutrients and aeration for optimal growth. Hence forested wetlands have greater potential for litter production than many tropical forests (Brown and Lugo, 1980).

Environmental factors not directly related to phenology also affect the seasonal patterns. In two riverine forests of Belgium, woody litter increased during the winter, during strong winds (Hermy, 1987). Christensen (1975) found that the fall of branches was determined by seasonal strong winds and that previous climatic conditions may predispose trees to higher litterfall.

2.5.1.4 Species composition of forest

Many authors have reported that species composition, basal area, age, structure (Stohlgren, 1988) are factors that strongly influence litterfall dynamics in natural forests. Litter production by individual species in a natural forest stand is dependent on their dominance in the stand and the total amount reflects its stocking density (Kotwal and Mall, 1977). George and Kumar (1998) related the interspecific variation in litterfall to the crown diameter of trees, trees with large crown diameter *e.g.* *Acacia* sp. gave highest litterfall compared to that of trees with low crown diameter like *Ailanthus* sp.

2.5.1.5 Management practices

A tropical tree plantations had higher litterfall than secondary forests of similar age growing under similar climatic and edaphic condition for their production and nutrient cycling characteristics was made by Lugo (1992). But, a study on the litter and biomass production from planted and natural fallows on degraded soils in South West Nigeria by Salako and Tian (2001) revealed no difference between annual litterfalls of planted and natural fallows with mean of 10.0 Mg ha⁻¹ yr⁻¹ and 13.6 Mg ha⁻¹ yr⁻¹ respectively. It was concluded that the annual litter flux was less in case of shelter wood than that of natural forests, thus, it revealed that forestry interventions significantly affects seasonal and annual contributions of organic residues. It was also observed that pruning operation

yielded less litter, albeit temporarily (George and Kumar, 1998) and altered leaf fall periodicity.

Since litterfall rates generally parallel the trend in biomass productivity, higher litter yield is probable in mixed species stands than sole stands (Binkley *et al.*, 1992). Parrota (1999) found that mixed species stands had usually higher litterfall rates than monospecific stands, despite variations on account of species composition.

2.5.2 Composition of litter

Many workers in the tropics and temperate countries have addressed the variations in the composition of litter. Leaf fraction predominates the fine litter in most studies. Typically, it represents 70 per cent of the total coniferous litter (Meentemeyer, *et al.*, 1982). Tropical workers, however, reported values ranging from 90 per cent (Kumar and Deepu, 1992; Lugo, 1992) to 100 per cent (Lodhiyal and Lodhiyal, 1997) of the total litterfall. A study by Sukardjo and Yamada (1992) in the *Rhizophora* plantation of Central Java, Indonesia revealed that the leaf litter constituted 73 to 84 per cent of the total litter weight, reproductive parts 26 to 49 per cent and woody litter 12 per cent to 14 per cent of total dry litter.

2.6 Litter decomposition

The mass of the litter accumulated may be reduced by physical and chemical degradation, heterotrophic consumption, and decomposition. These processes are tightly interrelated, either as competitive or sequential processes (Facelli and Pickett, 1991). Decomposition of plant litter includes leaching, break up by soil fauna, transformation of organic matter by microorganisms and transfer of organic and mineral compounds to the soil. This litter decomposition is probably the most important and widely studied aspect because of its essential role in soil formation, microbial metabolism and nutrient recycling (Couteaux *et al.*, 1998).

The decomposition of leaf litter plays an important role in nutrient cycling and supply of organic matter to the estuarine detritus food webs (Woodroffe, 1982; Twilley *et al.*, 1986). Decomposition rates vary greatly among ecosystems (Olson, 1963), faster rates are found in tropical forest (Jenny *et al.*, 1949) and slower rates in subalpine systems (Olson, 1963).

The decomposition of leaf litter in mangroves is fast. The half-life of Red mangrove leaves is less than a year and averages 70 days. A study was conducted

in three dominant tree species of mangroves in Hong Kong (Tam *et al.*, 1990). They estimated that *Kandelia candel* degraded most rapidly during first 6 weeks, followed by *Avicennia marina* and *Aegiceras corniculatum* with 12.7 per cent, 32.6 per cent and 60.2 per cent of the original leaf material present respectively at the end of the study period. A decomposition study conducted in *Avicennia marina* by Mackey and Smail (1996) under subtropical conditions, revealed that decay rates for both leaves and twigs were faster in summer (t_{50} ranging 59 to 44 days) than in winter (t_{50} ranging 98-78 days).

No such study has been reported from mangroves of South India particularly from Kerala. A through analysis of decay rates in various species of other ecosystems also awaits determination.

2.6.1 Factors affecting litter decomposition

Decomposition process is determined by interactions among three components, viz., organisms, physical parameters like climate and minerology of parent material and the quality of the decomposing resources. They all operate at different scales of space and time in a hierarchical fashion with high level factors dominating those acting at lower levels. Climatic factors are at the top most level in the hierarchy of factors affecting the decomposition rate, followed by soil physical properties, chemical properties of the resources and biological regulations through interaction between macro and micro-organisms (Lavelle *et al.*, 1993).

2.6.1.1 Climatic factors

Yearly environmental variations affect decomposition rates within a given system. Changes in temperature and moisture availability have been related to decomposition rates (Agbim, 1987; Woodwele and Dykeman, 1996). Mackey and Smail (1996) under subtropical condition revealed that the decay rate for both leaves and twigs were faster in summer than in winter. Since invertebrate shredders and microbes are very active during higher temperatures, warm and humid conditions of tropics favours break down and decomposition of litter.

2.6.1.2 Soil moisture

The microenvironment surrounding the litter affects the decomposition rate (Furniss and Ferrar, 1982). Litter decomposition is regulated mainly by temperature and water regimes, soil fertility may be secondarily important (Staaf,

1987). In flooded habitats, as we see in mangroves and other wetlands, biochemical decomposition may be limited by low oxygen concentration and low pH (Polunin, 1984). However, Day (1983) found that litter disappeared faster in the wettest sites of a lowland forest; pulses of flooding may hasten decomposition due to enhanced leaching, and the consequent changes in litter quality. Down shore position of the litter and hence exposure to the wetting action of the tides, is an important factor affecting decomposition (Mackey and Smail, 1996). Water soaking causes leaching of labile materials (Robertson, 1988; Chale, 1993) and promotes leaf conditioning by microbes (Tam *et al.*, 1990; Chale, 1993) both of which will increase decomposition rates. Litter bag studies in areas prone to flooding and extreme form of wetting and drying, have shown greater mass loss in seasonally flooded sites than in unflooded sites nearby (Brinson, 1977; Bell *et al.*, 1978). But the analysis is again complicated because inundation causes confounding effects such as nutrient import (Qualls, 1984), oxygen limitations and redox change (Brinson *et al.*, 1981) and fragmentation of moving water (Peterson and Rolfe, 1982). Day (1983) compared decomposition of red maple (*Acer rubrum* L.) in laboratory microsoms and found that, while flooding always promoted decomposition, fluctuating hydroperiods (i.e. repeated wetting and drying) had no further effect. A study by Witkamp (1969) showed that wetting and drying of litter increased loss of elements by leaching almost entirely because of lysis of dead microbial cells.

The export of organic material to the estuarine and offshore environments is an important function of mangrove ecosystems (Lugo and Snedaker, 1974) and the extent of this export is dependent upon tidal flushing (Lugo and Snedaker, 1975). Tide levels and their inundation regimes also affect decomposition rate. Mackey and Smail (1996) concluded that t_{50} 's of leaves placed in low tide levels on the shore were 20-25 per cent less than leaves placed in places with high tides. Similarly the t_{50} 's of twigs were 10-53 per cent less.

2.6.1.3 Soil temperature

Microbial activity increases exponentially with increasing temperatures and as a result, high temperature result in rapid decomposition (Waring and Schlesinger, 1985). Mackey and Smail (1996) studied decomposition rates in *Avicennia marina* in Australia and concluded that the t_{50} 's for leaves were on

average 42 per cent lower in summer than winter and similarly, twig t_{50} 's were 78 per cent lower. These differences were likely to be induced by the effects of warmer summer temperatures on the activity of bacterial and fungal decomposers. Since the summer months are wetter and more humid it is possible that this moist environment enhanced the activity of microbial decomposers. Invertebrate shredders are also more abundant in summer when large numbers of isopods and amphipods usually appear in litter bags (Mackey and Smail, 1996). In the tropics, with their higher temperatures, decomposers and shredder populations will be active throughout the year, but in temperate regions, most activity will occur during summer.

2.6.1.4 Biotic factors

There are many macro and micro fauna which help in decomposition of litter. Tropical ecosystems generally contain more diverse soil fauna than do temperate and subalpine forests. A greater earth worm activity (Anderson and Swift, 1983), higher bacterial cell counts and fungal hyphal lengths (Swift *et al.*, 1979) are frequently reported in the tropical soils compared to those in temperate and boreal forests. Mackey and Smail (1996) reported that macro fauna like burrowing isopod *Sphaeroma* to be a causative agent in break down *Avicennia* twigs in Australian mangroves. Twilley *et al.* (1997) concluded that the crabs (*Ucides occidentalis*) helped in leaf transportation and degradation of litter by minor consumption. The particulate organic matter left after leaching is highly dependent on the action of bacterial and fungal communities which develop rapidly on leaves (Wardle *et al.*, 1997).

2.6.1.5 Species composition

Litter decomposition rate varies from species to species in same biotic and abiotic conditions. A study conducted by Ashton *et al.* (1999) in mangrove forest of Malaysia predicted that the *Sonneratia alba* leaves decomposed very rapidly than that of *Rhizophora apiculata*, *Rhizophora mucronata* and *Bruguiera parviflora* at both the cleared and uncleared sites, the difference was due to difference in leaf morphology, texture and composition. A similar study in mangroves of Hong Kong (Tam *et al.*, 1990) revealed that *Kandelia candel* has the highest litter decomposition rate (daily loss of 1.13 %) followed by *Avicennia*

marina (daily loss of 0.85 %) and *Aegiceras corniculatum* had the lowest rate (daily loss of 0.47 %).

2.6.1.6 Litter quality

The chemical and physical characteristics of litter are thought to be key regulators of litter decomposition. The chemical composition of litter is another important variable affecting decomposition rates (Day, 1983; Furniss and Ferrar, 1982). The contents of lignin, nitrogen, cellulose, lignin cellulose and secondary compounds (particularly phenolic acids) are the most conspicuous variables (Horner *et al.*, 1988) which decide decomposition. Johansson *et al.* (1995) found that in a long climatic transect the substrate quality dominated over the climate. By tradition there appears to be a general opinion that climate rules decomposition on a regional scale whereas litter chemical composition dominates the process on a local scale (Berg, 2000).

2.6.1.6.1 Water soluble substances

Water soaking causes leaching of labile materials (Robertson, 1988; Chale 1993) and promotes leaf conditioning by microbes (Tam *et al.*, 1990; Chale, 1993) both of which will increase decomposition rate. Decomposition of mangroves is characterized by an initial leaching of soluble organic and inorganic compounds with subsequent colonization of bacteria, fungi and protozoan which utilize the labile substance and initiate the breakdown of plant material resulting finally in physical and biological fragmentation (Tam *et al.*, 1990). The water absorption pattern varies from species to species. In one such study by Taylor and Parkinson (1988) in the leaf litter of pine and aspen leaf, observed that aspen leaves lost all the leachable material in one day whereas in pine needles it was slow. The most easily leachable compounds like sugars and proteins are lost first (Woods and Raison, 1983; Berg and Wersen, 1984). Water absorption is in turn dependent on the physical structures of the leaf. Pine leaves with a low surface to volume ratio and thick cuticle layer compared to aspen leaves hinders absorption (Taylor and Parkinson, 1988).

2.6.1.6.2 Initial nitrogen

Nitrogen content of plant material is important in controlling rate of decomposition (Millar *et al.*, 1936). This initial nitrogen content is of importance in nutrient poor ecosystems, wherein exogenous supply of nitrogen for the

decomposing microorganisms is less (Melillo *et al.*, 1982). For non-leguminous litter, initial N and lignin percent or the ratio of lignin: N, correlated well with decomposition rates (Constantinides and Fownes, 1994). Under conditions where nitrogen limits the microbial growth, the rate of mass loss is determined both by the nitrogen concentration and by the lignin concentration (Brendse *et al.*, 1987). Berg and Staaf (1987) found that with an increase in the total nitrogen concentration, the concentration of both "lignin-bound" and "non-lignin-bound" nitrogen increased proportionally. Thus, there exists a positive linear relationship between nitrogen concentration and rate of mass loss (Brendse, *et al.*, 1987). Nitrogen immobilization pattern in litters is an important phenomenon during decomposition. Initial nitrogen is inversely related to the rate of N immobilization (Aber and Melillo, 1982). But highest immobilization rates (gram N immobilization per gram litter input per year) occur in litters high in both lignin and nitrogen. This is because total immobilization increases with lignin content, while rate of decay increases with nitrogen content (Aber and Melillo, 1982).

2.6.1.6.3 Lignin

Lignin in litter is usually recalcitrant to enzyme degradation, therefore, the higher proportion of this constituent is in a given leaf species, the lower is the relative amount of more readily available carbon compounds (Kumar, 2001). The intimate association of lignin with cellulose fibres results in marking of a large fraction of carbohydrate which otherwise would be accessible to the leaf associated microorganisms (Gessner and Chaunet, 1994). Hence lignin content in leaf litter is viewed an inverse index for the availability of carbon to decomposers. Melillo *et al.* (1982) suggested that the initial lignin concentration was highly correlated ($r^2 = 0.93$) with the slope of inverse relationship with the decomposition rate.

2.6.1.6.4 Lignin: N ratio

Thomas and Asakawa (1993) reported that of the structural attributes, lignin to N ratio is probably the best indicator of litter decomposition and it was significantly correlated with N release. A study by Melillo *et al.* (1982) in six hardwood species in Hubbard Brook forest of USA found that various initial litter quality parameters were correlated to that of decay constant k . Among them, the rates of decay were most highly correlated ($r^2 = 0.89$) with the initial lignin: initial nitrogen content of the leaf samples, both had an inverse relationship. However,

this relationship holds good only in case of species with a narrow initial lignin: initial N ratio. They also found a negative hyperbolic relationship between decomposition rate and initial lignin: nitrogen ratio.

2.6.1.6.5 C: N ratio

The dynamics of carbon and nitrogen in the substrate are determined by the uptake of carbon and nitrogen by microorganisms and by the return of both elements to the substrate as dead microbial biomass (Brendse *et al.*, 1987). A lower initial C: N ratio can enhance the rate of decomposition (Rao *et al.*, 1994), as seen in *Sonneratia* leaves which decomposed faster than other leaves (Ashton *et al.*, 1999). But in case of multi component substrates, C: N ratio of the individual components that can be assimilated by the microorganisms decide the immobilization and mineralization. Available reports indicate that, among all the factors, the litter quality especially the initial lignin and initial lignin: nitrogen ratios of the litter samples decide the decay pattern to a greater extent.

2.6.2 Pattern of decomposition

Berg (1986) divided decomposition into two parts (i) decomposition of labile fraction (hydrosolubles, non lignified cellulose and hemicellulose components) of the litter containing easily degradable compounds such as sugars, starches and proteins which can be rapidly utilized by decomposers to give the "rapid release phase". The phase is controlled by nutrients like nitrogen, phosphorous and sulphur. (ii) Decomposition of lignified carbohydrates (more recalcitrant materials such as cellulose, fats, waxes and tannins) which are chemically bound to native lignin, represents the slow release phase.

Decomposition of mangroves is characterized by an initial leaching of soluble organic and inorganic compounds with subsequent colonization of bacteria, fungi and protozoans which utilize the labile substance and initiate the breakdown of plant material. This results finally in physical and biological fragmentation. The decomposition of mangrove litter is principally the function of their chemical composition of the source material and thus are species specific (Tam *et al.*, 1990).

2.6.3 Nutrient release patterns

There are various patterns through which nutrients are released from decomposing litter like the triphasic or biphasic manner. Jamaludheen and Kumar (1999) reported that the nitrogen release from decomposing litter followed a three

phase release pattern for *Acacia*, *Casuarina* and *Artocarpus hirsutus*. In this phase the concentration of nitrogen of the decomposing litter declines rapidly after a brief initial increase and was followed by a final slower release phase. They also found that other MPTs followed a biphasic pattern, characterized by an initial rapid and a subsequent slow release phase. Phosphorous and potassium remaining in the residual litter mass exhibited an initial rapid release followed by slower, final release. Berg and Staaf (1987) also described a triphasic model for nutrient release from decomposing litter.

Sometimes, it is seen that the absolute nitrogen masses in the liter bags increase during initial stages of decomposition. This is due to the addition of nitrogen by fixation, absorption of atmospheric ammonia, through fall, dust, fungal translocation and/or immobilization.

The zonation, leaf phenology and litter dynamics decides the nutrient cycle pattern as well as the contribution of species to this particular ecosystem. This in turn is decided by the various physical and biological factors of this ecosystem. The whole correlation is very significant in it self, which binds the ecosystem together.

Materials and Methods

3. MATERIALS AND METHODS

3.1 Site description

3.1.1 Location:

The study was conducted at the Fisheries Research Station of Kerala Agricultural University at Pudukkottai in Ernakulam district, where about 100 ha of mangrove forests exists. The site (9°58' N latitude and 76°14' E longitude) falls under the Elangapuzha Panchayat of Kochi taluk with an altitude of approximately 1.7 m above mean sea level. It forms a part of the Vypeen island, located about 2 km east of the Vypeen – Munambam road, and is encircled by the Arabian Sea on three sides and the Murkumpadam Panchayat in the north. It is also surrounded by Cochin bar mouth and a canal (locally known as INTUC canal; 8 m wide) form the southern and eastern boundaries of the study area respectively.

3.1.2 Climate

The sea-board of Kerala has been categorized under the humid littorals with high temperature and high humidity throughout the year. The annual rainfall ranges from 2400 mm to 3000 mm (mean for 10 years; 1991-2001) with a bimodal distribution pattern; June-August (south west monsoon) represents the main peak (360-720 mm of monthly rainfall) and October – November (north east monsoon) a subsidiary peak (175-300 mm of monthly rainfall). Weather parameters during the study period (August 2001 to July 2002) are given in Table 1 and Fig. 1. Mean monthly temperature during the experimental study ranged from 29°C to 30°C with the maximum rarely exceeding 32°C and minimum rarely falling below 21°C. Mean maximum temperature at this site ranged from 29°C (July) to 32°C (April) and mean minimum from 22°C (January) to 25°C (April), with a relative humidity ranging from 67% (January) and 88% (July).

3.1.3 Geology and Soil

Pudukkottai represents a unique ecosystem, and is the result of land formation due to sediment deposition by rivers draining into the Vembanad lake. Low-lying water-logged marshy areas with criss-crossing channels and ditches are important physiographic features of Pudukkottai. Revenue records at Elangapuzha Panchayat suggest that this landmass at Pudukkottai was of recent origin owing to a high degree of sedimentation. The remarkable sedimentation process reported at this site can be explained by the fluvial dynamics of the suspension-rich rivers

Table 1. Weather parameter data of the study plot from August 2001 to July 2002

Months	Maximum Temperature (°C)	Minimum Temperature (°C)	Rainfall (mm)	Relative humidity (%)
Aug 01	29	23.7	376.8	89
Sep 01	29.6	23.8	289.4	86
Oct 01	30.2	23.9	302.3	84
Nov 01	30.9	23.6	175.1	81
Dec 01	31.3	22.7	48.3	75
Jan 02	31.4	22.1	21.9	73
Feb 02	31.8	23.4	22.9	76
Mar 02	32.4	25	35.3	75
Apr 02	32.7	25.4	124	77
May 02	31.7	25.3	395	82
Jun 02	29.7	24	720.7	89
Jul 02	28.9	23.5	697.2	91

Source: Meteorological Observatory, Naval Base, Kochi.

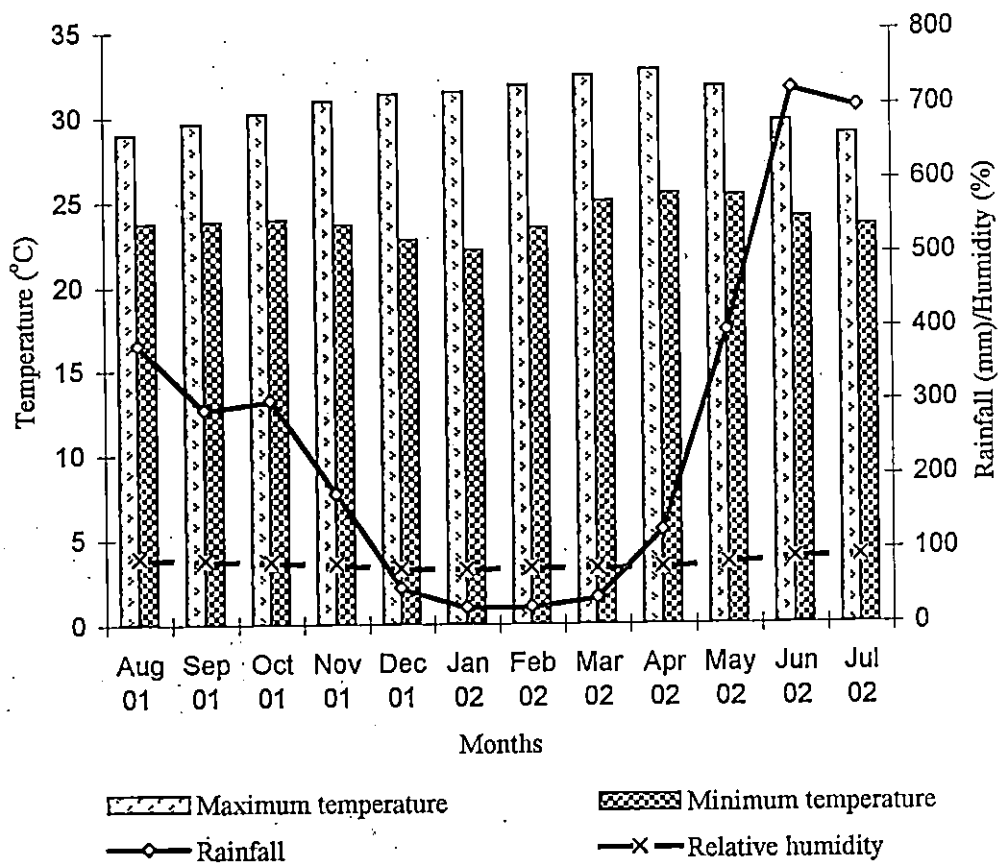


Fig. 1. Weather parameters of the study polt during August 2001 to July 2002.

draining into the Vembanad lake and/or the dredging operations in Cochin bar mouth.

Soil is silty clay textured and blocky in structure as reported by Kumar and Kumar (1997). The soil profile is characterized by a dark brown surface horizon (in the *Avicennia* zone) to a very dark grey top horizon (in the grass zone). Lower layers of the soil profile are however, uniformly black in both cases and sticky suggesting water logging or a shallow water table. Apart from fine sand, shell fragments, sillimanite, magnetite and rare earths are present in the *Avicennia* zone. This soil also contained high amounts of organic matter, but were low in total soluble solids and calcium carbonate. Relatively high concentrations of salts, N and P levels and humus were also present in the *Avicennia* zone.

3.1.4 Vegetation

A reconnaissance survey of the site revealed two distinct regions: the narrow shoreline strip with sandy soil and the inland mangrove area on a clayey substrate. The shoreline area consists of shrubs like *Clerodendron* sp. and *Premna* sp., with some climbers (*Ipomoea pes-carpa* L. Sweet) and grasses like *Cynodon* sp. and *Carex* sp. along with seedlings of *Calophyllum inophyllum* L. and *Bruguiera gymnorrhiza* L. Lamk. tree species. The inland mangrove areas, although discontinuous, consists of *Sonneratia caseolaris*, *Avicennia marina* (Forsk.) Vierh. (Plate 16), *Avicennia officinalis*, *Casuarina equisetifolia* L. on the outer side and a dense distribution of *Avicennia officinalis*, with patches of *Bruguiera cylindrica* and *Excoecaria agallocha* on the inner side. Previously, Nameer *et al.* (1992) reported seven species of strict mangroves and 16 mangrove associates while Kumar and Kumar (1997) reported seven major mangrove species and 19 mangrove associates at this site. Forest cover in Pudukkottai has been subjected to a variety of human impacts including extraction of firewood, Non-Wood Forest Products (NWFP's), lopping of leaves for cattle grazing and above all, commercial fisheries activities. Little quantitative information is available on the magnitude of such disturbances. It is, however, reasonable to assume that increasing level of disturbances are accompanied by changes in the floristic spectrum.

3.2 Description of the species under study

To estimate the litter decay and leaf phenology five locally important tree mangrove were selected. In addition a predominant mangrove shrub was included in the decay study. They are described below:

(a) *Avicennia officinalis* L. (white mangrove, Family: Avicenniaceae)

An evergreen perennial tree, attaining a height of about 15 to 20 m (Plate 11). It possesses a dense crown, with irregularly spreading branches and smooth bark, whitish, and deliquescent. Aerial roots are well-developed with spongy pencil-like pneumatophores having frequent lenticels and blunt apices. Leaves are opposite decussate, extipulate, cauline, petiolate, green, leathery and glabrous. The leaf lamina is elliptical, broadly ovate or obovate-oblong, entire or with occasionally rounded apex. The inflorescence is a compound spike with complete, bisexual, regular, cyclic, hypogynous, rosaceous and erect flowers. Capsules are fleshy, ovoid, opaque, green and densely hairy. The capsule is usually 3 cm long and 2.8 cm broad, flattened and wrinkled at the base with a short apical beak. Germination is epigeal, crypto-viviparous. Flowering and fruiting time is from March to early October (Naskar and Mandal, 1999).

(b) *Rhizophora mucronata* Lamark Encyd (long fruited stilted mangrove, Family: Rhizophoraceae)

A medium to tall tree, upto 15 m high, with deliquescent and horizontally spreading branches (Plate 12). Trunk is not conspicuous and is supported by profuse prop roots and stilt roots. Bark is brownish to whitish grey and is longitudinally fissured. Corky, woody, profuse stilt roots are present supporting the lower trunk regions and the lower branches. Leaves cluster in the short apex encircling the nodes and are elliptical. They are opposite decussate, simple, extipulate with a mucronate (pointed) at the tip. Inflorescence is upto 5.2 cm long cyme, opposite, decussate and ebracteate. Flowers are ebracteate, pedicellate, green, glabrous, complete, regular and hermaphrodite. The capsule is 5–7 cm long and has a 9.5 cm periphery with four persistent sepals. Flowering and fruiting are normally observed during February to October, but viviparous germinated hypocotyls hang in the mother plants, almost throughout the year (Naskar and Mandal, 1999).

(c) *Bruguiera cylindrica* L. (small leaved orange mangrove, Family: Rhizophoraceae)

A medium to large tree attaining upto 15 m height, perennial, evergreen, deliquescent, woody, erect with haphazardly arranged branches (Plate 13). Knee-like pneumatophores are common; leaves are simple, opposite decussate, cauline, extipulate, petiolate, reddish dark green and lamina ovate-lanceolate, acute or bluntly pointed. Inflorescence is cyme, three flowers in each peduncle, which is long, terete, green and glabrous. Flowers are ebracteate, pedicellate, greenish, bisexual and complete. Fruits are berries with persistent calyx, hypocotyls upto 16 cm long. Flowering and fruiting time extends from March to November, but viviparous seedlings are seen hanging on the mother plant throughout the year (Naskar and Mandal, 1999).

(d) *Sonneratia caseolaris* L. (mangrove apple, Family: Sonneratiaceae)

A small evergreen tree growing upto 8 m high, with a deliquescent branching pattern (Plate 10). Branches are horizontal with slender twigs and slightly pendulous but not drooping. Pneumatophores are slender, erect with a height of 1 m with spongy outer surface and secondary growth. Leaves are opposite, decussate, extipulate, simple, cauline, fleshy with short petioles and prominent reddish midribs. It has a cyme inflorescence, solitary or few flowered on the outer pendulous twig. Flowers are ebracteate, pedicellate and bisexual with a cup shaped calyx. Stamens are indefinite and are whitish above and reddish below. Fruit is a berry, green and globose. Vivipary is not seen. Flowering and fruiting is common during March and October (Naskar and Mandal, 1999).

(e) *Excoecaria agallocha* L. Syst. (blinding tree, Family: Euphorbiaceae)

A medium-sized deciduous tree, 15 to 20 m high, deliquescent, and much branched; bark grey, fissured, with poisonous milky latex, lenticels are prominent on young twigs (Plate 14). Roots are generally without any aerial growth and are usually superficial. Leaves are spirally arranged, somewhat clustered at the end. Leaves are simple, extipulate, cauline, petiolate, round, greenish and glabrous, with an ovate elliptical lamina. Mature leaves senescent during late winter or early summer. Male inflorescence is sessile and female inflorescence is a mixed cyme. Male flowers are bracteate, monochlamydous, dioecious and zygomorphic. Female flower is bracteate, sessile, round, glabrous and achlamydous. Fruits are three-

lobbed, schizocarpic, dehiscing into three cocci to release the solitary seeds and the pericarp is somewhat leathery but not fleshy. Flowering and fruiting times are February to August (Naskar and Mandal, 1999).

(f) *Acanthus ilicifolius* L. (holymangrove, Family: Acanthaceae)

A viny shrub or tall herb upto 1.5 m high, scarcely woody, bushy, with a very dense growth (Plate 15). Tap roots are shallow with fibrous roots. Leaf simple, opposite decussate, cauline, extipulate, petiolate, short glabrous, lamina oblong spiny to very spiny and wavy margin. Inflorescence is a racemose spike; flowers are bracteate, entire, acute, glabrous, greenish and bisexual. Fruits are capsules with four seeds in it, germination epigeal and non-viviparous. Flowering and fruiting is during May to August (Naskar and Mandal, 1999).

3.3 Methods

3.3.1 Phytosociological analysis

The study area approximately measured 1200 m in width from the sea coast to the land interior (where agricultural lands start) and 1.5 km in length along the sea coast (Fig. 2). The zonation attributes were evaluated by laying three transects, at 500 m interval, extending from the shoreline to the land interior of the mangrove forests up to the area where human settlements occur. Along each transect, 10 x 10m quadrats were established at 100 m intervals. For each quadrat, data on (i) number of species (ii) total number of individuals of each species and (iii) diameter of each individual at breast height (1.37 m) were collected. Number of species in each quadrat was plotted against distance from the land-ocean interface to evaluate the floristic changes. Stand basal area and dominance were computed using the enumeration data. In addition, community structure indices such as relative frequency, relative dominance and relative density and importance value of the species were computed using the formulae given here under.

1. Density = Number of individuals of a species 'i' per ha.

2. Abundance =
$$\frac{\text{Total number of individuals}}{\text{No. of quadrats of occurrence.}}$$

3. Basal area =
$$\frac{\text{GBH}^2}{4 \text{ 'PI'}}$$

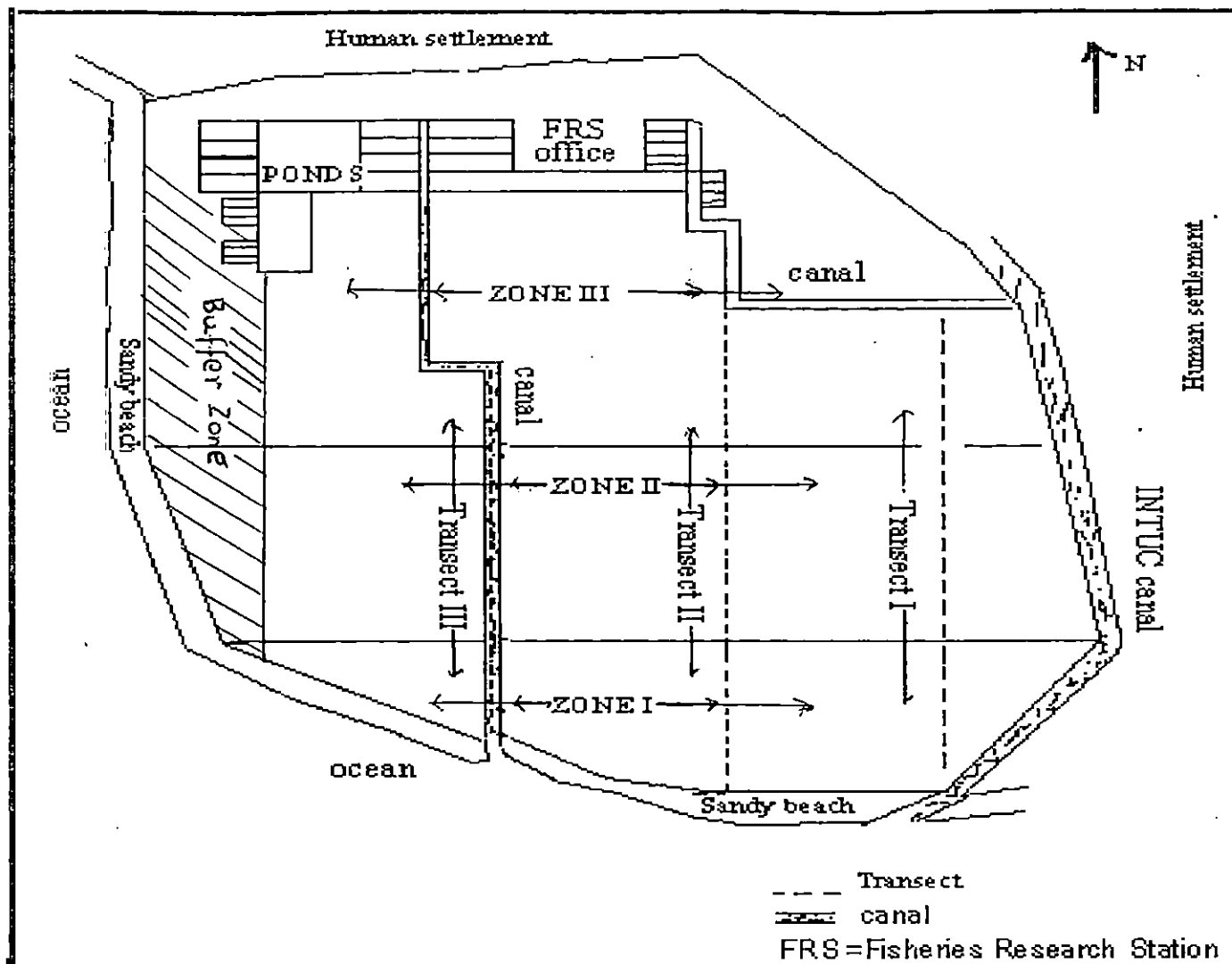


Fig .2 Map of the study site in the mangrove forest at Puduvelyppu

Only transect II reached the 1200 m distance from sea, whereas, transect I and transect III were extended only upto 700 m beyond which there was human settlement

$$4. \text{ Relative density} = \frac{\text{Number of individuals of a species} \times 100}{\text{Number of individuals of all species}}$$

$$5. \text{ Percentage frequency} = \frac{\text{Number of quadrats of occurrence} \times 100}{\text{Total number of quadrats studied}}$$

$$6. \text{ Relative Basal Area} = \frac{\text{Basal area of the species} \times 100}{\text{Basal area of all species}}$$

$$7. \text{ Importance value index (Curtis and McIntosh, 1950)} \\ = \text{Relative density} + \text{Relative frequency} + \text{Relative Basal area}$$

8. Simpson's floristic diversity index (Simpson, 1949)

$$D = \frac{1}{\sum_{i=1}^s \left(\frac{n_i}{N} \right)^2}$$

where: n_i = number of individuals of the, i^{th} species.

N = total number of individuals in the plot.

S = total number of species

D = Simpson's diversity index

9. Shannon - Wiener's species similarity index (Shannon and Wiener 1963)

$$H = - \sum_{i=1}^s \left(\frac{n_i}{N} \log_{10} \frac{n_i}{N} \right)$$

where: n_i = number of individuals of the species.

N = total number of individuals in the plot.

$$\text{Equitability (E)} = \frac{H}{H_{\text{max}}}$$

Where, H_{\max} is the maximum dispersion taking into account the number of species present in the plot, and $H_{\max} = 3.219 \log_{10} S$, where S is the total number of species.

3.3.2 Regeneration survey

Regeneration attributes of the area were quantified by laying nine 1 x 1m random grids in each 10 x 10m quadrat used for the phytosociological study. Number of seedlings in each height class (< 50, 50 to 100 and > 100 cm) were counted and recorded species-wise.

3.3.3 Leaf phenology

Ten trees of *Rhizophora mucronata*, *Avicennia officinalis*, *Bruguiera cylindrica*, *Sonneratia caseolaris* and *Excoecaria agallocha* spanning the entire range of mature reproductive trees (smallest to biggest) at the site were selected and marked for easy re-find in July 2001. Six shoots (two each at top, mid and low levels of crown canopy) were selected from each tree, and tagged at the base of each branch. The number and position of leaves present at the beginning were also recorded. Monthly observations regarding scores of new production and fall of leaves and any new side branches produced thereon were counted and their positions recorded till July 2002. Weather data, namely, rainfall, temperature and humidity hours were collected from the Meteorological Observatory, Naval Base, Kochi and correlated with the phenological events.

3.3.4 Litter collection

Litter collection was made using specially designed circular litter traps (Hughes *et al.*, 1987). For each trap, four 210 cm long galvanized (2-3 mm) iron wire was used. A tripod was made using three galvanized wires. The remaining one was made into a hoop of 45 cm diameter by overlapping the ends of the wire and tying them firmly. This hoop was tied horizontally on the tripod. A plastic grain bag was placed inside the hoop with tapering end downwards (Plate 17). Each trap had a collection area of 0.16 m². Sixty such traps were prepared. Based on the distance from the sea and/or floristic attributes the study site was broadly divided into three zones (Fig. 2) and 20 traps were placed in each zone. The traps were installed randomly in the interspaces of trees on (Plate 19) 1st August 2001. Litter collection was made from each trap at monthly intervals for a one-year period from 1st September 2001 to 1st August 2002. Litter was sorted out according

to species into leaves, twigs and reproductive parts in the laboratory. The samples were then oven dried at 70°C until constant weights and the mean monthly litterfall on unit area basis (g m^{-2}) computed.

3.3.5 Litter decomposition

Standard litter bag technique was employed for characterizing litter decomposition dynamics. Freshly fallen leaves of six dominant trees and plant species of the study site namely, *Avicennia officinalis*, *Bruguiera cylindrica*, *Rhizophora mucronata*, *Sonneratia caseolaris*, *Excoecaria agallocha* and *Acanthus ilicifolius* were collected and dried under shade for approximately 2 to 3 weeks. Twenty gram samples were placed in litter bags of 20 x 25 cm size made of 4 mm nylon wire mesh. Moisture content of samples (species-wise) at the time of transfer to the bag was estimated gravimetrically. The litter bags (in five replicates) were then placed in the field at representative locations (Plate 18) in each zone on 1st August 2001. Altogether, 1080 litter bags (180 samples per species: 6 species x 3 zones x 5 replication x 12 months) were installed in the litter layer of the soil and anchored to small plastic stakes to facilitate easy refined.

At monthly intervals, starting from 1st September 2001 litter samples were retrieved from the field by carefully removing the accumulated soil and litter over the bags (Plate 20). The bags were slowly and carefully dipped in a bucket of water and gently shaken to get rid of the clay particles adhering to the residual mass. The bags were then brought to the laboratory, the extraneous material like arthropods, fine roots, and soil was separated and the residual mass oven-dried.

The contents of the bags were analyzed for oven-dry mass, nitrogen, phosphorus and potassium following Jackson (1958). In addition, the initial nitrogen, phosphorus, potassium and lignin (Van Soest, 1963) contents of litter samples were assessed species wise, following standard methods. For lignin, 1 g of leaf sample (three replicates per species) was weighed out, and 100 ml cold acid detergent solution (prepared by adding 20 g of cetyl trimethyl ammonium bromide (CTAB) to 1 L of 1 N H_2SO_4) was added. This was refluxed for 60 min. on a refluxing rack. The sample was then filtered and washed. The filtrate was dried over night and then weighed to determine the acid detergent fiber percent. Seventy two percent H_2SO_4 was poured into this dried sample and intermittently stirred at half hourly intervals for 3 h. After filtering this solution, the sample was dried over

night and weighed, which was then kept in a muffle furnace for about 3 h at 600° C and weighed at the end of this period. The difference in weight between the sample before being kept in the muffle furnace to that afterwards, gave the lignin content of the sample.

Acid detergent lignin (%)

$$= \frac{(\text{Weight of crucible + lignin}) - (\text{Weight of crucible + ash}) \times 100}{\text{Weight of sample}}$$

3.3.5.1 Nutrients remaining in the litter

Nutrient content of the decomposing leaf was calculated using the following equation:

$$\text{Percentage nutrient remaining} = (C/C_0) \times (Dm/Dm_0) \times 10^2$$

Where C is the concentration of element in the leaf litter at the time of sampling, C₀ is the concentration of the initial litter kept for decomposition, Dm is the mass of dry matter at the time of sampling, and Dm₀ is the dry matter of initial litter kept for decomposition (Bockhiem *et al.*, 1991).

3.3.6 Soil analyses

Soil attributes along the transects were measured both *in situ* and in the laboratory. *In situ* redox potential (Eh) was measured using a combination of Pt-saturated Ag-AgCl electrode (TOA electronics, Ltd., Japan) during April 2002. For taking *in situ* redox potential measurements, the electrode was immersed (5 cm to 10 cm depth) in the submerged soil and the values were recorded. The observations were taken carefully to avoid any possible disturbance to the site.

In addition, soil samples upto a depth of 15 cm were collected from three locations in a quadrat during April-May 2002. They were brought to the laboratory and air-dried. The soil samples were ground to pass through a 2 mm sieve and analyzed as follows. Soil pH and electrical conductivity using a 1:2 mixture of soil and distilled water with ELICO (LI 613) pH meter and ELICO (CM 180) conductivity bridge respectively. Total nitrogen was estimated by micro Kjeldal method using H₂SO₄ and digestion accelerator (K₂SO₄ + CuSO₄) for digestion, followed by distillation and titration against 0.02 N H₂SO₄ with 0.5 per cent bromocresol green and 0.1 per cent methyl red in 95 per cent ethanol as indicator (Jackson, 1958). Available phosphorus was estimated by Olson's method, in which phosphorus was extracted using 0.5 N ammonium fluoride (NH₄F) solution (18.5 g

solid NH_4F L^{-1} of water adjusted to pH 7) and filtered through a Whatman No. 2 filter paper after dissolving activated charcoal in it. The filtrate was analyzed on a spectrophotometer (Spectronic 20, MAKEE) using a blue colour (molybdophosphoric reagent) reagent (Jackson, 1958). Available potassium was estimated after extraction with 1 N ammonium acetate extract (57 ml glacial acetic acid diluted to 800 ml, neutralized with concentrated ammonium hydroxide to pH 7 and diluted to 1 L) flame photometrically. Sodium was estimated using a magnesium uranyl acetate procedure and estimated using a flame photometer ELICO (CL 361).

3.4 Statistical analysis

Density and basal area of the stand and that of the individual species along the transect were analyzed using Repeated Measure ANOVA in SPSS 7.5 statistical package with distance (12 distances, *i.e.* 100 m to 1200 m) as within-subject variable and species (both mangroves and mangrove associates) and replications (three transects) as between subject variables. Data on stand density and regeneration counts were log transformed before the analysis. Regeneration data (seedling counts for different height classes) were also analysed using Repeated Measure ANOVA in a similar way.

The nature of interrelationships between stocking level (species wise) and soil parameters along the edge-to-interior transect gradient were assessed using factor analysis (principal component analysis) in SPSS 7.5 statistical package. Linear regression models were fitted to the data on species density and soil attributes to evaluate the nature of interdependence among them.

Frequency distributions (height and diameter) of important mangrove species (> 10 cm GBH) were compared using Page's *L* (trend) test (Meddis, 1975). In this method, the species were considered as matched sets and diameter and height classes were considered as groups (*y*). All the values in groups of each species were ranked in ascending order and the sum of the ranks (*R*) in each groups were calculated. The *L* value (sum of $R \cdot y$) was compared with the table values. For large *n* and *k* values, *Z* was estimated as follows.

$$Z = \frac{12L - 3nk(k+1)^2}{k \sqrt{(n(k^2 - 1)(K+1)}}$$

were: k = number of groups

n = number of matched sets of scores

Soil and phenological data (leaf production, leaf fall, number of old leaves, number of new leaves, number of scars and number of total leaves) were analysed using one-way ANOVA in MSTAT (version 1.2) statistical package. The derived means were compared using the Duncan's Multiple Range Test (DMRT). Phenological attributes were also related to the weather parameters (max. and min. temperatures, rainfall and relative humidity) using Carl Pearson's correlation in MSTAT.

The litterfall data were analyzed using split plot ANOVA involving zones (three zones- main plots), months (12 months - sub plots) and traps (20 in each zone - replications) in MSTAT (version 1.2) followed by Duncan's Multiple Range Test (DMRT) for mean separation.

3.4.1 Decay rate coefficient

The model for constant potential weight loss (Olson, 1963) represented by the equation below was fitted on the data on mass disappearance.

$$x/x_0 = e^{-kt}$$

Where x is the weight remaining at time t , x_0 is the original mass, e is the base of the natural logarithm, k is the decay rate coefficient and t is the time. The decay rate coefficient (k) was estimated by fitting the exponential decay function on the proportion of the original mass remaining (x/x_0) for each species in each zone for 12 months in SPSS 7.5 statistical package. Half lives ($t_{0.5}$) of the decomposing litter were estimated from the k value using the equation.

$$\begin{aligned} t_{0.5} &= \ln(0.5)/-k \\ &= -0.693/-k \end{aligned}$$

Decay rate coefficients (k) were also compared using two factor split plot ANOVA in MSTAT (version 1.2) with zone as main plot factor and species as sub plot factor. Nutrient release was analyzed with three factor split plot ANOVA, with zone and species as factorial main plot factors and months as the sub plot factor.

Results

4. RESULTS

Vegetation at Puduvely consists of seven true mangroves and 18 mangrove associates (Table 2). Among the mangroves *Avicennia officinalis* was predominant in most areas (Plate 3). In some areas, where the *Avicennia sp* opens the canopy, there has been an extensive growth of *Acanthus ilicifolius* covering the entire ground (Plate 6). In areas where *Avicennia officinalis* completely covers the canopy, restricted distribution of *Avicennia marina* has been observed (Plate 4). Also codominant and understory growth of *Bruguiera cylindrica* (shade loving) (Plate 7) and *Rhizophora mucronata* (very sparse) with lianas of *Derris trifoliata* Lour. were also found (Plate 5) along with them. Mangrove associates like *Thespesia sp* and *Hibiscus tiliaceus* L. were found towards the land-ward side.

4.1 Zonation pattern and the floristic and edaphic attributes

A comparison of the data presented in Fig.3 implies that the total number of species decreased along the sea-land ward transect. Broadly, three zones could be delineated on the basis of species diversity and distribution. Zone I (0-300 m) consisting of six true mangrove flora (*Avicennia sp* and *Sonneratia sp*) and 16 mangrove associates had the highest species diversity (Table 2, Plates 1 and 2). Zone II (300-800 m) has had five true mangrove species and was essentially dominated by *Avicennia officinalis*. However, a few scattered trees of *Avicennia marina*, *Bruguiera cylindrica* and *Derris trifoliata* (climber) besides the spiny scrub *Acanthus ilicifolius* were also present in this zone. In zone III (800-1200 m) only *Avicennia* and *A. ilicifolius* species were present. Both *A. officinalis* and *A. ilicifolius* were distributed along the entire transect length.

Simpson's floristic diversity index (D) decreased from Zone I (0.786) to Zone III (0.310) (Table 3), implying that higher mangrove floristic diversity was observed in the distal regions. Shannon Wiener's diversity index also showed a similar trend with H' values decreasing from 2.9 to 0.56 in Zone I and Zone III.

Phytosociological parameters such as stand density and basal area along the distance from the sea are presented in Tables 4-6, Fig.4 and 5. Although species richness and diversity (Table 3) decreased along the landward transect the

Table 2. Species distribution along a land-ocean interface to land interior transect at Puduvelyppu.

	Species	Habit	Distance from the sea (m)											
			100	200	300	400	500	600	700	800	900	1000	1100	1200
True mangroves	<i>Acanthus ilicifolius</i> L.	Shrub/ herb	x			x	x	x	x	x	x	x	x	x
	<i>Acrostichum aureum</i> L.	Fern												x
	<i>Avicennia marina</i> (Forsk.) Vierh.	Tree	x	x		x		x	x	x	x	x		
	<i>Avicennia officinalis</i> Linn.	Tree	x	x	x	x	x	x	x	x	x	x	x	x
	<i>Bruguiera cylindrica</i> (L) Bl.	Tree			x	x	x	x	x	x				x
	<i>Bruguiera gymnorrhiza</i> (L.) Lamk.	Tree	x	x										x [#]
	<i>Excoecaria agallocha</i> L.	Tree	x	x	x	x	x	x	x				x [#]	x [#]
	<i>Rhizophora mucronata</i> Lam.	Tree			x								x [#]	x [#]
	<i>Sonneratia alba</i> L.	Tree			x									
	<i>Sonneratia caseolaris</i> L.	Tree	x	x	x									
Mangrove associates	<i>Acacia auriculiformis</i>	Tree	x [#]											
	<i>Barringtonia racemosa</i> (L) Sprangel.	Tree	x											
	<i>Calophyllum inophyllum</i> L.	Tree	x	x										
	<i>Casuarina equisetifolia</i>	Tree	x [#]	x	x									
	<i>Carex sp.</i>	Grass	x											
	<i>Cerbera odollam</i> Gaertn	Tree	x											
	<i>Clerodendron inerme</i> (L.) Gaertn.	Shrub	x											
	<i>Cynodan dactylon</i> Pers.	Grass	x											
	<i>Cyperus sp.</i>	Grass	x											
	<i>Derris trifoliata</i> Lour.	Climber	x		x		x	x		x	x	x		
	<i>Erythrina indica</i>	Tree	x		x									
	<i>Fimbristylis sp.</i>	Grass	x											
	<i>Hibiscus tiliaceus</i> L.	Tree												x
	<i>Ipomoea pes-caprae</i> (L.) Sweet.	Herb	x											
	<i>Physalis minima</i>	Shrub	x											
	<i>Premna obtusifolia</i> Poir.	Shrub	x	x										
	<i>Sesbania grandiflora</i>	Shrub	x	x										
	<i>Thespesia populnea</i> L.	Tree												x
			Zone I			Zone II			Zone III					

Note: # Tree species were artificially planted.
 x Indicates occurrence of the species

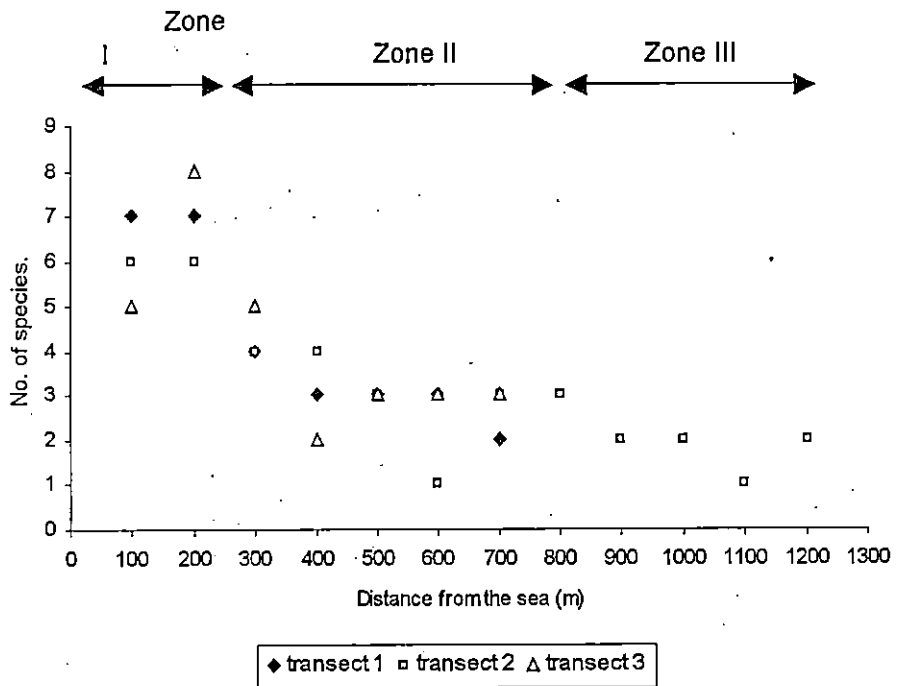


Fig. 3. Distribution of species diversity along the gradient from the sea-land interface to the land interior.

Table 3. Diversity indices of mangrove species (trees and shrubs) in different zones

Zones	Simpson's floristic diversity index	Shannon-Wiener's similarity index		
		H	H _{max}	Equitability
Zone I	0.786	2.9	3.20	0.91
Zone II	0.492	0.98	2.62	0.37
Zone III	0.310	0.56	1.72	0.09

phytosociological attributes such as density (1125 to 5478 no.ha⁻¹), abundance (21.3 to 80.5), percentage frequency (88 to 100%) and basal area (13.57 to 49.00 m² ha⁻¹) of important tree species increased from Zone I to Zone III.

Among the true mangrove flora, *A. officinalis* and *A. marina* had the highest IVI (Importance Value Index) in Zone III. However, *B. cylindrica* was abundant in zone II as a codominant species and *Sonneratia caseolaris* in Zone I. The density and basal area of *A. officinalis* and *A. marina* increased along the distance from sea. However, the basal area of *B. cylindrica* and *Excoecaria agallocha* decreased and stand density of both did not follow any predictable trends.

Mangrove associates were distributed only in the distal region (Zone I), with their densities ranging from 44 to 666 individuals ha⁻¹. Among the mangrove associates, *Calophyllum inophyllum* had the highest IVI and percentage frequency followed by *Barringtonia racemosa*, *Casuarina equisetifolia* (planted) and *Cerbera odollam*.

The diameter and height frequency distribution of the species varied significantly with Pages L test values of 5.57 and 3.88 respectively (Table 7, 8 and Fig. 6). Mangrove species were predominantly present in lower size classes, implying an inverse 'J' shaped distribution pattern (Fig. 6).

Soil attributes

Soil attributes differed significantly along the sea-land ward transect ($p < 0.01$). Data presented in Table 9 and Fig.7 show that electrical conductivity (51 to 86%), N (90 to 94%), K (15 to 71%) and Na (54 to 60%) increased markedly along the sea coast to land ward transect. Conversely, soil pH declined (45 to 80%) substantially along the transect. Available P and redox potential (Eh) however did not show any predictable pattern.

The association between soil parameters and distance from the ocean-land interface was evaluated using Carl Pearson's correlation coefficient (r). Electrical conductivity ($r = 0.895^{**}$) and the concentration of N ($r = 0.943^{**}$), K ($r = 0.849^{**}$) and Na ($r = 0.748^{**}$) were positively correlated to distance from the edge of the ocean. However, soil pH ($r = -0.903^{**}$) and Eh ($r = 0.615^{*}$) showed negative relationships (Table 10).

Table 4. Phytosociological attributes of mangrove trees and shrubs in different zones at Pudukkottai

Species	Density (no. ha ⁻¹)			Relative Density			Abundance			Percentage Frequency			Basal Area (BA) (m ² ha ⁻¹)			Relative Basal Area (RBA)			Importance Value Index (IVI)			
	Z ₁	Z ₂	Z ₃	Z ₁	Z ₂	Z ₃	Z ₁	Z ₂	Z ₃	Z ₁	Z ₂	Z ₃	Z ₁	Z ₂	Z ₃	Z ₁	Z ₂	Z ₃	Z ₁	Z ₂	Z ₃	
True Mangroves																						
<i>Avicennia marina</i>	625.8	2014.1	1600	12.9	26.6	18.6	8.7	47.0	20.0	61.1	41.7	50.0	0.89	9.92	45.60	9.5	20.9	44.9	83.6	89.2	113.5	
<i>Avicennia officinalis</i>	741.5	2942.1	6960	21.3	58.1	80.9	10.6	28.6	43.5	88.8	100.0	100.0	1.33	25.52	54.76	45.8	68.5	55.0	125.4	226.6	236.0	
<i>Bruguiera cylindrica</i>	-	657.9	40	-	17.8	11.5	-	8.3	1.0	-	80.5	25.0	-	2.62	0.05	-	13.0	0.05	-	111.3	25.5	
<i>Excoecaria agallocha</i>	1114.4	143.6	-	25.6	4.3	-	21.2	2.3	-	7.7	63.9	-	2.48	0.57	-	25.3	3.3	-	128.1	71.5	-	
<i>Rhizophora mucronata</i>	32.1	-	-	1.0	-	-	1.5	-	-	20.8	-	-	0.10	-	-	0.6	-	-	22.5	-	-	
<i>Sonneratia alba</i>	128.6	-	-	2.8	-	-	3.0	-	-	33.3	-	-	0.18	-	-	1.7	-	-	37.8	-	-	
<i>Sonneratia caseolaris</i>	540.1	-	-	12.0	-	-	6.3	-	-	88.9	-	-	1.46	-	-	16.0	-	-	116.9	-	-	
Mangrove associates																						
<i>Acacia auriculiformis</i>	85.72	-	-	1.8	-	-	2.0	-	-	33.3	-	-	0.22	-	-	2.1	-	-	37.2	-	-	
<i>Barringtonia racemosa</i>	214.3	-	-	5.5	-	-	3.5	-	-	66.7	-	-	0.48	-	-	5.6	-	-	77.8	-	-	
<i>Calophyllum inophyllum</i>	655.9	-	-	14.8	-	-	9.3	-	-	72.2	-	-	1.39	-	-	15.3	-	-	102.3	-	-	
<i>Casuarina equisetifolia</i>	184.3	-	-	4.1	-	-	3.8	-	-	55.5	-	-	0.29	-	-	3.0	-	-	62.7	-	-	
<i>Cerbera odollam</i>	42.9	-	-	0.8	-	-	1.0	-	-	50.0	-	-	0.01	-	-	0.1	-	-	51.0	-	-	
<i>Physalis minima</i>	42.9	-	-	0.9	-	-	1.0	-	-	33.3	-	-	-	-	-	-	-	-	34.2	-	-	
<i>Premna obtusifolia</i> Poir.	42.9	-	-	1.1	-	-	1.0	-	-	41.7	-	-	0.14	-	-	1.6	-	-	44.3	-	-	
<i>Sesbania grandiflora</i>	51.4	-	-	1.7	-	-	1.5	-	-	41.7	-	-	0.56	-	-	7.6	-	-	50.9	-	-	

Z I: Zone I, Z II: Zone II, Z III: Zone III.

Table 5. Density (no. ha⁻¹) of mangrove trees and shrubs (GBH ≥ 10 cm) along the distance from the sea land-land interface towards the land interior

Species	Distance from the sea (m)											
	100	200	300	400	500	600	700	800	900	1000	1100	1200
<i>Avicennia officinalis</i> .	793 ^a C(12)	831 ^{aC} (15)	932 ^{aC} (85)	3387 ^{aD} (56)	2569 ^b D(105)	1548 ^{aBC} 85)	2629 ^{aD} (86)	1904 ^{aBC} (102)	2629 ^{aB} (59)	99 ^{bD} (12)	8127 ^{aA} (56)	5247 ^{aAB} (77)
<i>Avicennia marina</i>	70 ^{bC} (12)	101 ^{abC} (6)	-	6 ^{cD} (1)	-	22 ^{abCD} (2)	17 ^{bcCD} (3)	99 ^{bC} (12)	890 ^{aB} (86)	3089 ^{aA} (88)	-	-
<i>Bruguiera cylindrica</i>	-	-	12 ^{abB} (1)	397 ^{abB} (45)	1023 ^{aCD} (45)	7 ^{cD} (1)	68 ^{bC} (1)	99 ^{bBC} (26)	-	-	-	-
<i>Rhizophora mucronata</i>	6 ^{bB} (2)	-	27 ^{abA} (2)	-	-	-	-	-	-	-	-	-
<i>Excoecaria agallocha</i>	73 ^{bB} (16)	911 ^{aA} (12)	6 ^{bD} (1)	36 ^{bcC} (1)	36 ^{bcC} (2)	34 ^{bC} (6)	44 ^{bBC} (11)	-	-	-	-	-
<i>Sonneratia caseolaris</i>	67 ^{bB} (13)	416 ^{aA} (52)	34 ^{abC} (2)	-	-	-	-	-	-	-	-	-
<i>Acacia auriculiformis</i>	4 ^{bA} (1)	4 ^{abA} (1)	5 ^{bA} (1)	-	-	-	-	-	-	-	-	-
<i>Casuarina equisetifolia</i>	94 ^{bB} (11)	114 ^{aAb} (23)	4 ^{bC} (1)	-	-	-	-	-	-	-	-	-
<i>Sonneratia alba</i>	-	-	6 ^{bA} (2)	-	-	-	-	-	-	-	-	-
<i>Calophyllum inophyllum</i>	5 ^{bB} (0)	274 ^{aA} (28)	-	-	-	-	-	-	-	-	-	-
<i>Cerbera odollam</i>	4 ^{bA} (1)	-	-	-	-	-	-	-	-	-	-	-
<i>Barringtonia racemosa</i>	6 ^{bB} (0)	43 ^{abA} (13)	-	-	-	-	-	-	-	-	-	-
<i>Premna obtusifolia</i>	4 ^{bA} (1)	4 ^{abA} (1)	-	-	-	-	-	-	-	-	-	-
<i>Sesbania grandiflora</i>	-	5 ^{abA} (1)	4 ^{bA} (1)	-	-	-	-	-	-	-	-	-
Total	1125 ^b	2702 ^{cD}	1028 ^D	3826 ^c	3628 ^c	1611 ^b	2758 ^{cD}	2102 ^{cD}	3521 ^c	3188 ^c	8127 ^A	5247 ^B
Comparison between species: p	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01
Comparison between distances: p	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01

Values in parenthesis indicate standard errors

Means followed by the same lower case letters are not significantly different within the same column

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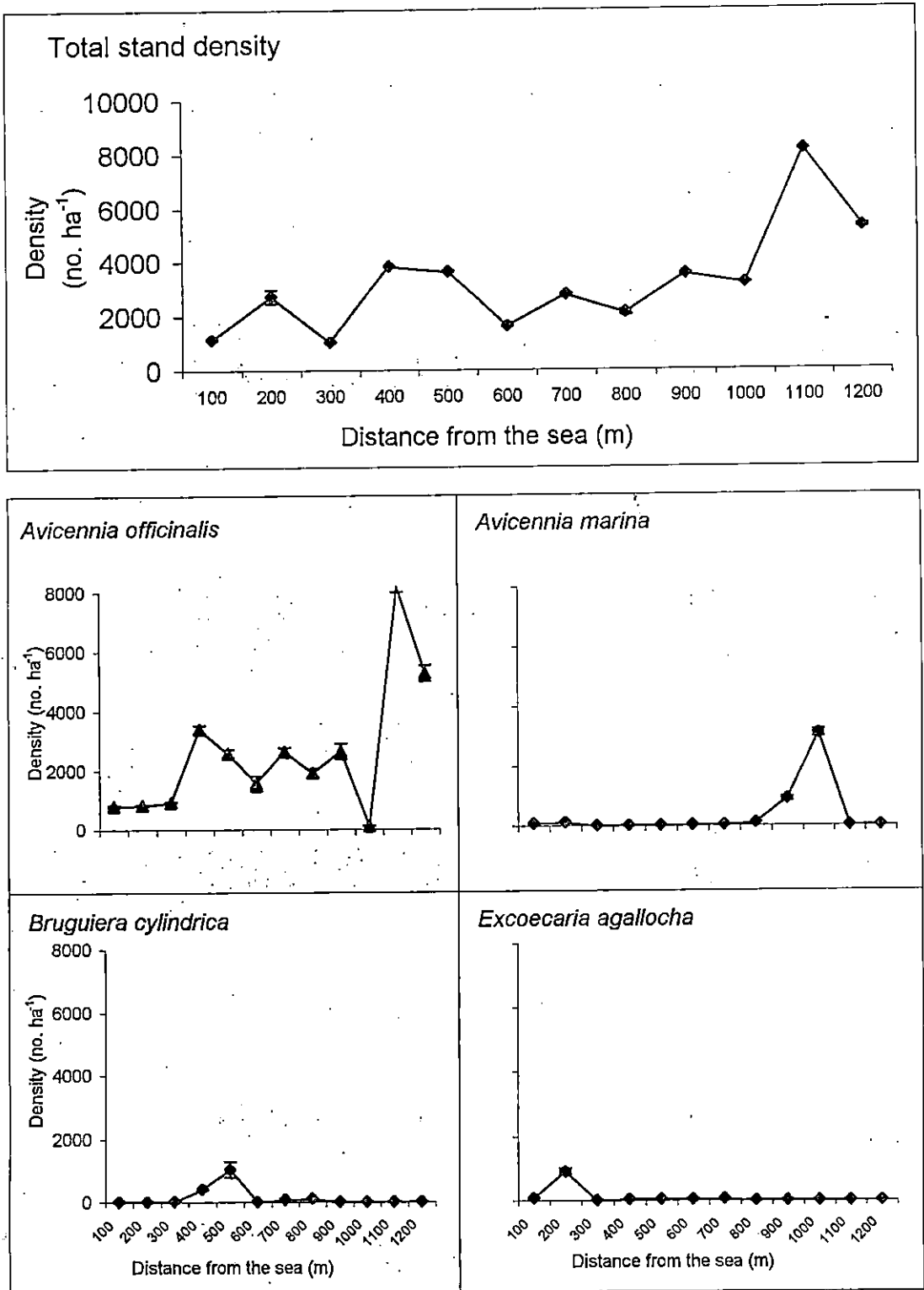


Fig. 4 Total stand density and stand densities of predominant mangrove species in the mangrove forest of Pudukkottai from the sea-land interface to the land interior (Error bars indicate standard errors)

Table 6. Basal area ($\text{m}^2 \text{ha}^{-1}$) of mangrove trees and shrubs ($\text{GBH} \geq 10 \text{ cm}$) along the distance from the sea-land interface towards the land interior

Species	Distance from the sea (m)											
	100	200	300	400	500	600	700	800	900	1000	1100	1200
<i>Avicennia officinalis</i>	1.68 ^{aD} (0.472)	1.22 ^{bD} (0.12)	7.33 ^{abCD} (1.23)	37.43 ^{aB} (4.56)	29.70 ^{aBC} (4.89)	12.66 ^{bCD} (2.36)	18.34 ^{aC} (3.65)	38.19 ^{aB} (4.39)	34.42 ^{aB} (5.45)	2.32 ^{bD} (0.32)	53.61 ^{aA} (5.29)	49.26 ^{aA} (5.84)
<i>Avicennia marina</i>	0.92 ^{bcdD} (0.126)	1.78 ^{abD} (0.03)	-	4.63 ^{bC} (1.23)	-	59.32 ^{aAB} (4.38)	9.36 ^{abC} (1.32)	0.39 ^{cD} (0.02)	32.54 ^{bB} (5.64)	81.48 ^{aA} (4.56)	-	-
<i>Bruguiera cylindrica</i>	-	-	12.11 ^{aA} (2.13)	4.19 ^{cB} (0.56)	2.35 ^{bBC} (0.89)	1.22 ^{cC} (0.15)	1.29 ^{bC} (0.29)	0.88 ^{bC} (0.01)	-	-	-	-
<i>Rhizophora mucronata</i>	-	-	0.43 ^{cA} (0.02)	-	-	-	-	-	-	-	-	-
<i>Excoecaria agallocha</i>	1.13 ^{bcdB} (0.66)	4.84 ^{aA} (1.12)	2.13 ^{bcB} (0.13)	0.93 ^{bB} (0.02)	1.08 ^{bB} (0.25)	0.64 ^{cC} (0.05)	0.94 ^{bC} (0.12)	-	-	-	-	-
<i>Sonneratia caseolaris</i>	3.00 ^{aA} (0.89)	1.12 ^{bB} (0.02)	0.51 ^{cC} (0.01)	-	-	-	-	-	-	-	-	-
<i>Acacia auriculiformis</i>	0.93 ^{bcdB} (0.07)	0.91 ^{bB} (0.03)	3.52 ^{bcA} (0.59)	-	-	-	-	-	-	-	-	-
<i>Casuarina equisetifolia</i>	1.48 ^{bcdAB} (0.09)	2.95 ^{abA} (1.03)	0.32 ^{cB} (0.02)	-	-	-	-	-	-	-	-	-
<i>Sonneratia alba</i>	-	-	0.34 ^{cA} (0.03)	-	-	-	-	-	-	-	-	-
<i>Calophyllum inophyllum</i>	0.76 ^{cdA} (0.05)	0.67 ^{bB} (0.06)	-	-	-	-	-	-	-	-	-	-
<i>Cerbera odollam</i>	0.02 ^{dA} (0.00)	-	-	-	-	-	-	-	-	-	-	-
<i>Barringtonia racemosa</i>	0.93 ^{bcdA} (0.02)	0.49 ^{bB} (0.02)	-	-	-	-	-	-	-	-	-	-
<i>Premna obtusifolia</i>	0.29 ^{cdA} (0.00)	0.3 ^{bA} (0.01)	-	-	-	-	-	-	-	-	-	-
<i>Sesbania grandiflora</i>	2.43 ^{abB} (0.01)	-	-	-	-	-	-	-	-	-	-	-
Total	13.57 ^D	14.28 ^D	26.69 ^C	47.18 ^B	33.13 ^C	73.84 ^A	29.83 ^C	39.46 ^{BC}	66.96 ^{AB}	83.8 ^A	53.61 ^B	49.26 ^B
Comparison between species: p	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01
Comparison between distances : p	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01

Values in parenthesis indicate Standard Error

Means followed by the same lower case superscript are not significantly different within the same column

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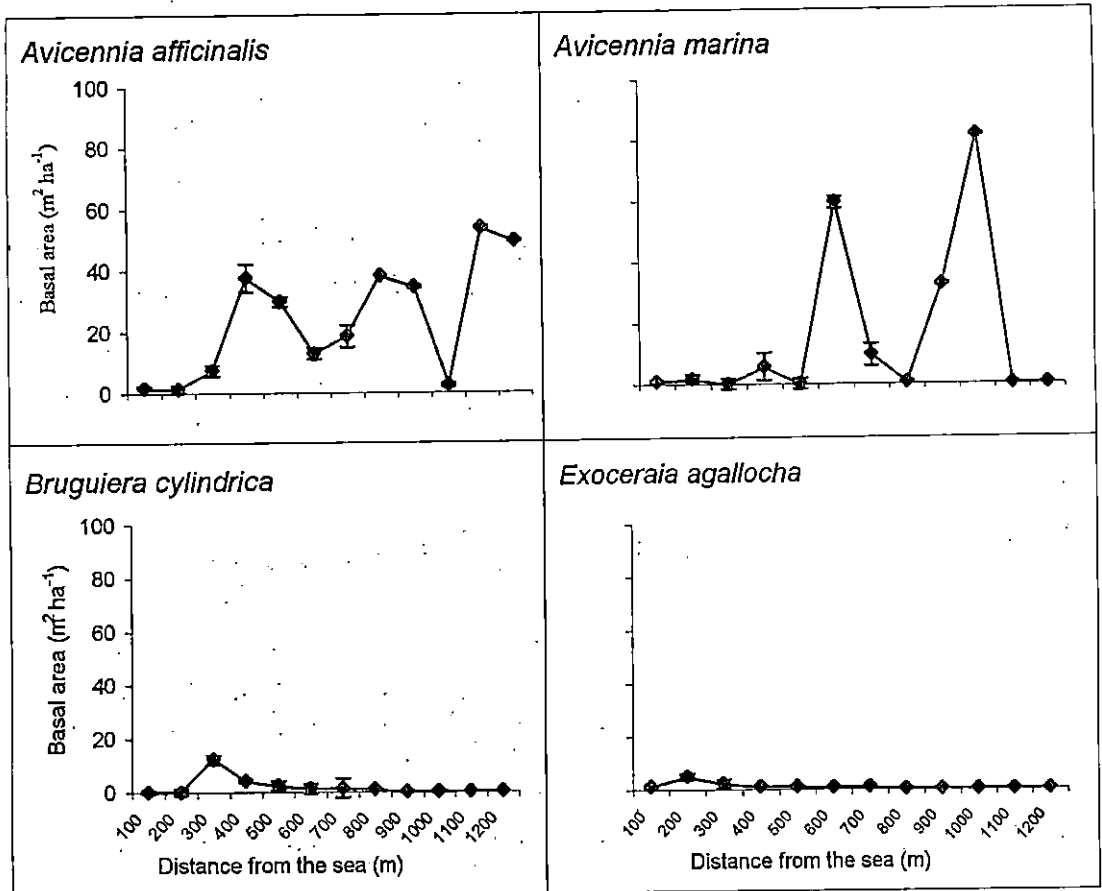
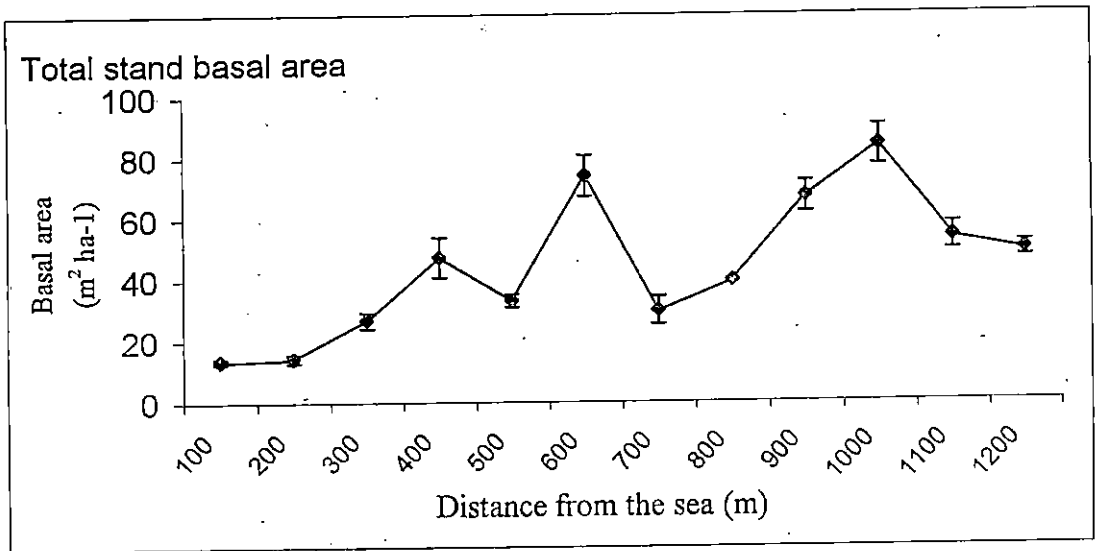


Fig. 5 Total stand basal area and basal areas of predominant mangrove species in the mangrove forest of Puduvely from the sea-land interface to the land interior (Error bars indicate standard errors)

Table 7. Frequency distribution (%) of different mangrove and mangrove associate tree species along the diameter classes

Species	Distance classes (cm)						
	1-5	6-10	11-15	16-20	21-25	26-30	31-35
<i>Avicennia officinalis</i>	31.3	43	15.7	7.6	1.8	0.36	-
<i>Avicennia marina</i>	46.6	33.3	9.6	3.7	4.4	0.7	1.5
<i>Bruguiera cylindrica</i>	85	5	5	5	-	-	-
<i>Excoecaria agallocha</i>	67.8	29.4	2.9	-	-	-	-
<i>Sonneratia caseolaris</i>	73.3	26.7	-	-	-	-	-
<i>Acacia auriculiformis</i>	50	50	-	-	-	-	-
<i>Casuarina equisetifolia</i>	16.6	83.3	-	-	-	-	-
<i>Calophyllum inophyllum</i>	60	40	-	-	-	-	-
<i>Cerbera odollam</i>	100	-	-	-	-	-	-

Pages L test value, $Z = 5.567^{**}$ ($n = 9, k = 7$)
 Values are expressed in per cent frequency (%)

Table 8. Frequency distribution (%) of different mangrove and mangrove associate tree species along the height classes

Species	Height classes (m)		
	1-4	5-8	9-12
<i>Avicennia officinalis</i>	54.4	42.7	2.9
<i>Avicennia marina</i>	66	33	1.5
<i>Bruguiera cylindrica</i>	85	15	-
<i>Excoecaria agallocha</i>	97	3	-
<i>Sonneratia caseolaris</i>	80	20	-
<i>Acacia auriculiformis</i>	-	100	-
<i>Casuarina equisetifolia</i>	77.8	22.2	-
<i>Calophyllum inophyllum</i>	100	-	-
<i>Cerbera odollam</i> Gaertn	100	-	-

Pages L test value, $Z = 3.88^{**}$ ($n = 9, k = 3$)
 Values are expressed in per cent frequency (%)

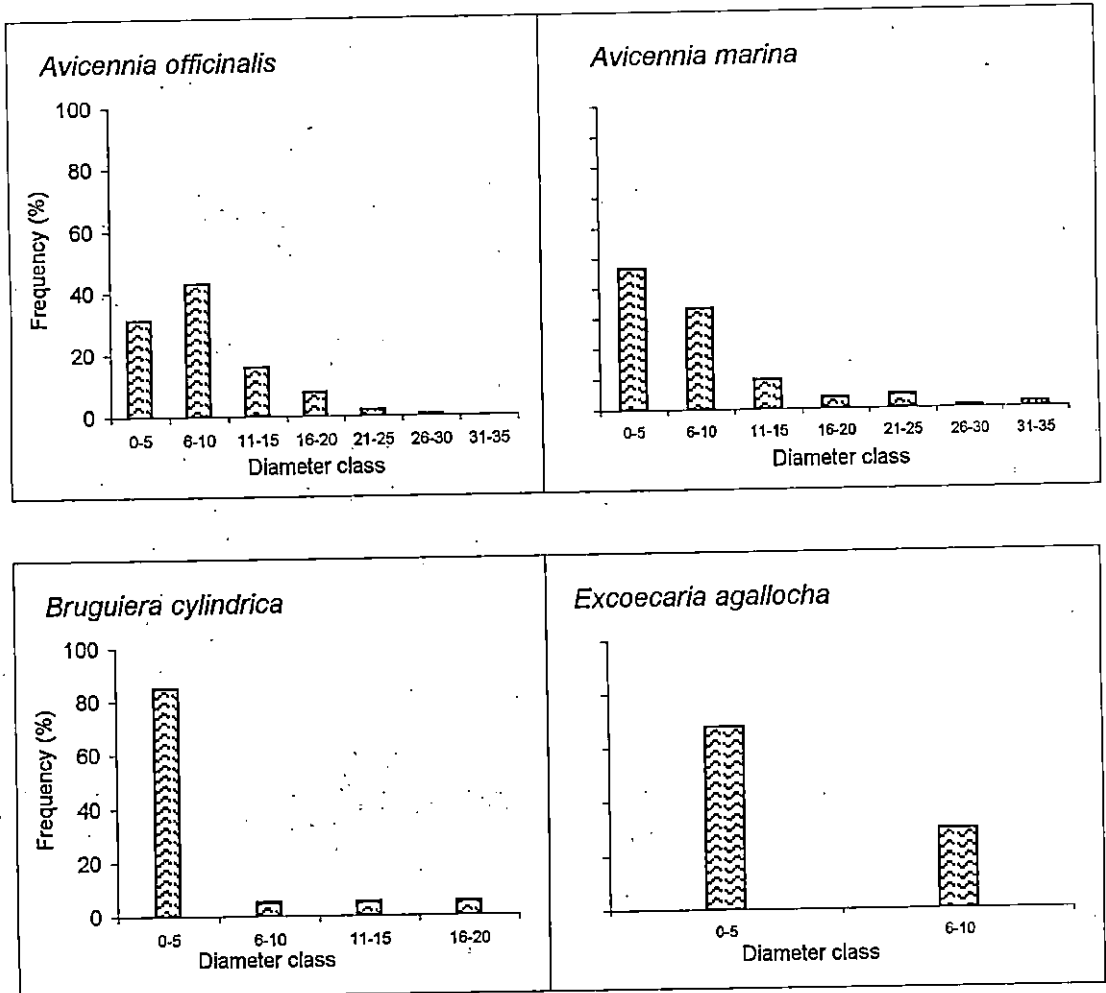


Fig. 6 Frequency distribution (%) of different mangrove species along the diameter class at Puduvely mangrove forest

Table 9. Soil chemical properties (15 cm depth except for *in situ* redox potential which is 5 - 10 cm) along the distance from the sea-land interface to the land interior.

Distance from the sea (m)	Electrical conductivity (dS m ⁻¹)	pH	N (mg kg ⁻¹)	P (mg kg ⁻¹)	K m (mg kg ⁻¹)	Na (mg kg ⁻¹)	<i>In situ</i> redox potential (mV)
100	2.18 ^c ± 0.12	7.75 ^a ± 0.21	00.00 [#]	0.00 [#]	0.00 [#]	0.00 [#]	-
200	4.58 ^c ± 0.75	6.66 ^{ab} ± 0.55	504 ^d ± 302.4	4.16 ^d ± 1.32	379.6 ^d ± 6.32	3512 ^c ± 958.2	-
300	5.74 ^c ± 4.36	7.76 ^a ± 0.28	352.8 ^b ± 64	73.21 ^b ± 25.6	3521 ^c ± 2788.2	3758 ^c ± 1256.1	-295 ^b ± 12.5
400	4.85 ^c ± 0.30	7.95 ^a ± 0.06	1008 ^{bc} ± 365.4	63.98 ^{bc} ± 28.61	2701.1 ^c ± 757.82	6956 ^b ± 956.2	-260 ^c ± 25.2
500	2.61 ^c ± 0.42	6.72 ^{ab} ± 0.83	1449 ^a ± 856	163.69 ^a ± 15.22	5041.6 ^b ± 1477.94	7986 ^a ± 1265.2	-380 ^a ± 12.3
600	12.33 ^b ± 1.60	5.31 ^b ± 0.43	2759.4 ^c ± 1026.9	40.47 ^c ± 13.95	5740.6 ^{ab} ± 547.68	7171 ^{ab} ± 1568.2	-260 ^c ± 15.3
700	12.42 ^b ± 2.93	5.34 ^b ± 0.59	5455.8 ^a ± 4087.12	184.72 ^a ± 65.23	6002 ^a ± 900.21	8365 ^a ± 1256.2	-200 ^d ± 26.5
800	17.25 ^a ± 4.54	4.78 ^{bc} ± 0.29	8044 ^{ab} ± 3670	62.50 ^{bc} ± 32.21	5271 ^b ± 456.32	7850 ^a ± 1455	-240 ^c ± 25.3
900	16.53 ^{ab} ± 1.20	4.56 ^{bc} ± 0.26	10684.0 ^a ± 4034.1	68.75 ^b ± 29.46	5302.4 ^b ± 804.16	7562 ^{ab} ± 256.2	-320 ^{ab} ± 36.5
1000	18.53 ^a ± 2.6	5.01 ^b ± 0.27	11560.2 ^a ± 3652.2	96.73 ^b ± 36.5	6502 ^a ± 625.3	7485 ^{ab} ± 1125.3	-260 ^c ± 23.5
1100	15.46 ^{ab} ± 0.35	4.46 ^{bc} ± 0.53	9561.2 ^{ab} ± 2354.2	193.75 ^a ± 65.2	5382 ^b ± 256.2	7584 ^{ab} ± 965.3	-340 ^a ± 56.2
1200	16.23 ^{ab} ± 0.39	4.21 ^c ± 0.21	10546.2 ^a ± 3654.2	78.84 ^b ± 28.9	6442 ^a ± 1156.2	7658 ^{ab} ± 956.2	-295 ^b ± 22.3
p ≤	0.01	0.01	0.01	0.01	0.01	0.01	0.01

0.00[#] values in N, P, K and Na is because of sandy soil

Values after ± are standard deviations

Means followed by the lower case superscript are not significantly different within the same column

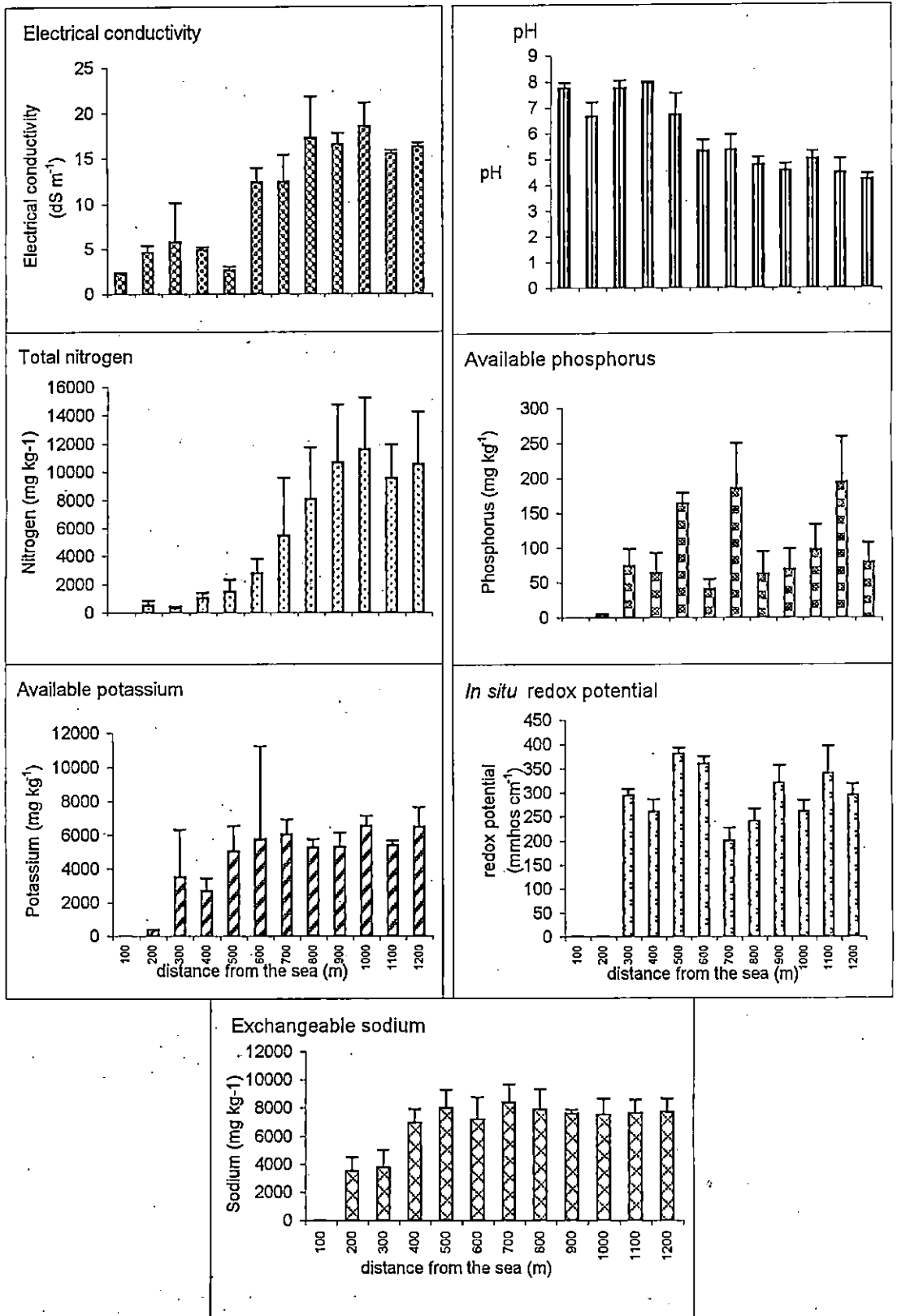


Fig. 7 Soil attributes along the sea-land interface to the land interior in the mangrove forest of Puduvypu
(Error bars are standard deviations)

Interestingly, population density of mangrove species was strongly dependent on *A. officinalis* density, implying the predominance of that species. Density, however, increased as the distance from land-ocean interface increased and was apparently related to available soil P ($r = 0.581^*$ and 0.600^* respectively for *A. officinalis* and total density). While density of *E. agallocha* was positively correlated with soil Eh ($r = 0.667^*$) and negatively correlated with K ($r = -0.608^*$), other species did not evince any significant relationships in this respect.

The interrelationships between population density and various edaphic attributes were evaluated by regressing the data on total density and density of the component species on soil physico-chemical properties and distances from the land-ocean interface (Table 11). R^2 values in general were modest, implying a weak relationship. Highest R^2 values ($p < 0.05$) were noted in respect of total stand density and distance ($R^2 = 0.45$). This was followed by *E. agallocha* density with Eh ($R^2 = 0.44$) and K ($R^2 = 0.37$) and *A. officinalis* density with available P ($R^2 = 0.36$) and distance ($R^2 = 0.34$).

4.2 Natural regeneration of mangrove species

Data on regeneration dynamics of important mangrove species at Pudukkottai are presented in Table 12. Regeneration density showed profound variability among species ($p < 0.01$) and distance along the land-ocean transect ($p < 0.01$). In general, 700-800 m from the land-ocean interface represented the zone with highest regeneration density (196-348 seedlings 100 m^{-2}) and it decreased both along the seaward and landward sides. The regenerant densities of individual species also showed considerable variations in all three size classes. Most of the seedlings of *Avicennia* species (70%) were in the lower height (< 50 cm) category (Plate 9). Whereas, *Bruguiera cylindrica* had well-established seedlings in the higher size classes (70% of seedlings in 50-100 cm and > 100 cm height class) (Plate 8).

As regards to smaller seedlings (< 50 cm in height), their density ranged from 32 to 348 seedlings 100 m^{-2} . *Avicennia officinalis* dominated this category with 59-348 seedlings 100 m^{-2} followed by *A. marina* with 63 to 196 seedlings 100 m^{-2} . Among other dominant species at the site, *B. cylindrica* had 61 to 89 seedlings 100 m^{-2} .

Table 10. Correlation matrix linking species stand densities with soil edaphic attributes and distance along the transect in Pudukkottai.

	AVM density	AVO density	BRC density	Total density	Distance	EC	Eh	EXA density	K	N	Na	P	pH
AVM density	1.00												
AVO density	-0.359	1.00											
BRC density	-0.189	0.034	1.00										
Total density	-0.023	0.911**	0.070	1.00									
Distance	0.347	0.586*	-0.199	0.667*	1.00								
EC	0.466	0.295	-0.477	0.369	0.895**	1.00							
Eh	-0.086	-0.473	-0.382	-0.456	-0.615*	-0.404	1.00						
EXA density	-0.121	-0.269	-0.114	-0.124	-0.455	-0.373	0.667*	1.00					
K	0.313	0.341	0.033	0.365	0.849**	0.776**	-0.780	-0.608*	1.00				
N	0.527	0.400	-0.338	0.537	0.943**	0.397**	-0.445	-0.380	0.735**	1.00			
Na	0.167	0.429	0.262	0.483	0.748**	-0.635*	-0.757**	-0.393	0.873**	0.611*	1.00		
P	0.003	0.581*	0.351	0.600*	0.512	0.271	-0.639*	-0.418	0.622*	0.358	0.650*	1.00	
pH	-0.271	-0.435	0.334	-0.498	-0.903**	-0.913**	0.386	0.232	-0.763**	-0.894**	-0.663*	-0.361	1.00

(2 tailed significance, n= 12)

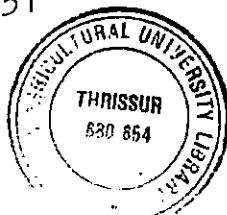
AVM: *Avicennia marina*, AVO: *Avicennia officinalis*, BRC: *Bruguiera cylindrica*, EXA: *Excoecaria agallocha*, EC: Electrical conductivity (dS m^{-1}), Eh: *In situ* redox potential (mV), K: Available potassium (mg kg^{-1}), N: Available nitrogen (mg kg^{-1}), Na: Exchangeable sodium (mg kg^{-1}), P: Available phosphorus (mg kg^{-1}).

Table 11. Regression linking density of important mangrove species to the distance from the sea and other soil attributes

Stand Density	Parameters	Intercept	SEE	Slope	SEE	R ²	p
Total density	Distance	872.99	943.16	3.63	1.29	0.45	0.018
	EC	1994.10	1131.54	115.50	92.10	0.14	0.238
	pH	7312.19	2306.03	694.25	382.54	0.25	0.099
	N	2059.79	768.18	0.23	0.11	0.29	0.072
	P	1654.80	816.88	18.37	7.74	0.36	0.038
	K	1839.51	1253.51	0.32	0.26	0.13	0.244
	Na	874.55	1447.46	0.37	0.21	0.23	0.111
	Eh	1471.14	1209.01	-7.42	4.58	0.24	0.136
<i>Avicennia officinalis</i>	Distance	191.68	117.43	3.64	1.59	0.34	0.045
	EC	1427.70	1328.10	105.10	108.08	0.09	0.352
	pH	6628.53	2733.30	-692.74	453.42	0.19	0.158
	N	1560.97	953.04	0.19	0.14	0.16	0.198
	P	814.11	949.10	20.30	8.98	0.34	0.047
	K	1071.81	1445.03	0.34	0.30	0.12	0.278
	Na	169.10	1705.31	0.38	0.25	0.18	0.164
	Eh	472.05	1366.60	-8.78	5.17	0.22	0.120
<i>Avicennia marina</i>	Distance	-202.55	542.23	0.86	0.74	0.12	0.269
	EC	-356.58	491.84	66.61	40.03	0.22	0.127
	pH	1371.58	1168.56	-172.52	193.85	0.07	0.394
	N	-167.39	353.44	0.102	0.051	0.28	0.078
	P	353.88	466.41	0.08	1.11	0.001	0.991
	K	-188.34	583.78	0.13	0.12	0.10	0.321
	Na	-13.06	744.37	0.06	0.11	0.03	0.605
	Eh	204.61	617.93	-0.64	2.34	0.01	0.790
<i>Bruguiera cylindrica</i>	Distance	242.37	190.96	-0.17	0.26	0.04	0.534
	EC	380.40	164.66	22.99	13.40	0.23	0.117
	pH	-287.50	385.66	71.70	63.98	0.11	0.289
	N	247.53	131.89	-0.02	0.02	0.11	0.282
	P	-8.22	147.19	1.65	1.39	0.12	0.263
	K	114.46	207.06	0.01	0.04	0.00	0.919
	Na	-63.20	245.53	0.03	0.64	0.07	0.410
	Eh	-93.58	193.16	-0.96	0.73	0.15	0.220
<i>Excoecaria agallocha</i>	Distance	306.81	148.33	-0.33	0.20	0.21	0.137
	EC	259.79	148.61	-15.37	12.09	0.14	0.233
	pH	-154	340.30	42.51	56.45	0.05	0.469
	N	204.04	110.85	-0.02	0.02	0.14	0.223
	P	239.34	122.12	-1.68	1.16	0.17	0.177
	K	400.68	140.59	-0.07	0.03	0.37	0.036
	Na	347.35	200.02	-0.04	0.03	0.15	0.206
	Eh	433.92	133.19	1.43	0.50	0.44	0.018

n = 12

EC: Soil Electrical Conductivity, Eh: *In situ* redox potential, K: Available potassium, N: Available nitrogen, Na: Exchangeable sodium, P: Available phosphorusR² = Coefficient of determination, SEE = Standard error of estimate, p = Probability value.



². Apart from the true mangroves, a few seedlings of mangrove associates (eg. *Calophyllum inophyllum*) were also found on the distal end of the transect.

Most species in the 50-100 cm seedling category followed a restricted distribution pattern. While *A. officinalis* was present in all quadrats in the 0-400 m zone it was conspicuously absent further inward (Table 12). *A. marina*, *R. mucronata* and *E. agallocha* among the true mangroves, were present only in solitary quadrats along the entire transect. However, *B. cylindrica* regenerated profusely in the middle stretch from 300-800 m of this mangrove patch. Significantly, *B. cylindrica* seedlings counts were higher in the larger size class (> 100 cm) too, where others except *R. mucronata* were not present. Regarding interzonal differences, regenerant density was highest in zone II followed by zone III and zone I.

4.2 Leaf phenology

Data on leaf and reproductive phenology of predominant mangrove species in Pudukkottai are presented in Tables 13-18. All tree species showed profound monthly variability ($p < 0.01$) in respect of their leaf production and leaf fall patterns. In general, leaf production peaked with the onset of rains (April to June). Incidentally, the site received 124-395 mm of summer rains during April-May (Table 1), which was followed by the monsoon rains. Increasing rates of leaf fall was observed during the winter season (October-February) (Table 13). *Sonneratia caseolaris* and *Excoecaria agallocha* remained completely leafless for a short period during February to March. They, however, did not show any distinct flowering and fruiting periodicity. As regards to *Rhizophora mucronata* and *Bruguiera cylindrica*, leaf production and leaf fall continued throughout the year, again without any clear-cut seasonal variability. However, in *A. officinalis*, profuse flowering and fruiting were noticed from February to May and April to October respectively. *R. mucronata* also flowered during February to May, but in *B. cylindrica* flowering was predominant in January-March. Interestingly, propagules were hanging from the branches of both tree species throughout the study period with peaks just after flowering.

The association between phenological attributes and weather parameters (rainfall, maximum and minimum temperature and relative humidity, Table 1) were evaluated using the Carl Pearson's correlation coefficient (Table 19 and Fig. 8). In

Table 12. Regeneration (no. 100 m⁻²) of mangrove species along the distance from the land-sea interface to the land-interior.

Seedling class	Species	Distance											
		100	200	300	400	500	600	700	800	900	1000	1100	1200
Height ≤ 50cm	<i>Avicennia officinalis</i>	70 ^{aC}	99 ^{aBC}	126 ^{aC}	142 ^{aC}	252 ^{aB}	101 ^{aBC}	348 ^{aA}	226 ^{aB}	256 ^{aB}	129 ^{aC}	59 ^{aC}	107 ^{aBC}
	<i>Avicennia marina</i>	-	-	63 ^{abBC}	-	-	109 ^{aB}	196 ^{aA}	-	-	77 ^{abBC}	-	-
	<i>Bruguiera cylindrica</i>	-	-	-	64 ^{abAB}	61 ^{bAB}	68 ^{abAB}	89 ^{aA}	32 ^{bB}	-	-	-	-
	<i>Rhizophora mucronata</i>	-	-	42 ^{abA}	-	-	-	-	-	-	-	-	-
	<i>Excoecaria agallocha</i>	49 ^{abB}	61 ^{abB}	-	102 ^{aA}	-	-	-	-	-	-	-	-
	<i>Sonneratia caseolaris</i>	-	58 ^{abA}	-	-	-	-	-	-	-	-	-	-
	<i>Calophyllum inophyllum</i>	49 ^{abA}	-	-	-	-	-	-	-	-	-	-	-
Height 50-100 cm	<i>Avicennia officinalis</i>	94 ^{aB}	99 ^{aB}	133 ^{aAB}	175 ^{aA}	-	-	-	-	-	-	-	-
	<i>Avicennia marina</i>	-	-	119 ^{aA}	-	-	-	-	-	-	-	-	-
	<i>Bruguiera cylindrica</i>	-	-	32 ^{abC}	159 ^{aB}	236 ^{aA}	79 ^{aBC}	229 ^{aA}	38 ^{aC}	-	-	-	-
	<i>Rhizophora mucronata</i>	-	-	32 ^{abA}	-	-	-	-	-	-	-	-	-
	<i>Excoecaria agallocha</i>	70 ^{abA}	-	-	-	-	-	-	-	-	-	-	-
	<i>Sonneratia caseolaris</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Calophyllum inophyllum</i>	61 ^{abA}	58 ^{abA}	-	-	-	-	-	-	-	-	-	-
Height ≥ 100 cm	<i>Avicennia officinalis</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Avicennia marina</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Bruguiera cylindrica</i>	-	38 ^{aC}	22 ^{abC}	153 ^{aB}	497 ^{aA}	85 ^{aBC}	151 ^{aB}	-	-	-	-	-
	<i>Rhizophora mucronata</i>	-	-	32 ^{abA}	-	-	-	-	-	-	-	-	-
	<i>Excoecaria agallocha</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Sonneratia caseolaris</i>	-	-	-	-	-	-	-	-	-	-	-	-
	<i>Calophyllum inophyllum</i>	-	-	-	-	-	-	-	-	-	-	-	-
Comparison between species: p	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01
Comparison between distances : p	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01	≤ 0.01
		Zone I			Zone II				Zone III				

Means followed by the same lower case letters are not significantly different within the same column
 Means followed by the same upper case letters are not significantly different between columns

Table 13. Leaf phenology of *Rhizophora mucronata* during August 2001 to July 2002.

Period (Months)	No. of old leaves per twig	No. of new leaves per twig	No. of leaves fallen per twig	Total number of leaves per twig
Aug 01	7.42 ^a ± 2.03	0.93 ^b ± 1.01	1.28 ^a ± 1.12	7.08 ^a ± 1.91
Sep 01	7.07 ^a ± 1.91	1.03 ^b ± 1.01	0.92 ^{ab} ± 1.00	7.22 ^a ± 2.03
Oct 01	5.60 ^{ab} ± 2.51	3.40 ^{ab} ± 3.74	0.63 ^b ± 0.84	4.52 ^b ± 3.35
Nov 01	7.16 ^a ± 1.98	0.40 ^c ± 0.81	1.23 ^a ± 1.16	6.12 ^{ab} ± 2.09
Dec 01	6.45 ^a ± 2.26	0.43 ^c ± 0.83	1.17 ^a ± 0.92	5.72 ^{ab} ± 2.15
Jan 02	3.35 ^b ± 1.72	5.42 ^a ± 1.92	0.53 ^b ± 0.89	7.13 ^a ± 0.91
Feb 02	4.82 ^b ± 1.65	1.47 ^b ± 1.21	0.78 ^{ab} ± 1.28	5.20 ^{ab} ± 1.88
Mar 02	5.20 ^b ± 1.88	1.07 ^b ± 1.01	0.73 ^{ab} ± 0.84	5.47 ^{ab} ± 1.49
Apr 02	3.50 ^b ± 1.72	5.47 ^a ± 1.49	1.13 ^a ± 1.00	6.93 ^a ± 0.80
May 02	5.67 ^a ± 1.58	1.30 ^b ± 0.96	0.68 ^b ± 0.87	6.28 ^{ab} ± 1.46
Jun 02	6.03 ^a ± 1.74	1.30 ^b ± 1.87	1.27 ^a ± 0.88	5.27 ^{ab} ± 2.25
Jul 02	5.77 ^a ± 1.72	1.00 ^b ± 1.01	0.73 ^{ac} ± 0.90	5.90 ^{ab} ± 1.73
	Sem ± 0.25 p ≤ 0.01	Sem ± 0.21 p ≤ 0.01	Sem ± 0.13 p ≤ 0.01	Sem ± 0.25 p ≤ 0.01

Mean values followed by same lower case superscript are not significantly different within the same column

Values after ± indicate standard deviations.

Table 14. Leaf phenology of *Bruguiera cylindrica* during August 2001 to July 2002.

Period (Months)	No. of old leaves per twig	No. of new leaves per twig	No. of leaves fallen per twig	Total number of leaves per twig
Aug 01	14.95 ^a ± 4.39	0.82 ^a ± 1.59	2.78 ^a ± 2.31	12.95 ^a ± 3.45
Sep 01	12.95 ^a ± 3.45	0.43 ^{ab} ± 0.98	1.92 ^a ± 1.29	11.47 ^a ± 2.96
Oct 01	11.47 ^a ± 2.96	0.80 ^{ab} ± 1.12	1.48 ^{ab} ± 1.16	10.73 ^a ± 3.33
Nov 01	10.73 ^{ab} ± 3.33	0.57 ^{ab} ± 0.98	2.08 ^a ± 1.43	9.20 ^{ab} ± 3.75
Dec 01	9.20 ^{ab} ± 3.75	1.33 ^a ± 1.36	1.42 ^{ab} ± 1.14	9.17 ^{ab} ± 3.95
Jan 02	9.17 ^{ab} ± 3.92	0.80 ^{ab} ± 1.05	1.40 ^{ab} ± 1.40	8.63 ^b ± 3.58
Feb 02	8.63 ^{ab} ± 3.58	1.07 ^a ± 1.07	1.32 ^{ab} ± 1.30	8.42 ^b ± 3.54
Mar 02	8.63 ^{ab} ± 3.58	1.07 ^a ± 1.07	1.32 ^{ab} ± 1.27	8.42 ^b ± 3.54
Apr 02	8.35 ^{ab} ± 3.56	0.87 ^{ab} ± 1.00	1.10 ^b ± 1.00	8.35 ^b ± 3.31
May 02	8.05 ^b ± 3.56	0.93 ^{ab} ± 1.01	1.08 ^b ± 1.01	7.97 ^b ± 2.82
Jun 02	8.13 ^{ab} ± 2.95	0.75 ^{ab} ± 0.97	1.05 ^b ± 0.95	7.83 ^b ± 2.95
Jul 02	7.63 ^b ± 7.74	0.83 ^{ab} ± 0.99	0.97 ^c ± 0.94	7.63 ^b ± 2.69
	Sem ± 0.45 p ≤ 0.01	Sem ± 0.14 p ≤ 0.01	Sem ± 0.17 p ≤ 0.01	Sem ± 0.43 p ≤ 0.01

Mean values followed by same lower case superscript are not significantly different within the same column

Values after ± indicate standard deviations.

Table 15. Leaf phenology of *Avicennia officinalis* during August 2001 to July 2002.

Period (Months)	No. of old leaves per twig	No. of new leaves per twig	No. of leaves fallen per twig	Total number of leaves per twig
Aug 01	9.65 ^a ± 2.95	1.03 ^{bc} ± 1.31	1.95 ^a ± 1.36	8.65 ^a ± 2.92
Sep 01	8.65 ^{ab} ± 2.92	2.03 ^b ± 3.87	1.45 ^{ab} ± 2.35	9.33 ^a ± 4.14
Oct 01	9.33 ^a ± 4.14	0.60 ^c ± 1.42	2.13 ^a ± 1.62	7.85 ^{ab} ± 4.26
Nov 01	7.85 ^b ± 4.26	1.25 ^{bc} ± 1.64	1.63 ^{ab} ± 1.51	7.50 ^{ab} ± 4.00
Dec 01	7.50 ^b ± 4.00	0.81 ^{bc} ± 1.05	1.15 ^{ab} ± 1.13	7.22 ^{ab} ± 3.63
Jan 02	7.21 ± 3.63 ^b	0.97 ^{bc} ± 1.12	1.28 ^{ab} ± 1.26	6.93 ^b ± 3.18
Feb 02	6.93 ^{bc} ± 6.95	1.08 ^{bc} ± 1.36	1.08 ^{ab} ± 0.96	6.95 ^b ± 3.04
Mar 02	6.95 ^b ± 3.04	0.92 ^{bc} ± 1.17	0.92 ^{ab} ± 0.87	6.92 ^b ± 3.08
Apr 02	5.95 ^c ± 3.12	2.48 ^{bc} ± 3.42	0.77 ^b ± 1.32	5.22 ^b ± 3.47
May 02	6.65 ^{bc} ± 2.63	0.50 ^c ± 0.90	0.43 ^b ± 0.72	6.72 ^b ± 2.77
Jun 02	3.50 ^c ± 1.72	6.72 ^a ± 2.77	0.43 ^b ± 0.81	9.79 ^a ± 3.68
Jul 02	6.45 ^{bc} ± 2.64	0.68 ^c ± 0.91	0.73 ^b ± 0.76	6.52 ^b ± 2.39
	Sem ± 0.42 p ≤ 0.01	Sem ± 0.26 p ≤ 0.01	Sem ± 0.17 p ≤ 0.01	Sem ± 0.42 p ≤ 0.01

Mean values followed by same lower case superscript are not significantly different within the same column

Values after ± indicate standard deviations.

Table 16. Leaf phenology of *Sonneratia caseolaris* during August 2001 to July 2002.

Period (Months)	No. of old leaves per twig	No. of new leaves per twig	No. of leaves fallen per twig	Total number of leaves per twig
Aug 01	7.60 ^a ± 2.12	0.82 ^b ± 1.19	2.78 ^a ± 2.19	5.73 ^a ± 2.11
Sep 01	5.63 ^{ab} ± 2.32	1.60 ^{ab} ± 2.31	1.37 ^{ab} ± 1.46	5.23 ^a ± 2.79
Oct 01	5.63 ^{ab} ± 2.32	1.60 ^{ab} ± 2.31	1.37 ^{ab} ± 1.46	5.23 ^a ± 2.79
Nov 01	5.28 ^{ab} ± 2.42	0.62 ^b ± 1.12	1.18 ^{ab} ± 1.31	4.82 ^{ab} ± 2.22
Dec 01	3.70 ^b ± 2.13	0.38 ^b ± 0.88	1.32 ^{ab} ± 1.05	2.78 ^b ± 2.19
Jan 02	2.78 ^b ± 2.19	0.28 ^b ± 0.87	1.63 ^{ab} ± 1.56	1.43 ^b ± 1.37
Feb 02	1.62 ^c ± 1.54	0.63 ^b ± 1.25	0.75 ^b ± 0.79	1.42 ^b ± 1.90
Mar 02	1.58 ^c ± 1.80	0.63 ^b ± 1.66	0.87 ^b ± 1.00	0.52 ^b ± 1.10
Apr 02	1.70 ^c ± 2.40	2.27 ^a ± 1.21	0.32 ^c ± 0.77	3.52 ^{ab} ± 2.33
May 02	3.37 ^b ± 1.41	1.97 ^a ± 0.78	0.37 ^c ± 0.61	4.83 ^{ab} ± 1.46
Jun 02	4.83 ^{ab} ± 1.46	1.83 ^a ± 0.56	0.28 ^c ± 0.58	6.18 ^a ± 1.58
Jul 02	6.18 ^a ± 1.58	1.40 ^{ab} ± 0.92	0.62 ^b ± 0.76	6.83 ^a ± 1.82
	Sem ± 0.26 p ≤ 0.01	Sem ± 0.18 p ≤ 0.01	Sem ± 0.16 p ≤ 0.01	Sem ± 0.26 p ≤ 0.01

Mean values followed by same lower case superscript are not significantly different within the same column

Values after ± indicate standard deviations.

Table 17. Leaf phenology of *Excoecaria agallocha* during August 2001 to July 2002.

Period (Months)	No. of old leaves per twig	No. of new leaves per twig	No. of leaves fallen per twig	Total number of leaves per twig
Aug 01	10.62 ^a ± 3.49	0.47 ^b ± 1.08	1.18 ^{ab} ± 1.41	9.87 ^a ± 3.65
Sep 01	9.87 ^a ± 3.65	0.50 ^b ± 1.17	1.50 ^{ab} ± 1.03	9.08 ^a ± 3.72
Oct 01	9.08 ^a ± 3.72	0.40 ^b ± 0.96	1.53 ^{ab} ± 1.40	8.02 ^a ± 3.95
Nov 01	8.02 ^a ± 3.95	0.17 ^b ± 0.56	2.28 ^a ± 2.16	5.93 ^{ab} ± 2.73
Dec 01	5.40 ^{ab} ± 2.91	1.62 ^{ab} ± 2.95	1.90 ^{ab} ± 1.74	3.70 ^{ab} ± 2.13
Jan 02	4.07 ^b ± 2.33	0.20 ^b ± 0.58	1.67 ^{ab} ± 1.36	2.60 ^b ± 1.78
Feb 02	2.60 ^b ± 1.78	0.05 ^b ± 0.39	2.10 ^a ± 1.13	0.37 ^c ± 0.58
Mar 02	0.37 ^b ± 0.58	0.00 ^b ± 0.00	0.30 ^b ± 0.50	0.07 ^c ± 0.36
Apr 02	0.07 ^b ± 0.36	3.12 ^a ± 1.62	0.00 ^c ± 0.00	3.18 ^b ± 1.57
May 02	3.18 ^{ab} ± 1.57	2.08 ^a ± 1.43	0.20 ^b ± 0.55	5.13 ^b ± 1.60
Jun 02	5.13 ^{ab} ± 1.60	1.17 ^{ab} ± 1.15	0.35 ^a ± 0.58	5.88 ^b ± 1.89
Jul 02	5.83 ^{ab} ± 1.89	0.95 ^{ab} ± 1.08	0.38 ^b ± 0.67	6.87 ^b ± 2.04
	Sem ± 0.34 p ≤ 0.01	Sem ± 0.17 p ≤ 0.01	Sem ± 0.15 p ≤ 0.01	Sem ± 0.31 p ≤ 0.01

Mean values followed by same lower case superscript are not significantly different within the same column

Values after ± indicate standard deviations.

Table 18. Reproductive phenology of important mangrove tree species at Pudukkottai.

Month	<i>Rhizophora mucronata</i>		<i>Bruguiera cylindrica</i>		<i>Avicennia officinalis</i>		<i>Sonneratia caseolaris</i>		<i>Excoecaria agallocha</i>	
	Flowering	Fruiting	Flowering	Fruiting	Flowering	Fruiting	Flowering	Fruiting	Flowering	Fruiting
Aug' 01	-	x	-	x	-	x	-	-	-	x
Sep' 01	-	x	-	x	-	x	x	-	-	-
Oct' 01	-	x	-	x	-	x	x	-	-	-
Nov' 01	-	x	-	x	-	-	x	-	-	-
Dec' 01	-	x	-	x	-	-	x	x	-	-
Jan' 02	-	x	x	x	-	-	x	x	-	-
Feb' 02	x	x	x	x	x	-	x	x	x	-
Mar' 02	x	x	x	x	x	-	x	x	x	-
Apr' 02	x	x	-	x	x	x	-	x	x	x
May' 02	x	x	-	x	x	x	-	-	-	x
Jun' 02	x	x	-	x	x	x	-	-	-	x
Jul' 02	x	x	-	x	x	x	-	-	-	x

x indicate occurrence of the event

Table 19 Correlation between phenological attributes of predominant mangrove species of Puduvyppu and weather parameters during August'01- July'02

Species	Phenological attributes	Maximum Temperature (°C)	Minimum Temperature (°C)	Rainfall (mm)	Relative humidity (%)
<i>Rhizophora mucronata</i>	Old leaves	-0.644	-0.094	0.364	0.592
	New leaves	0.385	0.015	-0.289	-0.387
	Leaf fall	-0.210	0.066	0.180	0.274
	Total leaves	-0.538	0.042	0.370	0.549
<i>Bruguiera cylindrica</i>	Old leaves	-0.498	-0.185	-0.041	0.334
	New leaves	0.474	-0.017	-0.360	-0.515
	Leaf fall	-0.392	-0.232	-0.142	0.216
	Total leaves	-0.471	-0.168	-0.066	-0.305
<i>Avicennia officinalis</i>	Old leaves	-0.225	-0.230	-0.343	0.012
	New leaves	-0.185	0.130	0.475	0.322
	Leaf fall	-0.317	-0.381	-0.279	0.061
	Total leaves	-0.064	-0.192	-0.451	-0.133
<i>Sonneratia caseolaris</i> F v	Old leaves	-0.929**	-0.243	0.634*	0.837**
	New leaves	-0.091	0.698*	0.554	0.473
	Leaf fall	-0.408	-0.494	-0.210	0.089
	Total leaves	-0.796**	0.106	0.871**	0.930**
<i>Excoecaria agallocha</i> u e	Old leaves	-0.820**	-0.403	0.346	0.623*
	New leaves	0.295	0.499	0.154	-0.015
	Leaf fall	-0.087	-0.726**	-0.426	-0.269
	Total leaves	-0.836**	-0.060	0.611*	0.821**

F value: Significant at 5% level: 0.5760

Significant at 1% level: 0.7079

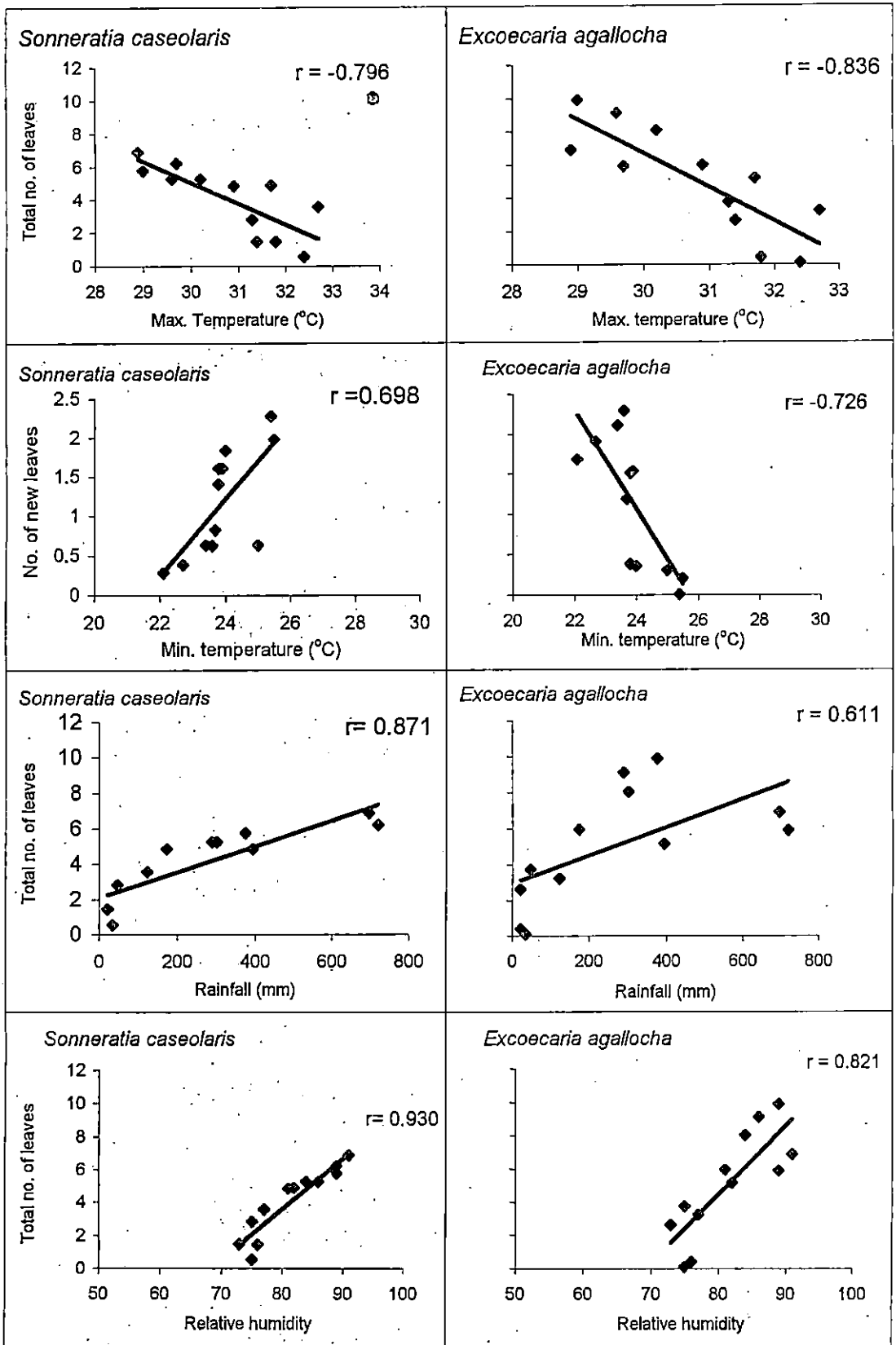


Fig. 8 A correlation between important weather parameters and phenological attributes of important mangrove species at Pudukkottai

general, rainfall and temperature determined the phenological cycles. Both *S. caseolaris* and *E. agallocha* yielded positive 'r' values when total number of leaves per shoot was related to rainfall ($r = 0.871^{**}$) and relative humidity ($r = 0.821^{**}$). However, maximum temperature exerted negative relationships with total number of leaves per shoot ($r = -0.796^{**}$) and leaf fall ($r = -0.726^{**}$). In other cases, the 'r' values were not statistically significant.

4.3 Litterfall

Data on litter production dynamics are presented in Tables 20-23 and Fig. 9. A comparison of the data in Table 20 indicates that total litterfall (leaves, twigs and reproductive parts of all species) in the mangrove forest of Pudukkottai ranged from $1031 \text{ g m}^{-2} \text{ yr}^{-1}$ to $1364 \text{ g m}^{-2} \text{ yr}^{-1}$. Interzonal differences were, however, not significant ($p = 0.056$).

As regards of the proximate composition of litter, leaf litter accounted for 58 to 62 per cent of the total litterfall. Although leaf fall showed a characteristic monomodal distribution pattern (Fig. 9), with a distinct peak during November-December, total litterfall did not exhibit such a pronounced seasonal pattern. Implicit in this is a marked seasonal variability in non-leaf litter contributing to total litterfall (as much as 84% in June 2002 and 12% in December 2001), which however, did not conform to the seasonal leaf fall pattern.

Monthly variations in litterfall and leaf fall of important species were also significant ($p < 0.01$) with peak values in November-December (Fig. 9). Among the predominant species that colonized the site, *Avicennia officinalis* accounted for about 50 to 72 per cent ($599\text{-}739 \text{ g m}^{-2} \text{ yr}^{-1}$) of the total litterfall in all three zones. This was followed by *S. caseolaris* (8-10%), *B. cylindrica* (6-8%), *R. mucronata* (5-6%) and *E. agallocha* (3-4%). In *A. officinalis*, twigs accounted for 14 per cent, fruits 18 per cent and flowers 5 per cent of the total litterfall. Interzonal variations in *Avicennia* litterfall were not significant ($p = 0.062$). *R. mucronata* showed less variability among months with a mean annual litterfall of $372 \text{ g m}^{-2} \text{ yr}^{-1}$ and leaf litter constituting about 39 per cent (29 to 46%) of the total litterfall. Among the other litter fractions, twigs (14%) and propagules (29%) formed major constituents (Table 23). Unlike most other species, *B. cylindrica* litterfall peaked in May 2002 (200 g m^{-2} , with a relatively lower

Table 20. Total litterfall and leaf fall in three zones of mangroves at Pudukkottai

Month	Zone I			Zone II			Zone III			Mean		
	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percenta ge leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter
Aug '01	60.58 ^f ± 31.73	36.14 ^{de} ± 32.12	59.66	98.42 ^h ± 39.89	65.07 ^{bcd} ± 35.90	66.12	129.49 ^{bc} ± 80.44	36.48 ^{cig} ± 33.94	28.18	96.16 ^b ± 50.67	45.90 ^{def} ± 34.78	47.73
Sep '01	60.20 ^{def} ± 36.50	41.30 ^{de} ± 28.22	68.60	132.69 ^a ± 67.50	95.85 ^b ± 44.57	69.98	92.25 ^d ± 55.81	62.72 ^{cde} ± 41.30	67.98	95.04 ^b ± 53.27	66.62 ^{bed} ± 39.09	70.09
Oct '01	103.8 ^{abc} ± 44.15	88.63 ^{ab} ± 38.63	85.32	24.90 ^f ± 19.26	18.17 ^f ± 18.29	72.96	55.81 ^c ± 55.31	43.23 ^{defg} ± 45.71	77.46	61.53 ^c ± 39.57	50.01 ^{cde} ± 48.06	81.27
Nov '01	130.06 ^a ± 61.42	112.68 ^a ± 57.42	86.63	64.13 ^{cde} ± 23.65	56.89 ^{cde} ± 21.69	88.71	95.20 ^d ± 67.78	76.62 ^c ± 55.68	80.48	96.46 ^b ± 50.94	82.06 ^b ± 62.12	85.07
Dec '01	118.50 ^{ab} ± 58.60	98.02 ^{ab} ± 57.02	82.71	143.87 ^a ± 52.72	134.93 ^a ± 50.17	93.78	178.04 ^a ± 99.42	153.18 ^a ± 83.09	86.04	146.80 ^a ± 70.25	128.71 ^a ± 72.33	87.68
Jan '02	72.20 ^{cdef} ± 31.55	56.44 ^{cd} ± 26.52	78.17	83.22 ^{bcd} ± 27.14	69.18 ^{bcd} ± 24.27	83.12	135.87 ^{bc} ± 64.97	111.49 ^b ± 50.35	82.06	97.09 ^b ± 41.22	79.03 ^{bc} ± 39.64	81.39
Feb '02	100.8 ^{abc} ± 63.90	74.45 ^{bc} ± 45.65	73.83	90.47 ^{bc} ± 33.95	72.72 ^{bc} ± 28.59	80.39	157.42 ^{ab} ± 106.22	120.70 ^b ± 47.99	76.67	116.24 ^b ± 68.02	89.29 ^b ± 49.42	76.82
Mar '02	45.61 ^f ± 29.33	28.09 ^{bc} ± 25.32	61.57	45.47 ^{cf} ± 18.23	29.38 ^{cf} ± 14.07	64.62	91.21 ^d ± 94.29	72.99 ^{cd} ± 31.86	80.02	60.76 ^c ± 47.28	43.48 ^{def} ± 40.09	71.58
Apr '02	79.58 ^{cde} ± 40.52	20.05 ^d ± 5.86	25.19	89.99 ^{bc} ± 35.47	39.79 ^{def} ± 26.31	44.21	95.32 ^d ± 71.82	47.57 ^{cdef} ± 41.33	49.90	88.30 ^{bc} ± 49.26	35.80 ^{def} ± 23.64	40.54
May '02	92.6 ^{bcd} ± 40.98	15.23 ^e ± 4.05	16.45	114.02 ^{ab} ± 78.27	22.47 ^f ± 12.44	19.71	133.27 ^{bc} ± 109.35	37.64 ^{cig} ± 20.19	28.24	113.30 ^b ± 76.20	25.12 ^{ef} ± 20.73	22.17
Jun '02	87.45 ^{bcd} ± 57.36	12.60 ^c ± 7.48	14.40	90.31 ^{bc} ± 50.56	13.50 ^f ± 9.51	14.95	106.52 ^{cd} ± 70.42	20.27 ^{fg} ± 16.52	19.03	94.76 ^b ± 59.95	15.45 ^f ± 14.27	16.3
Jul '02	102.21 ^{abc} ± 57.64	30.60 ^{de} ± 30.60	29.94	53.37 ^{def} ± 47.41	19.77 ^f ± 17.05	37.05	93.18 ^d ± 59.09	14.07 ^h ± 10.89	15.10	83.92 ^{bc} ± 54.71	21.48 ^{ef} ± 25.03	25.90
Total	1053.72	614.23		1030.85	637.72		1363.58	796.95		1149.38	682.96	
Z) Sem p	± 8.62	± 5.09		± 8.62	± 5.09		± 8.62	± 5.09		± 8.62	± 5.09	
M) Sem	<0.01	<0.01		<0.01	<0.01		<0.01	<0.01		<0.01	<0.01	
p	± 8.14	± 5.69		± 8.14	± 5.69		± 8.14	± 5.69		± 8.14	± 5.69	
	<0.01	<0.01		<0.01	<0.01		<0.01	<0.01		<0.01	<0.01	

Z: Comparison between zones, M: Comparison between months

Mean values followed by same lower case superscript are not significantly different within the same column

Values after ± indicate standard deviations.

Table 21 Total litterfall and leaf fall of *Avicennia officinalis* species in three zones of mangroves at Pudukkottai.

Month	Zone I			Zone II			Zone III			Mean		
	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter
Aug '01	36.33 ^{de} ± 12.39	15.69 ^{de} ± 4.08	44.71	85.04 ^b ± 47.08	63.68 ^{bc} ± 8.04	75.17	94.73 ^a ± 91.38	25.55 ^{bcd^{ef}} ± 5.15	27.74	72.03 ^{abcd} ± 50.29	34.97 ^{abcd} ± 5.76	48.55
Sep '01	49.48 ^{cde} ± 26.53	33.62 ^{cde} ± 5.88	68.59	114.89 ^a ± 54.74	83.63 ^{ab} ± 9.19	73.03	59.26 ^{bc} ± 54.81	39.39 ^{bcd} ± 6.35	67.03	74.54 ^{abc} ± 45.36	52.22 ^{bc} ± 7.15	70.06
Oct '01	87.51 ^{ab} ± 53.62	76.23 ^{ab} ± 5.79	87.25	15.89 ^f ± 11.11	14.76 ^{ef} ± 3.97	93.33	20.93 ^d ± 24.95	16.00 ^{def} ± 4.12	77.53	41.44 ^{cde} ± 29.89	35.66 ^{bcde} ± 5.63	86.05
Nov '01	98.77 ^a ± 64.76	84.43 ^a ± 9.24	85.62	62.96 ^{bcd} ± 38.59	41.57 ^{cdc} ± 6.52	66.56	65.40 ^b ± 81.92	49.70 ^{bc} ± 7.12	76.36	75.71 ^{ab} ± 61.76	58.57 ^{ab} ± 7.63	77.36
Dec '01	72.15 ^{abc} ± 48.41	64.26 ^{abc} ± 8.07	89.21	128.21 ^a ± 55.55	105.06 ^a ± 10.30	82.08	98.26 ^a ± 130.74	93.00 ^a ± 9.69	94.70	99.55 ^a ± 78.23	87.43 ^a ± 9.36	87.83
Jan '02	51.50 ^{cde} ± 28.56	38.24 ^{cde} ± 6.26	76.17	76.66 ^{bc} ± 35.47	55.67 ^{bcd} ± 7.53	72.96	42.23 ^{bcd} ± 45.94	37.66 ^{bcde} ± 6.22	89.51	56.47 ^{bcde} ± 36.66	43.86 ^{bcd} ± 6.67	77.67
Feb '02	66.64 ^{bcd} ± 58.19	48.31 ^{bcd} ± 7.02	72.89	66.42 ^{bcd} ± 34.36	46.23 ^{cde} ± 6.87	70.02	58.89 ^{bc} ± 52.01	55.60 ^b ± 7.54	94.51	63.98 ^{bcd} ± 48.19	50.05 ^{bc} ± 7.14	78.21
Mar '02	21.46 ^c ± 15.46	09.26 ^c ± 3.20	45.71	30.96 ^{ef} ± 16.29	18.11 ^{ef} ± 4.37	59.81	24.99 ^d ± 31.64	21.67 ^{cdef} ± 4.76	87.24	25.80 ^e ± 21.14	16.35 ^{de} ± 4.11	63.37
Apr '02	56.51 ^{bcd} ± 50.73	10.29 ^c ± 3.36	19.63	50.79 ^{cde} ± 43.29	29.39 ^{def} ± 5.51	59.68	42.60 ^{bcd} ± 45.30	26.63 ^{bcd^{ef}} ± 5.25	63.36	49.97 ^{bcde} ± 46.60	22.12 ^{cdc} ± 4.71	44.25
May '02	60.85 ^{bcd} ± 39.45	7.26 ^c ± 2.87	13.34	29.11 ^{ef} ± 43.77	4.04 ^f ± 2.24	16.74	29.63 ^{cd} ± 84.30	6.29 ^{ef} ± 2.70	23.79	39.86 ^{de} ± 51.51	5.86 ^e ± 2.61	14.69
Jun '02	70.36 ^{abc} ± 49.45	7.98 ^c ± 2.99	12.59	37.69 ^{def} ± 30.77	5.11 ^f ± 2.47	15.81	23.54 ^d ± 38.75	3.23 ^f ± 2.06	17.24	43.86 ^{bcde} ± 43.45	5.44 ^e ± 2.51	12.4
Jul '02	65.36 ^{bcd} ± 45.63	18.04 ^{de} ± 4.36	28.69	41.19 ^{def} ± 42.20	5.27 ^f ± 2.50	14.86	27.85 ^{cd} ± 24.95	5.06 ^{ef} ± 4.76	17.59	44.80 ^{bcde} ± 43.64	9.13 ^e ± 3.04	20.38
Total	735.90	413.61 ±		739.17	472.54		588.30	378.86		688.04	421.64	
Z) Sem P	± 8.96 <0.01	± 5.68 <0.01		± 8.96 <0.01	± 5.68 <0.01		± 8.96 <0.01	± 5.68 <0.01		± 8.96 <0.01	± 5.68 <0.01	
M) Sem P	± 6.39 <0.01	± 5.21 <0.01		± 6.39 <0.01	± 5.21 <0.01		± 6.39 <0.01	± 5.21 <0.01		± 6.39 <0.01	± 5.21 <0.01	

Z: Comparison between zones, M: Comparison between months

Mean values followed by same lower case superscript are not significantly different within the same column

Values after ± indicate standard deviations.

Table 22. Total litterfall and leaf litterfall of predominant mangrove species at Pudukkottai.

Month	<i>Rhizophora mucronata</i>			<i>Bruguiera cylindrica</i>			<i>Sonneratia caseolaris</i>			<i>Excoecaria agallocha</i>		
	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter	Total litter (g m ⁻²)	Leaf litter (g m ⁻²)	Percentage leaf litter
Aug '01	23.71 ^c ± 2.66	6.99 ^d ± 1.91	29.48	56.60 ^c ± 25.76	27.57 ^c ± 13.81	48.71	45.55 ^d ± 12.86	20.51 ^{ci} ± 13.22	36.92	11.83 ^h ± 0.56	4.37 ^b ± 0.57	36.93
Sep '01	25.91 ^{de} ± 3.08	11.48 ^c ± 1.93	44.29	32.87 ^{gh} ± 12.18	20.07 ^f ± 15.11	61.04	51.85 ^c ± 11.27	23.04 ^c ± 11.26	44.44	17.51 ^{lg} ± 0.82	10.13 ^f ± 0.17	57.87
Oct '01	29.55 ^{cd} ± 5.61	12.25 ^{bc} ± 2.99	41.41	17.07 ^f ± 5.96	10.85 ^g ± 7.20	63.53	87.26 ^d ± 13.27	60.39 ^c ± 23.25	57.75	20.57 ^f ± 1.21	11.71 ^f ± 1.04	38.29
Nov '01	21.58 ^{ci} ± 1.54	10.03 ^{cd} ± 0.95	46.47	32.13 ^h ± 2.04	28.51 ^{de} ± 27.82	88.74	167.19 ^a ± 24.26	115.63 ^a ± 26.51	62.58	21.81 ^f ± 1.00	27.85 ^c ± 1.00	56.11
Dec '01	41.20 ^a ± 5.24	18.90 ^a ± 4.14	45.88	92.56 ^c ± 2.58	85.37 ^a ± 27.85	92.23	70.13 ^b ± 18.26	66.78 ^b ± 13.26	33.37	99.88 ^a ± 1.12	100.16 ^a ± 3.48	82.06
Jan '02	32.04 ^{bc} ± 5.10	13.42 ^{bc} ± 2.20	41.88	49.72 ^f ± 15.50	31.30 ^{cd} ± 28.70	62.97	39.33 ^c ± 12.36	30.26 ^d ± 9.56	22.68	95.03 ^b ± 3.23	94.46 ^b ± 7.75	47.98
Feb '02	45.18 ^a ± 16.61	16.22 ^{ab} ± 5.13	35.89	93.56 ^c ± 25.86	68.82 ^b ± 41.75	73.55	46.47 ^d ± 13.26	18.14 ^{lg} ± 7.58	39.03	72.67 ^c ± 9.74	79.70 ^c ± 7.20	25.02
Mar '02	28.66 ^{cd} ± 4.81	12.35 ^{bc} ± 3.76	43.10	37.00 ^b ± 16.01	16.69 ^f ± 9.15	45.09	46.21 ^d ± 0.22	16.67 ^{lg} ± 6.27	78.59	43.43 ^d ± 6.91	36.27 ^d ± 2.26	20.10
Apr '02	35.16 ^b ± 0.85	11.99 ^{bc} ± 2.62	34.13	92.75 ^c ± 44.83	32.12 ^{cd} ± 20.78	34.62	26.46 ^f ± 0.15	11.70 ^{hi} ± 4.26	71.10	15.79 ^{gh} ± 2.17	11.40 ^f ± 2.66	22.89
May '02	40.83 ^a ± 6.68	13.57 ^{bc} ± 2.71	33.22	219.60 ^a ± 87.15	33.24 ^c ± 21.21	15.11	11.90 ^b ± 4.57	8.11 ^f ± 3.22	35.44	12.84 ^h ± 2.98	9.66 ^f ± 0.226	42.26
Jun '02	30.01 ^{cd} ± 5.70	9.73 ^{cd} ± 4.26	32.41	83.58 ^d ± 35.67	19.11 ^f ± 14.10	22.86	11.05 ^b ± 3.69	8.49 ^f ± 3.21	20.69	36.82 ^c ± 2.57	7.86 ^{lg} ± 0.21	46.74
Jul '02	17.99 ^f ± 2.90	6.33 ^d ± 0.37	35.17	120.86 ^b ± 27.97	29.31 ^{cd} ± 12.69	24.25	15.05 ^c ± 2.25	14.78 ^{gh} ± 7.26	26.37	12.38 ^d ± 1.25	4.40 ^b ± 0.68	35.56
Total	371.85	143.24		807.76	373.62		616.79	403.51		491.56	370.12	
Sem p	±5.80 ≤0.01	±4.73 ≤0.01		±5.80 ≤0.01	±4.73 ≤0.01		±5.80 ≤0.01	±4.73 ≤0.01		±5.80 ≤0.01	±4.73 ≤0.01	

Mean values followed by same lower case superscript are not significantly different within the same column
Values after ± indicate standard deviations.

Table 23. Reproductive parts and other litter fractions of mangrove species at Pudukkottai.

Month	<i>Rhizophora mucronata</i>				<i>Bruguiera cylindrica</i>				<i>Avicennia officinalis</i>		
	Twigs (g m ⁻²)	Flowers (g m ⁻²)	Fruits (g m ⁻²)	Bud (g m ⁻²)	Twigs (g m ⁻²)	Flowers (g m ⁻²)	Fruits (g m ⁻²)	Bud (g m ⁻²)	Twigs (g m ⁻²)	Flowers (g m ⁻²)	Fruits (g m ⁻²)
Aug '01	18.62 ± 13.55	-	-	-	-	-	36.74 ± 15.24	7.37 ± 1.56	8.94 ± 4.53	-	15.74 ± 2.41
Sep '01	4.83 ± 2.60	-	-	7.56 ± 1.25	5.53 ± 1.25	-	-	4.35 ± 0.58	12.19 ± 6.23	-	16.07 ± 5.56
Oct '01	2.78 ± 0.13	-	-	3.63 ± 1.56	-	-	12.46 ± 1.25	1.26 ± 0.56	9.64 ± 2.25	-	5.32 ± 2.69
Nov '01	3.15 ± 1.35	-	-	6.15 ± 1.62	0.88 ± 0.1	-	2.74 ± 1.21	1.26 ± 0.02	3.92 ± 1.24	-	-
Dec '01	0.93 ± 0.211	-	-	8.74 ± 2.54	-	-	-	5.35 ± 0.25	3.81 ± 1.63	-	-
Jan '02	4.49 ± 1.56	-	10.93 ± 3.25	5.03 ± 5.24	3.96 ± 2.36	2.45 ± 0.26	7.21 ± 2.35	2.62 ± 1.05	2.99 ± 0.23	-	-
Feb '02	12.80 ± 5.6	-	14.67 ± 2.98	4.92 ± 0.96	2.83 ± 1.02	3.40 ± 0.36	12.86 ± 5.62	1.95 ± 0.65	6.18 ± 1.12	2.37 ± 1.32	-
Mar '02	5.44 ± 2.23	-	-	1.51 ± 0.65	-	1.06 ± 0.59	13.01 ± 6.56	2.12 ± 0.21	5.07 ± 1.21	6.00 ± 2.35	-
Apr '02	10.62 ± 6.98	-	-	-	2.14 ± 1.25	-	54.87 ± 13.5	1.64 ± 0.23	12.48 ± 3.25	7.13 ± 1.26	2.55 ± 2.35
May '02	10.13 ± 5.25	11.45 ± 6.23	19.53 ± 5.21	3.05 ± 1.56	-	-	146.56 ± 56.87	-	13.03 ± 3.25	23.45 ± 16.25	9.36 ± 3.52
Jun '02	10.96 ± 6.58	9.76 ± 5.62	11.46 ± 3.5	11.86 ± 2.23	6.29 ± 0.25	-	42.51 ± 12.53	-	12.77 ± 6.54	4.34 ± 1.23	36.24 ± 16.52
Jul '02	8.40 ± 2.56	9.46 ± 1.23	15.25 ± 4.56	4.50 ± 0.25	2.64 ± 0.36	-	54.33 ± 15.96	-	11.27 ± 2.31	1.38 ± 0.25	48.27 ± 11.56
Total	93.15	30.67	117.32	56.95	24.27	6.91	383.29	25.30	102.29	44.67	133.57

Values after ± indicate standard deviations.

Table 23 (Contd). Reproductive parts and other litter fractions of mangrove species at Pudukkottai

Month	<i>Sonneratia caseolaris</i>			<i>Excoecaria agallocha</i>			Miscellaneous (g m ⁻²)
	Twigs (g m ⁻²)	Flowers (g m ⁻²)	Fruits (g m ⁻²)	Twigs (g m ⁻²)	Flowers (g m ⁻²)	Fruits (g m ⁻²)	
Aug '01	12.77 ± 1.25	-	-	3.27 ± 0.21	-	-	15.98 ± 6.95
Sep '01	23.63 ± 9.65	3.33 ± 0.12	14.71 ± 2.51	12.83 ± 5.62	0.31 ± 0.01	-	11.84 ± 2.31
Oct '01	16.97 ± 3.25	2.01 ± 0.12	-	4.06 ± 0.25	0.34 ± 0.01	-	3.96 ± 0.21
Nov '01	27.45 ± 3.56	0.11 ± 0.06	-	3.51 ± 1.25	1.76 ± 0.25	-	4.24 ± 0.21
Dec '01	16.99 ± 5.65	4.47 ± 1.25	-	1.43 ± 0.95	2.52 ± 0.25	-	3.07 ± 0.35
Jan '02	13.86 ± 2.35	0.98 ± 0.13	-	2.51 ± 0.25	0.06 ± 0.01	-	6.31 ± 0.69
Feb '02	22.41 ± 5.68	0.42 ± 0.06	14.28 ± 2.36	1.87 ± 0.85	0.94 ± 0.06	-	4.48 ± 1.23
Mar '02	7.80 ± 2.35	0.06 ± 0.01	-	0.88 ± 0.12	-	-	4.16 ± 0.21
Apr '02	10.00 ± 2.51	-	-	1.45 ± 0.21	0.06 ± 0.05	-	6.43 ± 0.25
May '02	-	-	-	1.23 ± 0.25	-	-	2.09 ± 0.25
Jun '02	-	-	-	1.00 ± 0.5	-	20.44 ± 5.62	22.45 ± 11.25
Jul '02	-	-	-	2.32 ± 0.52	-	35.10 ± 13.25	8.69 ± 2.36
Total	151.88	11.38	28.99	36.36	5.99	55.54	93.7

Values after ± indicate standard deviations.

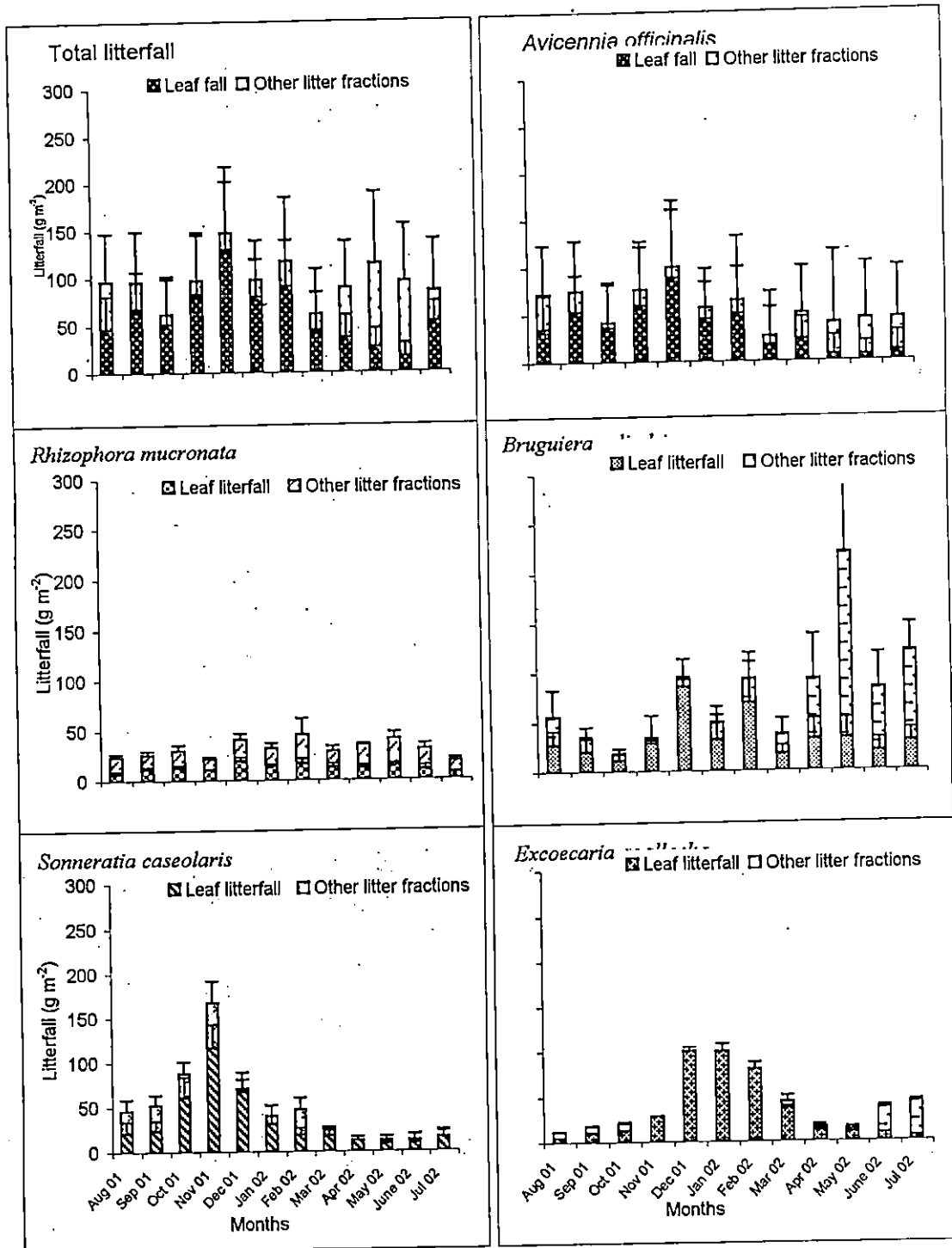


Fig. 9 Total litterfall and leaf fall of mangrove species in the mangrove forest of Puduvypu. (Error bars are standard deviations)

leaf fall content of about 15%). Conversely, reproductive parts (propagules) formed a major component of the total litterfall (147 g m^{-2}) in *B. cylindrica* during that period (Table 23).

4.4 Leaf litter decay

Mass loss data of decomposing leaf litter for six species in the three zones of mangrove forest are furnished in Tables 24-26. Mass loss rates differed significantly among species ($p < 0.01$) and zones ($p < 0.01$). Out of the six species studied only three namely, *A. ilicifolius*, *E. agallocha* and *S. caseolaris* showed complete mass loss during the period of experimentation (8, 6 and 9 months respectively). Among the remaining species, *R. mucronata* in particular showed very slow decay rates with as much as 45 to 71 per cent of the original litter mass remaining at the end of the 12th month, when the study culminated. *B. cylindrica* and *A. officinalis* also showed moderately slow decay rates, respectively retaining 10 to 27 per cent and 12 to 43 per cent of the original litter mass at the end of the 12 months decomposition period.

Mass disappearance data in all the four species namely, *A. ilicifolius*, *E. agallocha*, *A. officinalis* and *S. caseolaris* showed a negative exponential pattern, whereas, in *R. mucronata* and *B. cylindrica* showed a linear pattern (Table 27 and Fig. 10). The model for constant (k) gave a reasonably good fit with r^2 value ranging from 0.9 to 0.99. In general, there was a high decay rate constant (k) in zone I and it decreased as the distance from land ocean interface increased ($p < 0.01$). Furthermore, differences in decay rates among the species were statistically significant ($p < 0.01$). Among the species, *E. agallocha* (0.42) had the highest decay rate constant (k) followed by *A. ilicifolius* (0.31), *S. caseolaris* (0.21), *A. officinalis* (0.16), *B. cylindrica* (0.17) and *R. mucronata* (0.05) with their R^2 values > 0.90 . Half life ($t_{0.5}$) of the six species ranged from 1.62 to 15.64 months with highest in lowest in *E. agallocha* and *R. mucronata*, implying significant interspecific variations (Table 27).

4.4.1 Biochemical quality of leaf litter

Interspecific differences in initial per cent lignin, initial per cent nitrogen and initial per cent lignin: initial per cent nitrogen ratio were significant ($p < 0.01$). Low initial lignin and comparatively high nitrogen levels were recorded in *Excoecaria*

Table 24. Leaf mass loss for *Rhizophora mucronata* and *Bruguiera cylindrica* in three zones of mangrove forest at Pudukkottai.

Months	<i>Rhizophora mucronata</i>			<i>Bruguiera cylindrica</i>		
	Zone I (g)	Zone II (g)	Zone III (g)	Zone I (g)	Zone II (g)	Zone III (g)
0	14.71 ± 0.00	14.71 ± 0.00	14.71 ± 0.00	12.06 ± 0.00	12.06 ± 0.00	12.06 ± 0.00
1	12.84 ± 0.44	12.03 ± 1.19	12.57 ± 1.00	5.69 ± 0.53	4.01 ± 0.38	5.04 ± 0.63
2	11.62 ± 0.43	11.00 ± 0.81	11.97 ± 1.22	4.42 ± 0.50	3.92 ± 0.38	4.86 ± 0.59
3	11.12 ± 0.64	11.32 ± 0.68	11.95 ± 1.14	4.30 ± 0.31	3.90 ± 0.37	4.62 ± 0.41
4	11.13 ± 0.45	11.56 ± 0.74	11.45 ± 0.62	4.48 ± 0.29	3.79 ± 0.82	4.78 ± 1.41
5	11.36 ± 0.35	11.94 ± 0.81	12.23 ± 0.48	4.02 ± 0.63	3.57 ± 0.54	4.97 ± 0.08
6	11.01 ± 0.20	11.04 ± 0.91	12.42 ± 0.65	3.43 ± 0.99	3.45 ± 0.62	4.34 ± 0.45
7	10.02 ± 1.47	12.08 ± 0.24	12.75 ± 0.05	2.54 ± 0.27	3.53 ± 0.53	4.46 ± 0.29
8	8.91 ± 0.55	11.25 ± 2.39	12.94 ± 0.28	2.46 ± 0.59	3.68 ± 0.56	4.60 ± 0.07
9	8.76 ± 0.33	10.71 ± 0.71	11.61 ± 1.56	2.20 ± 0.71	3.23 ± 0.87	3.78 ± 0.22
10	8.37 ± 0.49	9.17 ± 0.96	12.38 ± 0.62	2.01 ± 0.57	2.13 ± 0.41	3.65 ± 0.22
11	6.81 ± 0.55	8.23 ± 0.12	11.67 ± 0.65	1.75 ± 0.25	2.34 ± 0.37	3.62 ± 0.28
12	6.61 ± 0.65	6.62 ± 0.97	10.45 ± 0.46	1.30 ± 0.27	2.11 ± 0.44	3.25 ± 0.53
Z: Sem	± 0.030	± 0.030	± 0.030	± 0.030	± 0.030	± 0.030
p	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
M: Sem	± 0.08	± 0.08	± 0.08	± 0.08	± 0.08	± 0.08
p	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
CD (5%)	0.53	0.53	0.53	0.53	0.53	0.53

Z: Comparison between zones, M: Comparison between months, Values after ± indicate standard deviations

Table 25. Leaf mass loss for *Avicennia officinalis* and *Sonneratia caseolaris* in three zones of mangrove forest at Puduvyppu.

Months	<i>Avicennia officinalis</i>			<i>Sonneratia caseolaris</i>		
	Zone I (g)	Zone II (g)	Zone III (g)	Zone I (g)	Zone II (g)	Zone III (g)
0	15.35 ± 0.00	15.35 ± 0.00	15.35 ± 0.00	13.96 ± 0.00	13.96 ± 0.00	13.96 ± 0.00
1	10.30 ± 1.63	10.47 ± 0.85	9.343 ± 1.23	9.99 ± 1.36	10.41 ± 1.15	10.19 ± 0.81
2	7.12 ± 1.10	9.22 ± 0.68	10.78 ± 1.08	8.83 ± 1.72	5.96 ± 1.62	8.07 ± 0.95
3	6.06 ± 1.18	8.04 ± 0.87	8.85 ± 1.05	5.69 ± 0.55	5.33 ± 0.34	6.14 ± 0.58
4	6.15 ± 1.39	7.73 ± 2.22	8.09 ± 0.35	5.54 ± 0.85	5.24 ± 0.53	6.19 ± 0.64
5	5.64 ± 0.61	7.77 ± 0.51	8.36 ± 0.48	4.38 ± 0.54	5.10 ± 0.99	5.70 ± 1.055
6	6.00 ± 0.55	7.13 ± 0.67	8.68 ± 1.15	5.81 ± 0.50	4.11 ± 2.01	5.29 ± 0.28
7	4.99 ± 1.22	5.63 ± 0.19	8.47 ± 0.63	4.01 ± 1.23	3.62 ± 1.34	5.31 ± 0.59
8	3.57 ± 0.59	4.70 ± 0.99	8.16 ± 0.55	4.20 ± 0.34	3.62 ± 2.05	4.98 ± 1.18
9	2.68 ± 0.24	4.73 ± 2.90	7.00 ± 0.45	0.56 ± 0.17	3.31 ± 0.53	4.66 ± 0.86
10	2.37 ± 1.10	2.80 ± 0.88	7.52 ± 1.36	0.57 ± 0.25	3.46 ± 0.37	4.45 ± 0.27
11	1.72 ± 0.82	2.20 ± 0.36	7.43 ± 0.92	0.37 ± 0.05	2.20 ± 0.52	3.17 ± 0.64
12	1.88 ± 0.66	1.97 ± 0.46	6.56 ± 1.91	0.39 ± 0.29	1.28 ± 0.25	1.56 ± 0.59
Z: Sem	± 0.030	± 0.030	± 0.030	± 0.030	± 0.030	± 0.030
p	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
M: Sem	± 0.08	± 0.08	± 0.08	± 0.08	± 0.08	± 0.08
p	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
CD (5%)	0.53	0.53	0.53	0.53	0.53	0.53

Z: Comparison between zones, M: Comparison between months, Values after ± indicate standard deviations

Table 26. Leaf mass loss for *Excoecaria agallocha* and *Acanthus ilicifolius* in three zones of mangrove forest at Pudukkottai.

Months	<i>Excoecaria agallocha</i>			<i>Acanthus ilicifolius</i>		
	Zone I (g)	Zone II (g)	Zone III (g)	Zone I (g)	Zone II (g)	Zone III (g)
0	14.83 ± 0.00	14.83 ± 0.00	14.83 ± 0.00	13.74 ± 0.00	13.74 ± 0.00	13.74 ± 0.00
1	7.45 ± 0.15	4.10 ± 1.36	6.73 ± 0.65	9.20 ± 1.76	4.27 ± 1.09	6.77 ± 1.14
2	3.50 ± 0.78	2.99 ± 0.46	4.09 ± 0.77	4.74 ± 0.50	2.42 ± 0.49	3.34 ± 0.37
3	1.40 ± 0.18	2.78 ± 0.91	3.86 ± 1.03	4.01 ± 1.36	2.32 ± 0.71	3.67 ± 0.97
4	1.31 ± 0.34	2.77 ± 1.20	1.47 ± 1.09	4.51 ± 1.43	2.08 ± 0.33	3.22 ± 1.09
5	1.07 ± 0.10	1.92 ± 0.41	0.67 ± 0.22	2.11 ± 0.41	2.31 ± 1.09	2.22 ± 0.54
6	0.57 ± 0.29	1.27 ± 1.08	0.35 ± 0.04	1.40 ± 0.14	1.81 ± 1.16	2.66 ± 0.66
7	0.49 ± 0.13	0.52 ± 0.30	0.62 ± 0.34	1.25 ± 0.79	1.10 ± 0.19	2.49 ± 0.43
8	0.43 ± 0.25	0.48 ± 0.15	0.52 ± 0.12	0.49 ± 0.15	0.84 ± 0.07	1.41 ± 0.55
9	0.33 ± 0.10	0.45 ± 0.22	0.43 ± 0.33	0.42 ± 0.20	0.78 ± 0.11	1.26 ± 0.36
10	0.30 ± 0.11	0.41 ± 0.21	0.33 ± 0.11	0.39 ± 0.27	0.67 ± 0.20	1.18 ± 0.53
11	0.28 ± 0.14	0.24 ± 0.09	0.30 ± 0.15	0.34 ± 0.02	0.26 ± 0.14	1.15 ± 0.60
12	0.12 ± 0.01	0.19 ± 0.04	0.26 ± 0.08	0.33 ± 0.04	0.39 ± 0.27	0.96 ± 0.06
Z: Sem	± 0.030	± 0.030	± 0.030	± 0.030	± 0.030	± 0.030
p	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
M: Sem	± 0.08	± 0.08	± 0.08	± 0.08	± 0.08	± 0.08
p	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
CD (5%)	0.53	0.53	0.53	0.53	0.53	0.53

Z: Comparison between zones, M: Comparison between months, Values after ± indicate standard deviations

Table 27. Decay rate coefficients of six species in three different zones of mangrove forest at Pudukkottai.

Species	Zone I					Zone II					Zone III					Mean	
	k	R ²	SEE	n	t _{0.5}	k	R ²	SEE	n	t _{0.5}	k	R ²	SEE	n	t _{0.5}	k	t _{0.5}
<i>Excoecaria agallocha</i>	-0.44 ^{a A}	0.98	0.02	8	1.58	-0.41 ^{a B}	0.99	0.02	10	1.67	-0.43 ^{a AB}	0.98	0.02	8	1.62	-0.42 ^a	1.62
<i>Acanthus ilicifolius</i>	-0.30 ^{ab AB}	0.99	0.01	7	2.29	-0.35 ^{ab A}	0.97	0.02	11	1.95	-0.27 ^{ab BC}	0.97	0.01	12	2.58	-0.31 ^{ab}	2.27
<i>Sonneratia caseolaris</i>	-0.29 ^{ab A}	0.93	0.02	9	2.35	-0.19 ^{abc B}	0.98	0.01	12	3.67	-0.15 ^{bc C}	0.96	0.01	12	4.5	-0.21 ^{abc}	3.5
<i>Avicennia officinalis</i>	-0.20 ^{bc A}	0.99	0.01	12	3.54	-0.17 ^{bc AB}	0.99	0.01	12	4.10	-0.13 ^{bc C}	0.90	0.01	12	5.2	-0.16 ^{bc}	4.28
<i>Bruguiera cylindrica</i>	-0.20 ^{bc A}	0.97	0.01	12	3.42	-0.18 ^{bc AB}	0.92	0.02	12	3.89	-0.14 ^{bc C}	0.90	0.01	12	5.1	-0.17 ^{bc}	4.14
<i>Rhizophora mucronata</i>	-0.06 ^{c A}	0.99	0.01	12	10.87	-0.05 ^{c AB}	0.96	0.01	12	12.95	-0.03 ^{c BC}	0.98	0.01	12	23.1	-0.05 ^c	15.64
p	≤0.01					≤0.01					≤0.01					≤0.01	

k : Decay rate coefficient

R² : Coefficient of determination

SEE : Standard error of estimate

p : Probability level of significance for the fitted -ve exponential decay model

t_{0.5} : Half life (months)

Means followed by the same lower case superscript are not significantly different within the same column

Means followed by the same upper case superscript are not significantly different among zones.

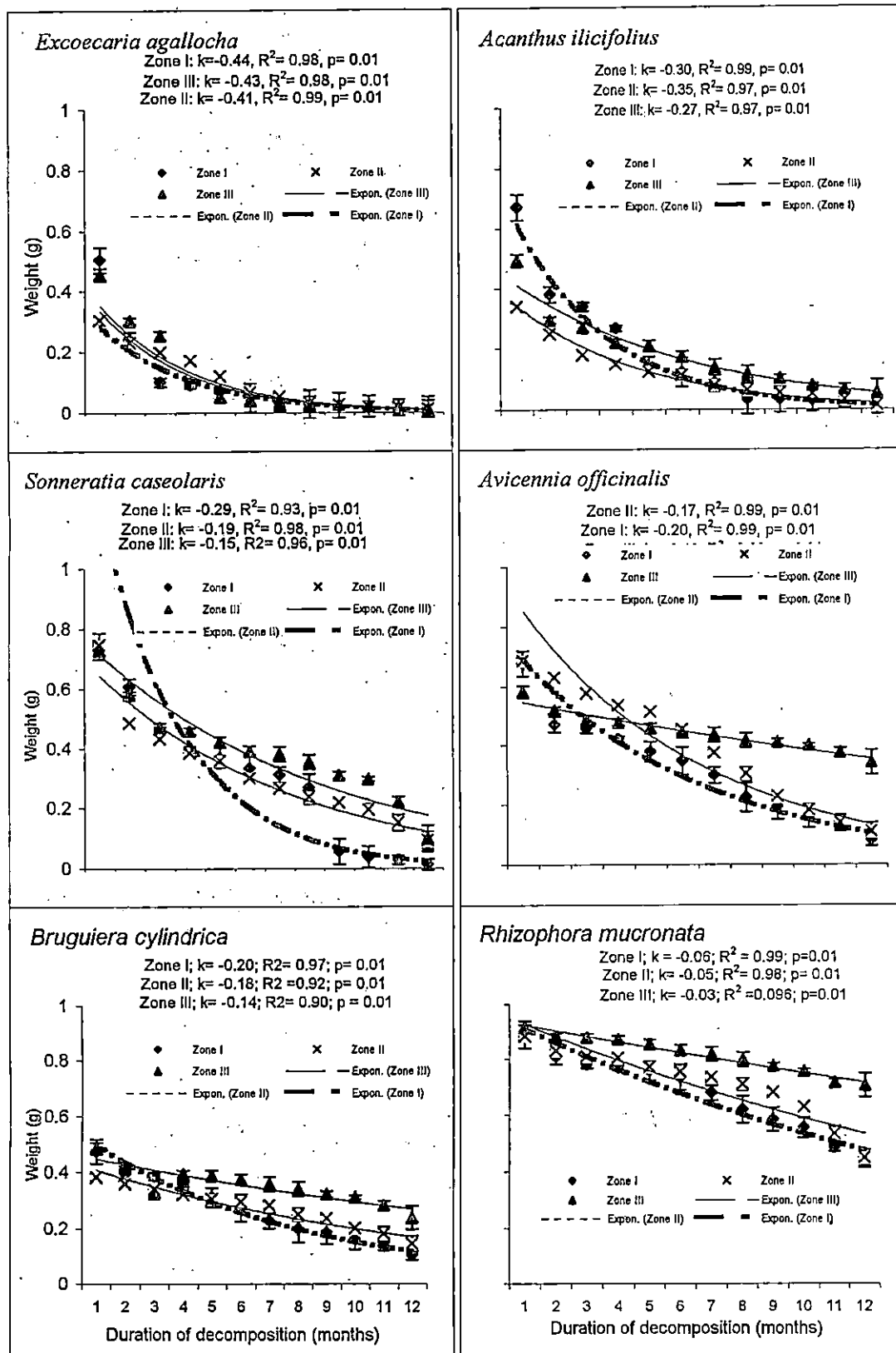


Fig. 10 Decay curves for six species in three zones of mangrove forest at Puduvypu (Error bars indicate standard deviations)

agallocha, *Acanthus ilicifolius* and *Sonneratia caseolaris* (Table 28). In contrast, high initial lignin and low initial nitrogen concentrations were observed in *Avicennia officinalis* and *Rhizophora mucronata*. *Bruguiera cylindrica*, however, showed higher initial nitrogen and lignin contents. Variations in lignin: nitrogen ratio followed a similar pattern as that of the initial per cent lignin. *A. ilicifolius* and *R. mucronata* recorded the lowest and the highest values respectively. Linear regression linking decay rate coefficients and biochemical properties of decomposing leaves are presented in Table 29 and Fig. 11. Decay rate coefficient was negatively correlated ($p < 0.01$) with initial lignin ($R^2 = 0.84$) and initial lignin: nitrogen ratio ($R^2 = 0.81$).

4.4.2 Nutrient dynamics of decomposing litter mass

Data on NPK concentrations (absolute and relative) of the decomposing leaf litter at different intervals in different zones are furnished in Tables 30-35. Differences in the N, P and K concentrations were significant among intervals ($p < 0.01$), zones ($p < 0.01$) and species ($p < 0.01$).

The N concentration in the decomposing samples of *R. mucronata* and *S. caseolaris* did not show much variations until the last sampling, except for *A. officinalis* and *E. agallocha* (Fig 12). In both cases, N concentration of litter mass increased initially, and was followed by a decline at about 3 months, thereafter it followed an asymptotic pattern. Whereas, N concentration decreased in case of *A. ilicifolius* and *B. cylindrica*. As regards to P concentrations, *R. mucronata*, *B. cylindrica*, *S. caseolaris*, *E. agallocha* and *A. officinalis* increased moderately during the course of decomposition, whereas, in *A. ilicifolius* it decreased. For K concentrations, there was a significant decrease except in *B. cylindrica*, which increased. Regarding interzonal variations, nutrient levels in zone III was greater than that of zone II and zone I ($p < 0.01$).

Relative proportion of nutrients remaining during the decomposition period showed profound variations among months ($p < 0.01$) and species ($p < 0.01$). As regards to interzonal differences, only variations in relative proportion of N ($p < 0.01$) were significant while P ($p = 0.433$) and K ($p = 0.069$) did not show statistically significant differences. The relative proportion of nutrient left at the end of the study period ranged from 50 to 1 per cent, 20 to 3 per cent and 15 to 1 per cent for N, P and

Table 28. Initial lignin percentage, initial nitrogen and initial lignin and nitrogen ratio of six mangrove species

Species	Initial lignin %	Initial nitrogen (%)	Initial lignin: nitrogen
<i>Excoecaria agallocha</i>	3.08 ^f	1.12 ^c	2.80 ^c
<i>Acanthus ilicifolius</i>	4.09 ^e	1.90 ^a	2.15 ^f
<i>Sonneratia caseolaris</i>	10.57 ^d	1.54 ^b	6.94 ^d
<i>Avicennia officinalis</i>	20.87 ^c	1.18 ^c	19.58 ^b
<i>Bruguiera cylindrica</i>	22.93 ^b	1.42 ^b	14.96 ^c
<i>Rhizophora mucronata</i>	24.86 ^a	0.84 ^d	29.69 ^a
	Sem ± 0.992	Sem ± 0.059	Sem ± 1.248
	p < 0.01	p < 0.01	p < 0.01

Table 29. Regression linking decay rate coefficient to the biochemical properties of decomposing leaf samples.

Decay rate coefficient	Biochemical properties of leaf	Intercept	SEE	Slope	SEE	R ²	p
	Initial lignin (%)	0.395	0.045	-0.012	0.003	0.84	0.01
	Initial nitrogen (%)	0.035	0.220	0.139	0.160	0.16	0.43
	Initial lignin: nitrogen ratio	0.357	0.041	-0.011	0.003	0.81	0.01

n = 6, R² = Coefficient of determination, SEE = Standard error of estimate, p = Probability value.

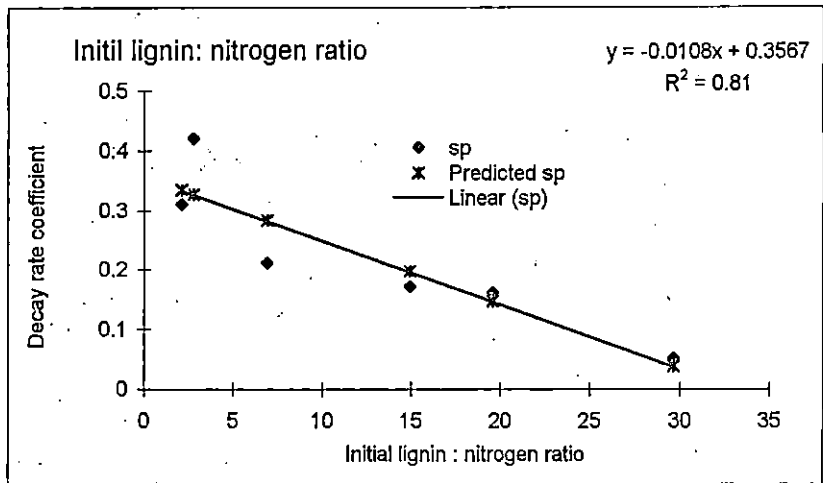
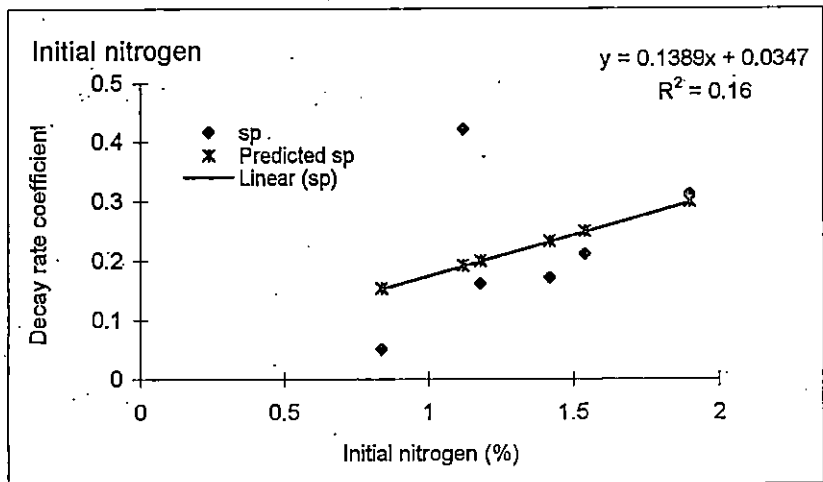
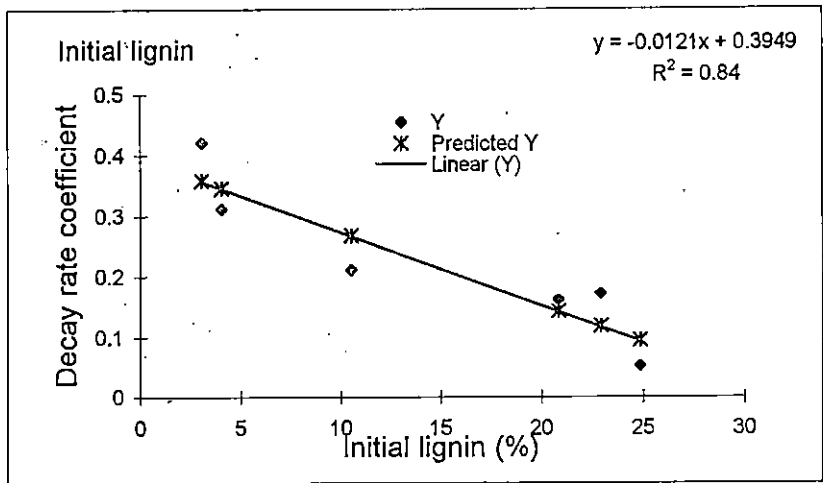


Fig. 11 Relationships between decay rate coefficient and biochemical properties of mangrove leaf litter

Table 30. Nutrient remaining in the decomposing leaf litter of *Rhizophora mucronata* in three zones of mangrove forest of Pudukkottai.

Duration of decomposition	Zone I						Zone II						Zone III					
	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR
0	0.89	100	0.061	100	0.515	100	0.89	100	0.061	100	0.515	100	0.89	100	0.061	100	0.515	100
1	1.22	121	0.052	53	0.197	28	1.09	108	0.073	74	0.071	10	1.06	108	0.055	58	0.103	15
2	1.09	98	0.043	40	0.094	12	1.22	114	0.069	66	0.103	14	1.25	123	0.062	63	0.028	4
3	0.82	71	0.058	52	0.133	16	1.29	117	0.073	53	0.072	10	0.97	96	0.087	88	0.110	16
4	1.41	122	0.064	57	0.201	25	1.27	114	0.061	57	0.165	21	1.05	103	0.073	73	0.174	25
5	0.41	35	0.046	40	0.175	21	1.04	90	0.056	49	0.175	22	1.22	117	0.060	59	0.152	21
6	1.19	98	0.070	27	0.340	41	1.29	109	0.034	29	0.172	21	1.06	99	0.085	46	0.224	30
7	0.80	60	0.044	34	0.219	24	1.51	124	0.048	40	0.176	21	1.02	93	0.058	54	0.200	27
8	1.60	110	0.085	61	0.220	22	1.22	97	0.052	42	0.188	22	1.13	101	0.092	69	0.150	19
9	1.09	71	0.047	31	0.239	23	0.95	72	0.089	69	0.181	20	1.16	100	0.029	26	0.142	18
10	1.73	107	0.041	26	0.194	17	1.17	83	0.028	20	0.385	39	0.61	52	0.121	46	0.137	17
11	1.36	74	0.040	22	0.158	12	1.21	73	0.097	59	0.244	21	0.68	54	0.137	25	0.094	11
12	1.29	62	0.033	16	0.145	10	0.95	48	0.044	23	0.253	18	0.68	54	0.162	19	0.096	11
Z) Sem	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19
p	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07
M) Sem	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53
p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CD (5%)	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64

PR: Relative Proportion of Nutrient Remaining (%)

Z : Comparison between zones, M : Comparison between months

Table 31. Nutrient remaining in the decomposing leaf litter of *Bruguiera cylindrica* in three zones of mangrove forest of Pudukkottai

Duration of decomposition	Zone I						Zone II						Zone III					
	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR
0	1.42	100	0.065	100	0.294	100	1.42	100	0.065	100	0.294	100	1.42	100	0.065	100	0.294	100
1	2.50	83	0.136	91	0.252	40	1.78	48	0.056	30	0.077	10	1.70	58	0.126	86	0.121	20
2	1.83	51	0.165	62	0.197	26	1.40	35	0.136	69	0.115	14	1.63	48	0.203	120	0.169	24
3	0.99	27	0.190	103	0.172	22	1.37	33	0.192	91	0.143	16	1.81	51	0.120	38	0.260	36
4	0.95	24	0.147	83	0.193	23	1.11	25	0.093	42	0.195	21	1.2	33	0.110	50	0.244	33
5	1.04	23	0.120	57	0.219	23	1.16	25	0.092	26	0.218	23	1.09	30	0.079	43	0.234	31
6	0.48	92	0.066	26	0.414	38	1.37	28	0.116	48	0.225	23	1.22	32	0.097	41	0.368	47
7	1.28	20	0.101	32	0.262	20	1.12	22	0.111	50	0.331	32	1.32	33	0.090	46	0.356	43
8	1.38	19	0.131	37	0.245	16	1.12	20	0.087	47	0.333	32	1.13	27	0.068	33	0.304	35
9	0.92	12	0.103	18	0.212	13	1.23	20	0.103	34	0.296	25	1.20	27	0.095	43	0.241	26
10	1.50	17	0.137	31	0.208	11	1.16	16	0.149	42	0.364	15	1.09	24	0.138	52	0.190	20
11	1.29	12	0.281	24	0.209	10	1.22	15	0.119	26	0.320	20	1.09	22	0.199	39	0.220	21
12	1.36	10	0.226	16	0.253	9	1.30	13	0.154	18	0.356	17	0.88	15	0.115	34	0.469	38
Z) Sem	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19
p	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07
M) Sem	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53
p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CD (5%)	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64

.PR: Relative Proportion of Nutrient Remaining (%)

Z : Comparison between zones, M : Comparison between months

Table 32. Nutrient remaining in the decomposing leaf litter of *Avicennia officinalis* in three zones of mangrove forest of Pudukkottai.

Duration of decomposition	Zone I						Zone II						Zone III					
	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR
0	1.23	100	1.105	100	0.552	100	1.23	100	1.105	100	0.552	100	1.23	100	1.105	100	0.552	100
1	1.95	144	0.168	98	0.069	8	2.42	134	0.232	138	0.138	17	2.48	117	0.080	41	0.052	48
2	2.58	99	0.230	85	0.131	11	2.65	135	0.131	129	0.088	10	3.17	134	0.149	67	0.252	24
3	2.24	83	0.178	70	0.237	20	2.63	123	0.130	76	0.151	16	1.77	69	0.109	46	0.245	21
4	1.27	43	0.124	54	0.312	24	1.09	47	0.134	72	0.203	20	1.56	61	0.118	42	0.294	26
5	1.02	31	0.109	44	0.330	23	1.07	45	0.075	24	0.209	19	1.16	43	0.056	22	0.193	16
6	1.83	51	0.066	20	0.215	13	1.58	58	0.157	62	0.165	14	1.56	56	0.080	31	0.414	33
7	2.13	51	0.065	17	0.249	13	1.49	45	0.130	53	0.220	15	1.68	59	0.121	46	0.335	26
8	2.02	36	0.107	21	0.200	8	1.70	42	0.156	46	0.234	13	1.31	44	0.105	30	0.242	18
9	1.90	29	0.104	17	0.198	7	1.43	26	0.046	9	0.360	15	1.43	47	0.125	44	0.227	17
10	1.77	22	0.128	17	0.178	5	1.77	26	0.115	18	0.134	4	1.59	51	0.167	58	0.376	27
11	1.50	16	0.169	21	0.327	7	1.40	16	0.171	12	0.542	13	1.60	48	0.106	34	0.496	34
12	0.44	3	0.138	9	0.146	2	1.11	10	0.138	11	0.325	6	1.54	43	0.075	22	0.404	25
Z) Sem	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19
p	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07
M) Sem	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53
p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CD (5%)	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64

PR: Relative Proportion of Nutrient Remaining (%)

Z : Comparison between zones, M : Comparison between months

Table 33. Nutrient remaining in the decomposing leaf litter of *Sonneratia caseolaris* in three zones of mangrove forest of Puduvyppu.

Duration of decomposition	Zone I						Zone II						Zone III					
	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR
0	1.53	100	0.091	100	0.630	100	1.53	100	0.091	100	0.630	100	1.53	100	0.091	100	0.630	100
1	2.13	103	0.167	77	0.285	34	2.81	137	0.281	150	0.157	19	2.17	130	0.204	107	0.237	27
2	2.20	87	0.205	89	0.327	32	2.83	89	0.226	78	0.195	15	2.69	101	0.224	93	0.206	19
3	1.43	42	0.080	49	0.286	21	1.54	43	0.243	75	0.271	19	2.26	70	0.282	95	0.272	20
4	1.31	34	0.135	50	0.327	20	2.06	52	0.134	37	0.307	19	2.31	69	0.138	45	0.170	12
5	1.86	45	0.105	36	0.334	19	1.63	38	0.127	32	0.346	20	2.45	67	0.150	45	0.386	26
6	2.04	44	0.080	19	0.203	11	2.31	45	0.107	23	0.319	15	2.13	54	0.102	28	0.306	19
7	1.91	39	0.149	31	0.347	17	1.31	23	0.158	30	0.317	13	2.24	55	0.116	32	0.307	18
8	1.02	18	0.159	30	0.310	13	1.50	23	0.148	25	0.426	16	2.27	61	0.121	30	0.255	14
9	1.02	40	0.114	4	0.313	3	2.26	32	0.059	9	0.379	13	2.31	46	0.116	25	0.379	18
10	1.86	4	0.103	3	0.391	2	1.99	25	0.075	10	0.194	6	2.45	47	0.186	39	0.204	10
11	1.77	3	0.205	2	0.152	1	1.49	15	0.165	12	0.352	8	1.90	27	0.198	31	0.216	8
12	0.84	1	0.217	0	0.171	0	1.76	11	0.135	9	0.125	2	1.54	10	0.175	12	0.433	7
Z) Sem	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19
p	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07
M) Sem	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53
p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CD (5%)	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64

PR: Relative Proportion of Nutrient Remaining (%)

Z : Comparison between zones, M : Comparison between months

Table 34. Nutrient remaining in the decomposing leaf litter of *Excoecaria agallocha* in three zones of mangrove forest of Pudukkottai.

Duration of decomposition	Zone I						Zone II						Zone III					
	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR
0	1.17	100	0.071	100	1.064	100	1.17	100	0.071	100	1.064	100	1.17	100	0.071	100	1.064	100
1	2.26	55	0.228	142	0.203	10	2.15	49	0.292	87	0.323	9	2.42	55	0.165	96	0.197	8
2	3.08	34	0.235	56	0.308	7	3.85	44	0.179	61	0.185	4	2.53	43	0.229	96	0.327	9
3	2.04	12	0.237	29	0.308	3	1.98	28	0.203	66	0.289	5	2.56	30	0.198	61	0.389	9
4	0.99	10	0.173	21	0.383	3	1.90	13	0.156	24	0.243	4	1.83	11	0.152	18	0.393	4
5	1.64	6	0.141	12	0.601	4	2.00	12	0.113	16	0.391	4	1.83	6	0.114	4	0.394	2
6	1.43	3	0.131	8	0.348	2	0.91	6	0.115	11	0.443	3	1.66	4	0.112	6	0.238	1
7	1.22	2	0.112	5	0.318	1	1.19	5	0.167	10	0.444	2	2.38	3	0.119	5	0.367	1
8	1.02	2	0.106	4	0.236	1	1.68	2	0.184	7	0.425	1	1.27	2	0.104	4	0.212	1
9	0.91	2	0.110	3	0.383	1	1.09	2	0.034	1	0.409	1	1.1	2	0.167	4	0.364	1
10	0.66	1	0.189	4	0.347	1	1.86	2	0.230	2	0.584	1	1.36	2	0.056	1	0.326	1
11	1.09	1	0.234	2	0.228	0	1.74	2	0.200	1	0.574	1	1.36	2	0.139	2	0.427	1
12	0.95	07	0.155	1	0.229	0	1.61	1	0.227	1	0.561	1	1.11	1	0.117	1	0.013	0
Z) Sem	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19
p	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07
M) Sem	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53
p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CD (5%)	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64

PR: Relative Proportion of Nutrient Remaining (%)

Z : Comparison between zones, M : Comparison between months

Table 35. Nutrient remaining in the decomposing leaf litter of *Acanthus ilicifolius* in three zones of mangrove forest of Pudukkottai.

Duration of decomposition	Zone I						Zone II						Zone III					
	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR	N (%)	PR	P (%)	PR	K (%)	PR
0	1.9	100	0.112	100	2.190	100	1.9	100	0.112	100	2.190	100	1.9	100	0.112	100	2.190	100
1	1.30	80	0.310	128	0.388	12	1.70	38	0.240	50	0.243	4	1.43	63	0.256	77	0.161	5
2	1.68	61	0.262	61	0.395	6	2.26	50	0.274	42	0.200	2	1.70	39	0.262	47	0.252	3
3	1.36	36	0.221	40	0.261	3	1.65	19	0.243	27	0.216	2	1.38	36	0.174	29	0.226	4
4	1.24	14	0.134	22	0.579	7	0.93	12	0.182	23	0.433	3	1.27	21	0.194	26	0.247	2
5	0.97	8	0.170	15	0.636	4	1.16	13	0.103	10	0.343	2	1.25	20	0.112	14	0.319	3
6	0.60	9	0.123	11	0.337	3	1.23	5	0.146	10	0.581	3	1.08	15	0.132	15	0.379	2
7	0.68	5	0.143	8	0.252	1	1.22	5	0.177	8	0.446	2	0.73	17	0.208	15	0.523	3
8	0.86	2	0.166	3	0.013	0	0.66	6	0.127	5	0.301	1	0.92	8	0.122	9	0.372	2
9	1.09	1	0.090	2	0.011	0	1.04	3	0.109	4	0.362	1	1.09	5	0.100	6	0.437	2
10	0.91	1	0.187	3	0.487	1	1.36	5	0.083	3	0.022	0	1.38	6	0.176	8	0.339	1
11	0.77	1	0.157	2	0.492	1	1.25	3	0.189	4	0.340	0	1.25	5	0.123	5	0.217	1
12	0.36	1	0.090	1	0.335	0	1.41	1	0.135	1	0.189	0	1.22	3	0.252	4	0.482	1
Z) Sem	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19	±0.02	±0.76	±0.01	±3.14	±0.01	±0.19
p	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07	<0.01	<0.01	<0.01	0.39	<0.01	0.07
M) Sem	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53	±0.04	±1.35	±0.01	±5.26	±0.01	±0.53
p	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
CD (5%)	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64	0.20	6.73	0.031	26.18	0.049	2.64

PR: Relative Proportion of Nutrient Remaining (%)

Z : Comparison between zones, M : Comparison between months

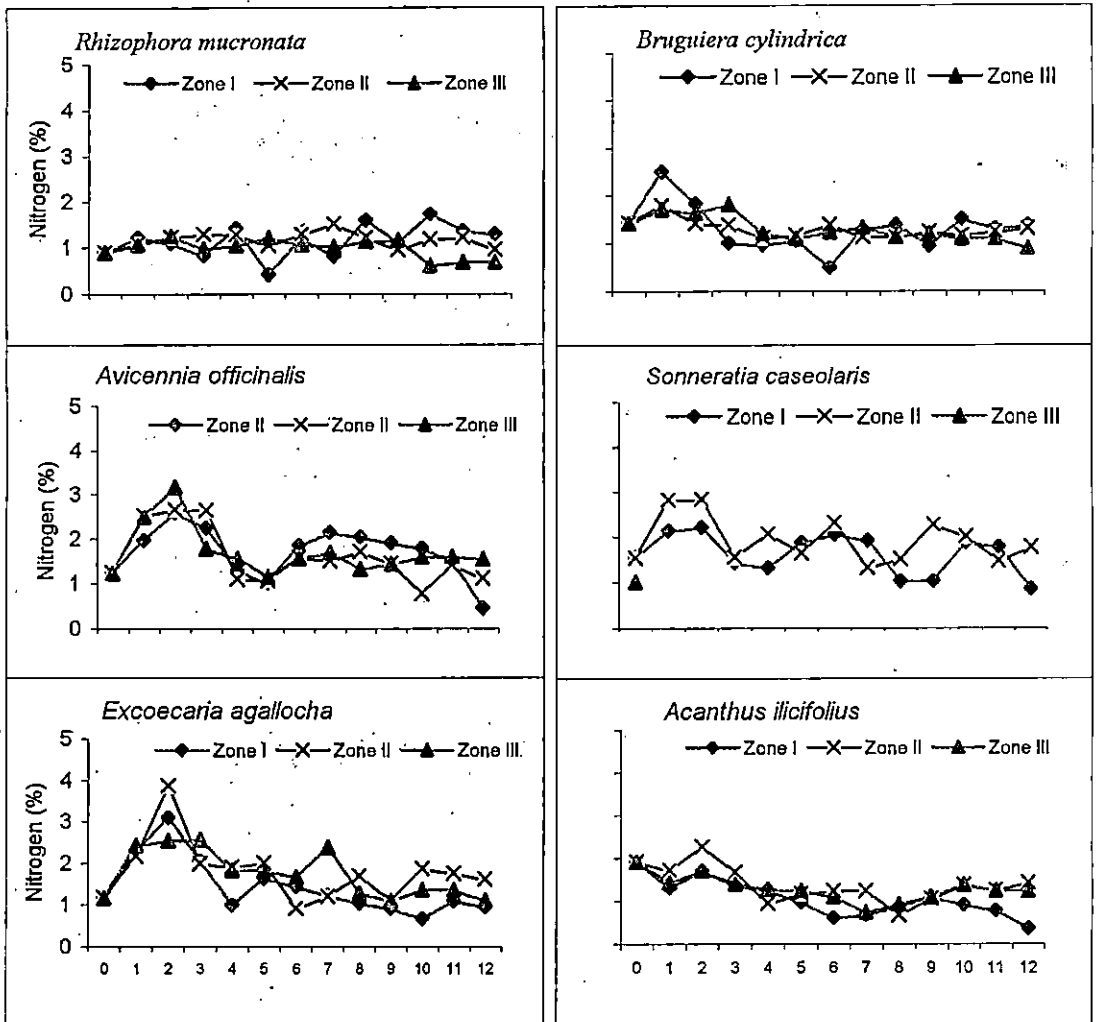


Fig. 12a Time course of change in absolute nitrogen concentration of decomposing litter mass

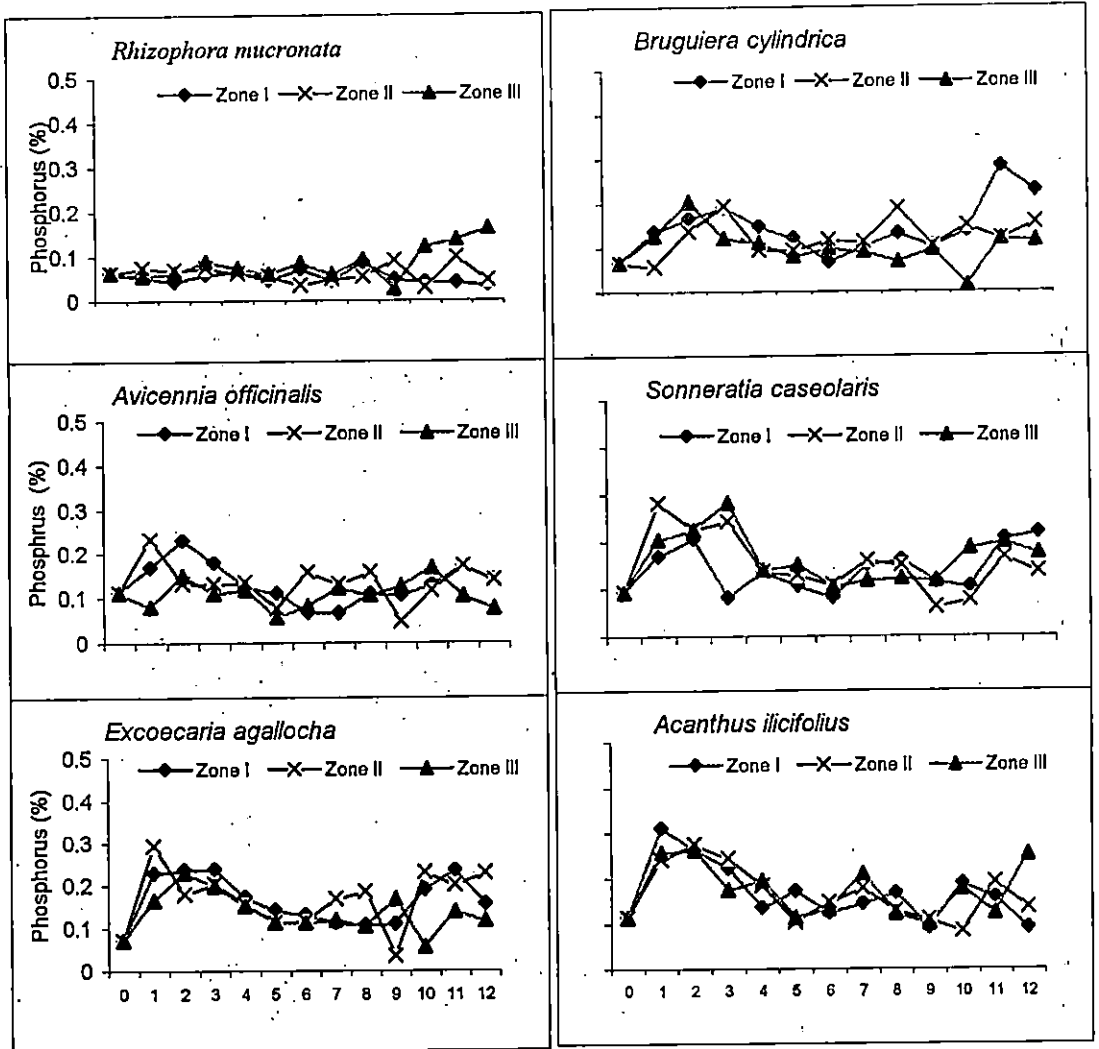


Fig. 12b Time course of change in absolute phosphorus concentration of decomposing litter mass

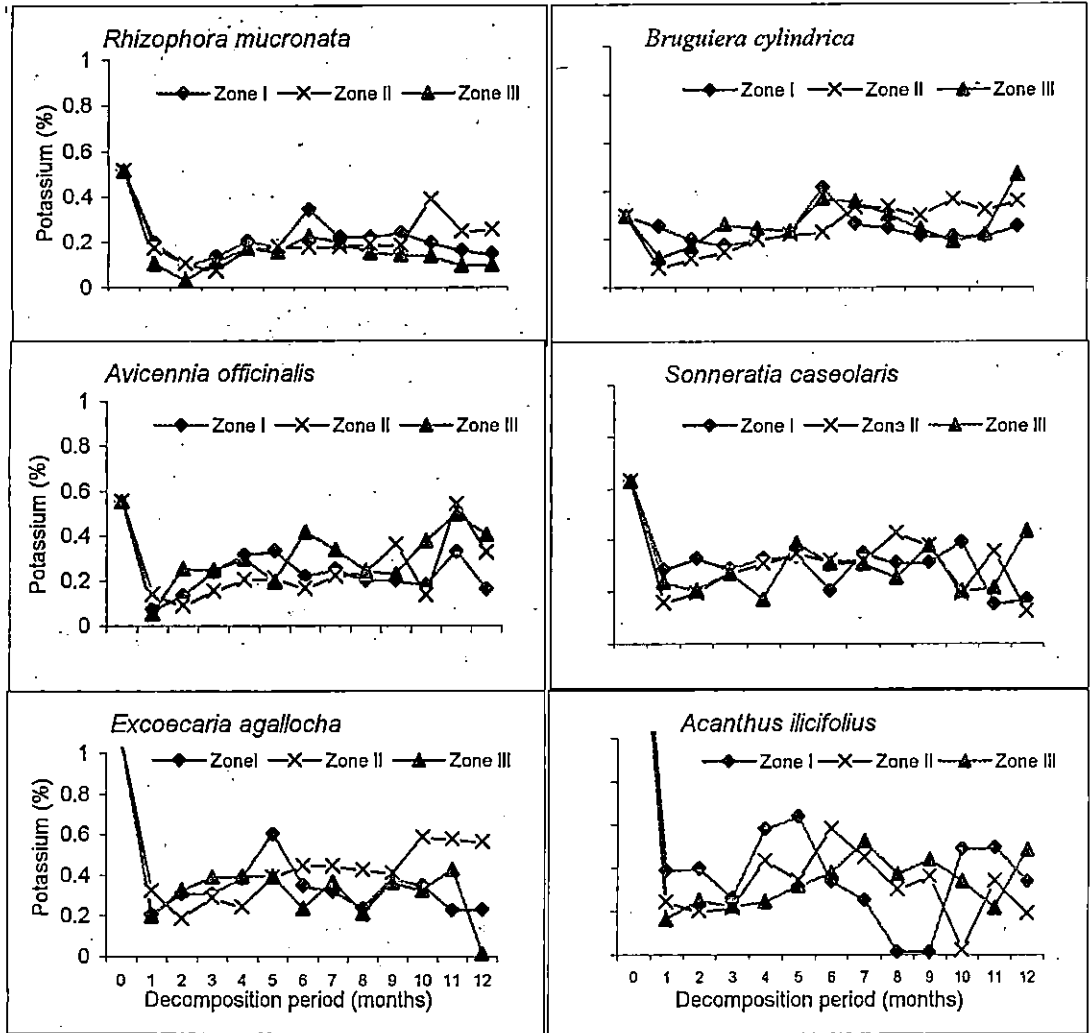


Fig. 12c Time course of change in absolute potassium concentration of decomposing litter mass

K respectively. Species differences were also profound in this respect. *Rhizophora mucronata* had the highest proportion of N (50%), P (20%) and K (15%) followed by *Avicennia officinalis* (N: 15%, P: 16%, K: 29%), *Bruguiera cylindrica* (N: 10%, P: 15%, K: 20%) and *Sonneratia caseolaris* (10%, 5% and 5% NPK respectively). *Excoecaria agallocha* and *Acanthus ilicifolius* had only traces of NPK. In general, Zone III had higher nitrogen accumulation than Zone II and Zone I.

Discussion

5. DISCUSSION

5.1 Zonation pattern and the floristic and edaphic attributes of Pudukkottai mangroves.

Zonation is a unique feature of a well developed mangrove ecosystem (Rodriguez, 1987). Zonation implies the existence of more or less well defined vegetation zones along an environmental gradient, each dominated by distinct species associations. Many previous studies (Watter, 1991; Mckee, 1993; Singh, 1996; Bunt, 1996; Chen and Twilley, 1998) reported clear zonation patterns in the mangrove ecosystems around the world. In respect of Pudukkottai mangroves, although a clear zonation pattern with distinct species associations was not discernible, characteristic variations in diversity and distribution of species were noticeable (Table 2 and Fig.3). Accordingly, the mangrove area were broadly delineated into three zones, zone I (0-300 m from the sea), zone II (300-800 m from the sea) and zone III (800 to 1200 m from the sea). Data presented in Table 2 and Fig. 3 also show that zone I has had five true mangroves (*Sonneratia* sp., *Avicennia* sp., *Excoecaria agallocha*, *R. mucronata* and *Bruguiera gymnorhiza*) and 18 mangrove associates, Zone II was almost entirely dominated by *A. officinalis*. However, a few scattered individuals of *A. marina* and *B. cylindrica* were recorded in this zone. Conversely, zone III has had a near total dominance of *A. officinalis* and *A. marina*. Watter (1991) also reported a three-zone system in the mangroves of Mumbai, where the 1st zone was comprised of *Sonneratia apetalla* and *Avicennia officinalis*. *Avicennia alba* and *Rhizophora apiculata* colonized the second zone, while *Acanthus ilicifolius*, *Ceriops tagal* and *Aegicerus corniculatum* occupied the third zone.

Species diversity at Pudukkottai decreased from the sea-land interface to the land-interior (Table 3). Simpson's diversity index (D) was highest (0.786) in zone I and lowest (0.310) in zone III. Likewise, Shannon-Wiener's diversity index (H') decreased along the transect from land-ocean interface (zone I = 2.9 to zone III = 0.56). Although the H' values presently reported for the interior zones is in agreement with that of Nameer *et al.* (1992) (0.56) and Kumar and Kumar (1997) (0.48) at this site, they are substantially higher in the distal regions. Furthermore, Shannon-Wiener's

indices (H') presently reported are lower than that of other ecosystems and mangrove formations elsewhere. For example, Pascal (1988) reported H' values ranging from 3.6 to 4.3 for evergreen forests of Western Ghats. For mangrove ecosystem, several authors (Steve, 1993; Licum Li *et al.*, 1993; Karlapkar and Bhosale, 1993) have reported H' values ranging from 1.0 to 3.2.

Stand density (13.57 to 49.00 $m^2 ha^{-1}$), abundance (21.3 to 80.5), and percentage frequency (88 to 100%) increased along the land ward transect (Tables 4-6 and Figs. 4 and 5). Such diametrically opposite trends in diversity and phytosociological parameters are not unusual and may be attributed to the restricted distribution of some species (Rabinowitz, 1978) and/or their monospecificity (Selvam *et al.*, 1991). The high concentration dominance ($cd = 0.86$) and importance value index (259) for the Puduvyppu forest (Kumar and Kumar, 1997) further reinforces the argument of *A. officinalis* domination at this site.

Propagule availability (Jimenez and Sauter, 1991) and edaphic attributes (Tilman, 1982) co-determine species composition of a forest stand. Propagule availability of mangrove forests in particular is dependent on tidal inundations (Rabinowitz, 1978) and is perhaps less dependent on the occurrence of reproductive trees (Jimenez and Sauter, 1991). As a result, the zonation pattern observed at this site may be explained based on the tidal sorting of propagules: small mangrove propagules (eg. *A. officinalis*, *B. cylindrica* and *A. marina*) requiring freedom from tidal disturbances, get established in the shallow sections of the forest (land ward side, *i.e.*, zone II and zone III). Wherein, large and heavy mangrove propagules, like that of *S. caseolaris*, *B. gymnorhiza* and *R. mucronata* due to their inability to be carried into shallow inland waters, become established in the deeper distal sections of the forests. Although, previous studies at this site (Nameer *et al.*, 1992; Kumar and Kumar, 1997) did not reveal clear zonation patterns owing to the juvenility of the stand, present results indicate that clear mangrove zones may emerge at this site in the near future. Presently, however, these are 'fuzzy' zones having less distinct boundaries, except in the case of the *Avicennia* zone (III).

As regards to edaphic attributes, a marked spatial variability in soil nutrient and salinity levels was observed along the sea-land ward transect (Table 9 and Fig. 7).

NPK concentrations and electrical conductivity increased as the distance from the land-ocean interface increased, whereas, pH decreased. Tam and Wong (1998) also reported similar changes in soil characteristics in the mangrove forests of Hong Kong. In addition, there may be seasonal variations in salinity levels (Zeng and Zueng, 2000). Furthermore, spatial heterogeneity of resources (nutrients) favours different plant species to colonize different locations (Tilman, 1985). Coincidentally, larger trees and higher density (Tables 5 and 6, Figs. 4 and 5) for *A. officinalis* and *A. marina* was observed in the inland locations where N (8044-10546 mg kg⁻¹), P (69-193 mg kg⁻¹), K (5000-6442 mg kg⁻¹) availabilities were higher.

Distribution of species is also related with soil salinity levels. For instance, electrical conductivity at the site ranged from 2.18 to 17.25 dS m⁻¹ along the transect. Clough (1984) reported that the optimum soil salinity for *Avicennia marina* ranged from 3.5 to 17.5 dS m⁻¹, implying that *A. officinalis* can tolerate relatively higher levels of salinity. In the present study, a decrease in salinity levels towards the seaward side of the study site may be a case of "flushing the substrate" during rains where the canopy is sparse (sampling was done in May when about 395 mm rainfall was received, Table 1). However, in the absence of data on seasonal variations in soil salinity levels it is impossible to draw firm conclusion in this respect.

5.2 Natural regeneration of mangrove species

Regenerant density was high (196-348 seedlings 100 m⁻²) in the central part of the forest (700-800 m from the sea) and it decreased both along the sea-ward and land-ward side (Table 12). In his context, Jimenez (1990) reported that seedling mortality is high in a monospecific stand than in mixed species stand. Perhaps, monospecific stand development by *Avicennia* towards the landward end reduced seedling density. Whereas, seedlings of *A. officinalis* and *B. cylindrica* owing to their smaller seed size cannot establish themselves towards the seaward side because of frequent tidal inundation.

Among the tree species, *Avicennia* sp. had more than 70 per cent of the seedling population in the lower height class (< 50 cm), whereas, *B. cylindrica* was well represented (70%) in the higher size classes (Table 12). Although *A. officinalis* seedlings in the two higher size classes (50-100 cm and >100 cm) were poorly

represented, the diameter structure of the stand (>10 cm diameter) indicated a negative 'J' shaped pattern implying adequate regeneration status for most species (Table 7 and Fig. 6).

The truncated seedling distribution pattern for *A. officinalis* (Table 12) can be explained based on its shade intolerant nature (Clarke and Allaway, 1993). This means that *A. officinalis* which are abundant in the smaller seedling category (<50 cm) is perhaps incapable of maturing into the higher size classes under its own understorey. Whereas, *B. cylindrica* being shade tolerant (Boto and Wellington, 1984), had well-established seedlings in all the seedling height classes. As a result, the 'pioneer' *A. officinalis* which is presently most abundant at Pudukkottai may give way to a more mixed species stand with greater occurrence of other shade tolerant species (e.g. *B. cylindrica* and *R. mucronata*) if the site is protected from large scale disturbances. However, forests at Pudukkottai are under a constant threat of firewood collection and other forms of disturbances such as aquaculture, non-wood forest product collection and so on. In these circumstances, *A. officinalis* may continue to be established in the canopy gap and the forests are likely to retain the monospecificity of *A. officinalis*.

5.3 Leaf phenology

Mangrove ecosystems are subjected to various kinds of stresses. Water stress (changing salinity levels and associated "physiological drought") and temperature stress are probably the most important. They not only decide the growth and abundance of mangrove species but also their physiological traits, which in turn determine the phenological patterns (Borchert, 1994). However, very few attempts have been made to characterize the phenological trends of the mangrove ecosystems in Kerala, although such studies are abundant elsewhere (Stienke and Charles, 1984; Lopez-Portillo and Ezcurra, 1985; Duke, 1990; Gwada *et al.*, 2000).

Data on phenological traits of important mangrove species at Pudukkottai (Tables 13 to 18) reveal that leaf production and leaf fall in all species except *R. mucronata* and *B. cylindrica* increased during the rainy season (April-July) and winter (October-February) respectively. Leaf flushing during the rainy season was reported by many authors (Fournier and Fournier, 1986; Boinski and Fowler, 1989; Porras,

1991; Spencer *et al.*, 1986). In the instant case, April-May was characterized by summer rains, with moderately higher temperatures (Table 1). This apparently stimulated leaf production in *E. agallocha*, *S. caseolaris* and *A. officinalis*. Pearson's correlation values also showed that rainfall ($r = 0.877^{**}$) and relative humidity ($r = 0.821^{**}$) most influenced the total number of leaves per shoot (Table 19 and Fig. 8) in *E. agallocha* and *S. caseolaris*.

Though temperature seems to be a key factor influencing leaf production, higher temperatures ($> 30^{\circ}\text{C}$) may retard leaf production (Gwada *et al.*, 2000). Present data show that temperature exerted a negative impact on total number of leaves ($r = -0.786^{**}$). Temperature effect on leaf number can be explained either by accelerated leaf fall and/or by reduced leaf production under high temperature regimes (Table 1). However, leaf fall in *A. officinalis*, *S. caseolaris* and *E. agallocha* peaked during winter season (Tables 13, 14 and 15). This phenomenon is comparable to that described by Gwada *et al.* (2000) for *Kandelia candel* in Japan. The winter period at Pudukkottai is associated with relatively lower rainfall and moderately low temperatures (Table 1 and Fig. 1). Thus, evapo-transpirational demands may increase resulting in higher solute concentrations in the soil. The consequent lower osmotic potential may affect plant water balance (Ranjan *et al.*, 2001). Thus, an episode of stress can lead to a greater abscisic acid (ABA) production resulting in greater leaf fall.

Among the major species at Pudukkottai, *E. agallocha* and *S. caseolaris* were leafless for a short period (1-2 months) during February-April (Tables 14 and 15). This may be explained based on the "salt accumulation" mechanism of these species (Dagar *et al.*, 1991). Large amounts of sodium and chloride ions accumulate in the leaves to make them fleshy. However, during an episode of water stress (high salinity in water) these ions are excluded through leaf fall and the trees remain leafless for a short period.

B. cylindrica and *R. mucronata* showed less variations in respect of leaf production and leaf fall and they persisted throughout the study period (Table, 16 and 17). Similar observations were made by Christensen and Wiium-Andersen (1977) for *R. apiculata* in Australia. They further reported that *R. apiculata* had continuous and

erratic leaf fall and a highly variable and aseasonal (no particular season) leaf production. Fruit fall in all species peaked during rainy season (Table 18), which is comparable with the observations made by Naskar and Mandal (1999).

Results of the present study also indicate that there is a pronounced climatic influence on vegetative and reproductive phenology of the mangroves, which is not unusual. The Pudúvypu mangrove ecosystem, which has a distinctive array of species, has been less studied in terms of their phenology. Information on the phenological traits is helpful in predicating the interaction between plants and the aquatic fauna. This is particularly important for the fish population in mangrove ecosystem, which derive a significant part of feed requirements either directly or indirectly through the detritus cycle. In addition, the mangrove flora and their phenological pattern may influence the water temperature by providing shade. When the trees are leafless possibly water temperature may rise and the light regimes on the surface of the land also get altered. Thus, mangrove vegetation impacts the aquatic fauna significantly by affecting their migration, abundance, feeding, breeding and diversity.

5.4 Litterfall

Litter production dynamics in the estuarine ecosystems is the primary mechanism of export of organic matters and nutrients (Tam *et al.*, 1990). The importance of mangrove leaf litter in the maintenance of detrital-based food webs in the coastal environment also has been well recognized (Ashton *et al.*, 1999). In view of this, several attempts were made around the world to quantify litterfall in these ecosystems (Hardiwinoto *et al.*, 1989; Steinke and Ward, 1990; Sukardjo and Yamada, 1992; May, 1999). However, very few studies on this (only two) has been carried out in the respect in the Indian subcontinent (Dagar and Sharma, 1991; Sengupta and Chaudhuri, 1993), none of them are, however, from the western coast of India.

The present study therefore is aimed to characterize litterfall in the newly formed mangrove forests at Pudúvypu among other mangroves. Results show that annual litterfall ranged from 1031 to 1364 g m⁻² yr⁻¹ with a mean production of about 1149 g m⁻² yr⁻¹ (Table 20). Although this is comparable with the litterfall values (680-1280 g m⁻² yr⁻¹) reported for the mangroves of Florida and Peurto Rico by Pool *et al.*

(1977), it is substantially greater than that reported for the *Avicennia marina* and *B. gymnorhiza* stands ($450 \text{ g m}^{-2} \text{ yr}^{-1}$) in South Africa (Steinke and Ward, 1990). Woodroffe *et al.* (1988) also claimed that annual litterfall in mangroves at Darwin harbour, Australia to be $> 1000 \text{ g m}^{-2} \text{ yr}^{-1}$.

A comparison of the mangrove litterfall rates with other forest ecosystems show that depending on the vegetation type and stocking levels, litterfall rates may be more or less. For instance, Stohlgren (1988) reported a total annual litterfall of 450 to $640 \text{ g m}^{-2} \text{ yr}^{-1}$ from the temperate ecosystems. Likewise, Pascal (1988) reported that annual litterfall is approximately $850 \text{ g m}^{-2} \text{ yr}^{-1}$ in the evergreen forests of Western Ghats. However, Kumar and Deepu (1992) reported a much higher value of 1220 to $1440 \text{ g m}^{-2} \text{ yr}^{-1}$ for the tropical moist deciduous forest in peninsular India.

Notwithstanding the above, Brown and Lugo (1980) concluded that forested wetlands have greater potential for litter production than tropical forests. This in turn, can be explained by the frequent water movements (tides) in these ecosystems, which may act as "energy subsidies" to ecosystem production (Twilley *et al.*, 1986). Frequent inundations also provide a source of nutrients and aeration for optimal growth of the tree species (Wharton and Brinson, 1979).

A non-significant interzonal variation in total litterfall (Table 20) can be explained by the remarkable domination of *Avicennia officinalis* along entire transect length (Table 2). Coincidentally, this species accounted for about 50 to 70 per cent of the total litterfall (Table 21) and 60 to 85 per cent of the total stand basal area (Table 4). Furthermore, Kumar and Kumar (1997) estimated the above ground biomass of 47 t ha^{-1} of this forest. In general, a one-to-one correspondence between stocking level and litterfall is expected. The present trend of a substantial *A. officinalis* litterfall and the lack of interzonal variation is therefore not surprising. Corroboratory results were also obtained by Dawes *et al.* (1998) in the mangroves of Florida where no significant variations in litterfall between fringing and interior zones dominated by *Rhizophora* species were noted.

Annual litterfall in *A. officinalis* ranged from 588 to $739 \text{ g m}^{-2} \text{ yr}^{-1}$. May (1999) also reported similar values for *A. marina* (620 to $780 \text{ g m}^{-2} \text{ yr}^{-1}$) in Rangannu mangroves of New Zealand. Among the other species at Pudukkottai, *R. mucronata*

showed an annual litterfall of $372 \text{ g m}^{-2} \text{ yr}^{-1}$. However, authors who studied *Rhizophora* dominated mangrove forests elsewhere reported values ranging from 370 to $1050 \text{ g m}^{-2} \text{ yr}^{-1}$ (Anwar, 1987; Sukardjo, 1984; Dagar and Sharma, 1991; Sengupta and Chaudhuri, 1993). This is not surprising as litterfall is primarily a function of the above ground biomass productivity (Weber, 1987) and/or stand basal area. The stand basal area of *R. mucronata* at the present study site did not exceed $0.43 \text{ m}^2 \text{ ha}^{-1}$ (Table 6). Annual litterfall in *Bruguiera cylindrica* ($808 \text{ g m}^{-2} \text{ yr}^{-1}$) at this site is however, comparable to that in *Bruguiera gymnorhiza* mixed stand (773 to $872 \text{ g m}^{-2} \text{ yr}^{-1}$) at Ohura Bay, Okinawa (Hardiwinoto *et al.*, 1989).

Leaf fall contribution at Puduvelyppu ranged from 50 to 74 per cent of the total litterfall (Tables 20-22). Many previous observers have reported mangrove leaf fall ranging from 69 to 84 per cent (Stienke and Ward, 1990; Dagar and Sharma, 1991; Sukardjo and Yamada, 1992; May 1999) of the total litterfall. Peak values in leaf fall were noted in November and December (Fig. 9). However, leaf fall timings reported in the literature is tremendously variable depending on species and site factors. For instance, Dagar and Sharma (1991) observed that in Andaman mangroves leaf fall peaked in August to September. May (1999) recorded a high leaf fall during November to February in the mangrove forest of New Zealand, whereas, in the Indonesian *Rhizophora mucronata* forests Sukardjo and Yamada (1992) observed that leaf fall peaked during the rainy season. Lugo and Musa (1993) observed a high leaf fall in rainy season in the fringe and basin mangroves of Laguna Joyuda, Puerto Rico. Kumar and Deepu (1992) explained that seasonality of peak in leaf fall is due to changes in hormonal balance, exerted by external stresses. Water stress is the most common exogenous factor that triggers leaf senescence in tropical forests (Moore, 1980). Incidentally, a relatively lower rainfall intensities (81-74 mm) during November-December and relatively lower temperatures (23.6 to 22.7°C) (Table 1) was recorded at their site during November to December (period of peak leaf fall) compared to previous months. This coupled with accumulation of salts in the substrates on account of lower leaching during non-rainy season, may cause water stress triggering a *de novo* synthesis of abscisic acid in the foliage of plants, which in turn, stimulates leaf senescence.

5.5 Leaf litter decay

Decomposition of leaf litter plays an important role in nutrient cycling and the supply of organic matter to the estuarine detritus food web (Twilley *et al.*, 1986). In addition, litter decomposition is a key process in maintaining soil fertility and forms a major source of nutrients for tree growth. Litter decomposition rates, however, are dependent on the environmental conditions and the litter quality attributes. Mangrove forests often involve diverse tree species and their litter quality attributes are correspondingly variable. Hence, it is important in characterising the litter decay rates of the estuarine vegetation. Despite this, mangrove litter decay in the peninsular India has been seldom studied.

Results of the present study show that decay parameters for mangrove litter are shown to be site and species dependent (Tables 24-27 and Fig.10). The pattern of mass loss and decay rate coefficients of different species was substantially variable. Out of the six species studied, all except *Rhizophora mucronata* and *Bruguiera cylindrica* followed negative exponential decay pattern (Fig.10). *R. mucronata* and *B. cylindrica*, however, followed a linear pattern. Decay rate coefficients (k) for the six mangrove species studied decreased in the order *E. agallocha* > *A. ilicifolius* > *S. caseolaris* > *A. ilicifolius* > *B. cylindrica* > *R. mucronata* (Table 27). Interspecific variations in decay rates (Table 27) are comparable to that observed by Ashton *et al.* (1999) for four mangrove species in Malaysia. They reported that *S. caseolaris* had greater k values compared to *R. mucronata* and *B. praviiflora*.

In general, differences in decomposition dynamics reflect differences in leaf morphology, texture and the biochemical quality of litter. Data presented in Table 28 also show that the species like *R. mucronata*, *B. cylindrica* and *A. officinalis* with higher initial lignin and initial lignin: nitrogen ratios and lower nitrogen concentrations decomposed slower. Conversely, *S. caseolaris*, *E. agallocha* and *A. ilicifolius* with lower lignin and higher nitrogen concentrations decomposed faster. Several previous workers (Robertson, 1988; Tam *et al.*, 1990; Basguren and Pozo, 1994; Twilley *et al.*, 1997) also reported that leaf quality (initial N concentrations, lignin concentrations, initial lignin: nitrogen concentrations) affects decay rates.

Regression linking decay rate coefficient and biochemical properties of leaf litter (Table 29 and Fig. 11), showed a strong negative relationship ($p < 0.01$) between decay rates and initial lignin ($R^2 = 0.84$) and initial lignin: nitrogen ratio ($R^2 = 0.81$). While the initial nitrogen showed a positive relationship although the R^2 value was modest ($R^2 = 0.16$) (Table. 29). Mellilo *et al.* (1982) also noticed a significant negative relationship between initial lignin concentrations and decay rates of litter.

Half life ($t_{0.5}$) of the decomposing leaf litter sample followed a pattern similar to that of the decay rates. Highest $t_{0.5}$ was for *R. mucronata* (15.7 months) > *A. officinalis* (4.28 months) > *B. cylindrica* (4.14 months) > *S. caseolaris* (3.5 months) > *A. ilicifolius* (2.27 months) > *E. agallocha* (1.62 months) (Table 27). This is comparable with the previous reports. For example, Robertson *et al.* (1992) reported a half-life of 12 months for *R. mucronata*. Mackey and Smail (1996) reported $t_{0.5}$ values of 1.5 to 2 months for *A. marina*.

Regarding interzonal variations along the sea-land ward transect, zone I (0-300 m from the sea) had higher decay rates than zone II (300 to 800 m from the sea) and zone III (800 to 1200 m from the sea) (Table 27). Interzonal variations in decay rates may be due to variable tidal influence in different zones along the transect and the associated soil physico-chemical and microbiological properties. Obviously, zone I experienced frequent tidal inundations than the rest. Frequent tidal inundation results in soaking of litter fragments and leaching of labile materials (Chale, 1993; Robertson, 1988) and promotes microbial activity (Tam *et al.*, 1990; Chale, 1993), both of which accelerate the decomposition process. In this context, Robertson *et al.* (1992) reported that leaf decay might be faster in sub tidal region than in intertidal zones.

5.5.1 Nutrient dynamics of decomposing litter mass

Absolute concentrations of NPK in the decomposing species showed considerable variations during the decomposing period (Tables 30 to 35, Fig.12). However, there was no consistent pattern in respect of the changes in nutrient concentrations of the species studied.

As regards to N, the time-course of its changes in the samples of *A. officinalis* and *E. agallocha* showed substantial variations. In both cases, N concentration of litter mass increased initially, and was followed by decline at about 3

months, thereafter it followed an asymptotic pattern. For *A. ilicifolius* and *B. cylindrica*, the N concentration declined more or less steadily through the decomposition period. However, *R. mucronata* and *S. caseolaris* did not show much variation until the last sampling

The frequent tidal inundation to which these litter decay bags were exposed to may have caused a decrease in N concentrations. Since N is a leachable nutrient, it is perhaps lost by tidal flushing. In view of this, the observed increase in N concentration of decaying litter in *A. officinalis* and *E. agallocha* is interesting. A further study on mangrove decay to characterize the N dynamics of these two species is needed to gain insights into that aspect.

The P concentration of *R. mucronata*, *B. cylindrica*, *S. caseolaris*, *E. agallocha* and *A. officinalis* increased moderately during the course of decomposition, whereas, in *A. ilicifolius* it decreased. Many previous reports also indicate increased P levels in decomposing litter (Bockhiem *et al.*, 1991; Tam *et al.*, 1990; Jamaludheen and Kumar, 1999), which may be on account of P immobilization.

The time course of K changes in the decomposing mangrove litter at Puduvyppu showed that K levels declined constantly during the decay, except in case of *B. cylindrica*. Since K is not bounded as a structural component, it is probable that leaching losses are high. The recurring tidal inundations may therefore explain the lower concentrations compared to the initial values.

On a final note, litterfall accounts for approximately 92 to 112 kg ha⁻¹ of N, 5 to 7 kg ha⁻¹ of P and 54 to 69 kg ha⁻¹ of K annually. Out of which on an average 52 to 84 kg ha⁻¹ of N, 4 to 5 kg ha⁻¹ of P and 43 to 55 kg ha⁻¹ of K is annually mineralised through litter decomposition.

Summary

SUMMARY

The present study was conducted in the mangrove forest of Pudukkottai, Kochi to characterize ecological attributes of the mangrove formations on recent substrates. Specific objectives included evaluating the interzonal differences in vegetation distribution and to assess the regeneration status of the mangrove forests along an environmental gradient (ocean-edge-to-land interior). Litter dynamics and leaf phenology of dominant tree species in this area were also characterized. The results are summarized as below.

- 1) Based on diversity and distribution of species along the land-ocean interface to the land-interior transect, the mangrove areas of Pudukkottai could be broadly divided into three zones: Zone I (0-300 m), Zone II (300-800 m) and zone III (800-1200 m from sea). Implicit in this is probably variations in the edaphic attributes and site specificity of the colonizing species. Eco-restoration activities at this site should, therefore, consider these factors, especially in deciding the most appropriate species for afforestation.
- 2) Simpson's diversity index (d) was highest in zone I (0.786) followed by zone II (0.492) and zone III (0.310), suggesting that the distal region exhibits a higher propensity for receiving mangrove propagules through tidal movements. In addition, some of the slow growing, less frequent and shade intolerant species that originally colonized the interior regions may have become extinct as the overstorey developed. This, in turn, leads to the formation of a more or less pure patch of *A. officinalis* on the interior site, which incidentally was colonized earlier than the distal portions.
- 3) Interestingly, phytosociological parameters such as density (1125-5478), abundance (21.3-80.5), percentage frequency (88 to 100%) and basal area (13.57 to 49.00 m² ha⁻¹) of trees increased from zone I to zone III, mainly because of the earlier colonization of this site.
- 4) Furthermore, a shade tolerant species such as *S. caseolaris* was found only in zone I along with a few other mangrove associates. Both *A. officinalis* and *A. ilicifolius* were, however, evenly distributed along the entire transect. *B. cylindrica*, a shade tolerant species was abundant in zone II along with *A. officinalis*. Artificial

regeneration program thus, if planned, should therefore, focus on *S. caseolaris* in zone I and *B. cylindrica* in zone II. However, judging from the wide distribution of *A. officinalis*, it may be suited for the entire transect length.

- 5) Mangrove diameter structure exhibited an inverse 'J' shaped distribution pattern, implying a balanced size class distribution and adequate regeneration of these forest.
- 6) Among the electrochemical properties of the soil, *in situ* redox potential (Eh) was positively ($r = 0.581^{**}$) related to *E. agallocha* density. However, soil pH increased while electrical conductivity decreased towards the landward side.
- 7) As expected, soil N, K, Na concentrations increased towards landward side, but did not alter stand density substantially. However, soil P was found to be positively related to stand density ($r = 0.600^{*}$).
- 8) As far as natural regeneration is concerned, 700-800 m from the land-ocean interface represented the zone with highest regeneration capacity (196-348 seedlings m^{-2}) and it decreased along the seaward and landward side. It seems that the more exposed conditions to frequent tides towards the seaward side and monospecific conditions towards landward side may retard regeneration capacity of *A. officinalis* and *B. cylindrica*.
- 9) Moreover, most of the seedlings of *A. officinalis* (70%) were in the lower height (<50 cm) category. Being shade intolerant *A. officinalis* seedlings did not reach the sapling stage under its own canopy. Conversely, *B. cylindrica* being shade tolerant had well established seedlings in the higher size classes (70% of seedlings in 50-100 cm and > 100 cm height class). *R. mucronata* another shade tolerant species also was evenly represented in all seedling height classes. This indicates that a pioneer species like *A. officinalis* may be replaced by other shade tolerant species like *R. mucronata* and *B. cylindrica* eventually transforming the present monospecific stand at Pudukkottai (Zone III) into a mixed species vegetation.
- 10) Phenological cycles of the tree species were determined by rainfall and temperature. Apparently, rainfall ($r = 0.871^{**}$) and relative humidity ($r = 0.821^{**}$) stimulated leaf production, while temperature ($r = -0.726^{*}$) and low rainfall caused leaf fall. This implies a pronounced climatic cue in determining the physiological processes, which in turn, control the phenological patterns.

- 11) Total litterfall in the mangrove forests of Pudukkottai ranged from $1031 \text{ g m}^{-2} \text{ y}^{-1}$ to $1364 \text{ g m}^{-2} \text{ y}^{-1}$ with no marked interzonal variations. Leaf litter constituted 58 to 68 per cent of the total litterfall and formed a significant component of the food web of this ecosystem. Leaf fall peaked during winter (November-December) in *S. caseolaris*, *E. agallocha* and *A. officinalis*, whereas, it was erratic in *R. mucronata* and *B. cylindrica*.
- 12) *A. officinalis* leaf fall, is paramount in deciding the litterfall trends of Pudukkottai mangroves owing to its monospecificity. In particular, *A. officinalis* accounted for 50 to 70 per cent of the total litterfall. This was followed by *S. caseolaris* (8-10%), *B. cylindrica* (6-8 %), *R. mucronata* (5-6 %) and *E. agallocha* (3-4 %).
- 13) Litter bag studies reveal that mass loss followed an exponential pattern in *E. agallocha*, *A. ilicifolius*, *A. officinalis* and *S. caseolaris*. However, *R. mucronata* and *B. cylindrica* had a linear pattern of mass loss with slow to moderate mass loss rates. Furthermore, zone I (subtidal) had higher decay rates than zone II and zone III (intertidal).
- 14) Decay rate coefficient (k) was high in species with higher lignin concentrations and lignin: nitrogen ratio and lower nitrogen concentrations. Whereas, lower k values were observed in species with lower lignin and lignin: nitrogen ratio and higher nitrogen concentration.
- 15) Regarding nutrient dynamics of decomposing litter, N concentrations decreased in most of the species due to leaching, whereas, P decreased moderately due to immobilization. However, K concentrations decreased steadily as they were loosely bound to the plant structure.
- 16) Approximately 92 to 112 kg ha^{-1} of N, 5 to 7 kg ha^{-1} of P and 54 to 69 kg ha^{-1} of K are annually added to the soil through leaf litterfall. Out of which, on an average 52 to 84 kg ha^{-1} of N, 4 to 5 kg ha^{-1} of P and 43 to 55 kg ha^{-1} of K is mineralized into the ecosystem through decomposition every year. This return will enrich the soil and water bodies and provide significant inputs to the food web.

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Plates



Plate 1: A complex association of *Sonneratia caseolaris* with other shrubs in zone I



Plate 2: Association of *Sonneratia caseolaris* and *Avicennia marina*



Plate 3: *Avicennia officinalis* tree sand.



Plate 4: Monospecific stand of *Avicennia marina*



Plate 5: *Derris trifoliata* creepers forming a dense growth in the *Avicennia* stand



Plate 6: *Acanthus ilicifolius* growing up in the open areas along with *Avicennia officinalis*

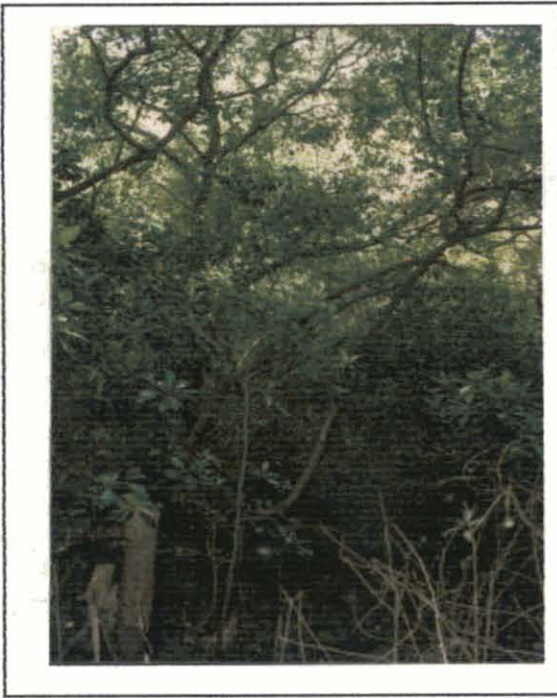


Plate 7: *Bruguiera cylindrica* as a codominant species with the dominant *Avicennia officinalis*



Plate 8: Regeneration of *Bruguiera cylindrica*



Plate 9: Regeneration of *Avicennia officinalis*



Plate 10: *Sommeratia caseolaris*

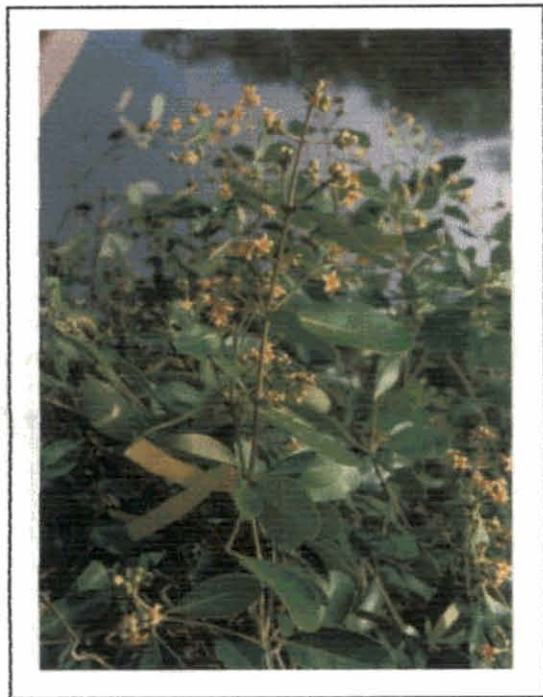


Plate 11: *Avicennia officinalis*



Plate 12: *Rhizophora mucronata*



Plate 13: *Bruguiera cylindrica*



Plate 14: *Excoecaria agallocha*

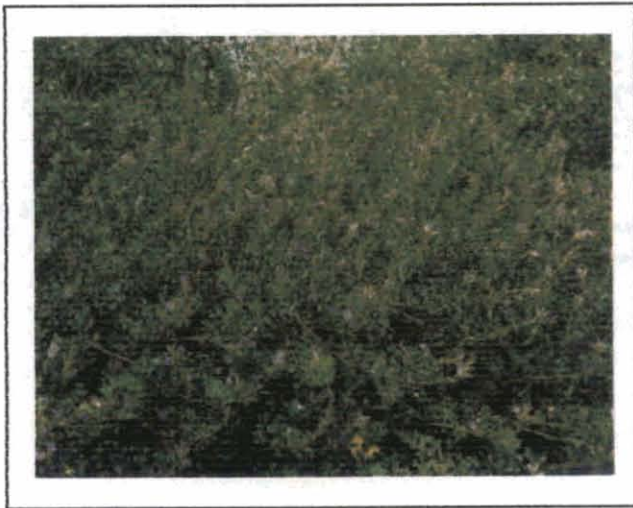


Plate 15: *Acanthus ilicifolius*



Plate 16: *Avicennia marina*



Plate 17: A close up of a litter trap



Plate 18: Litter decomposition study site

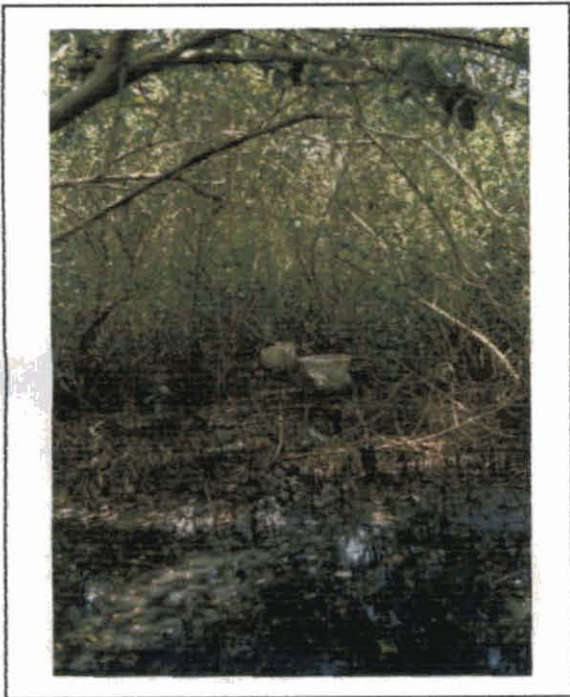


Plate 19: Litter traps under the *Avicennia officinalis* canopy



Plate 20: Retrieving litter decay bags.

Appendices

Appendix I

Abstracts of ANOVA tables for total and leaf litter fall, *Avicennia officinalis*
total and leaf litterfall between zones during August 01 to July 02

Sources	df	Mean square			
		Litterfall components			
		Total litterfall	Leaf litterfall	<i>Avicennia</i> total litterfall	leaf litterfall
Between zones	2	43176.694	12352.625	9319.29	2805.72
Between months	11	24355.117**	49906.169**	18907.07**	27872.19**

** indicates significant at 1% level

Appendix II

Abstracts of ANOVA tables for litterfall of other mangrove species at
Puduvyppu during August 01 to July 02

Sources	df	Mean square	
		Litterfall components	
		Total litterfall	Leaf litterfall
Between species	3	15377.01	3218.37
Between months	4	6276.13**	2837.63**

** indicates significant at 1% level

Appendix III

Abstracts of ANOVA tables for mass loss of six mangrove species in three zones of mangrove forest at Puduvyppu

Sources	df	Mean square
		Mass loss for species
Between zones	2	213.87**
Between species	5	2063.23**
Between months	11	232.365**

**indicates significant at 1% level

Appendix IV

Abstracts of ANOVA tables for decay rate coefficient of different species in three zones

Sources	df	Mean square
		Decay rate coefficient
Between zones	2	0.026*
Between species	5	0.257**

** indicates significant at 1% level

* indicates significant at 5% level

Appendix V

Abstracts of ANOVA tables for initial lignin, initial nitrogen and initial lignin: nitrogen ratio of six mangrove species

Sources	df	Mean square		
		Lignin %	Initial nitrogen	Initial lignin: nitrogen
Within species	3	10.132	0.004	5.615
Between species	5	378.595**	0.544**	466.685**

** indicates significant at 1% level

Appendix VI

Abstracts of ANOVA tables for nutrients (NPK) content in the decomposing leaf litter during 12 months in three zones of mangrove forest at Puduvyppu.

Sources	df.	Mean square		
		Nitrogen	Phosphorus	Potassium
Between zones	2	2.4**	0.01**	0.00**
Between species	5	12.58**	0.16**	0.00**
Between months	11	5.09**	0.052**	0.00**

** indicates significant at 1% level

Appendix VII

Abstracts of repeated measure analysis (MANOVA) for basal area of the species along the distance from the sea – land interface to the land interior transect.

A. Tests of Between-Subjects effects and tests of significance for T₁ using UNIQUE sums of square

Source	DF	Mean square	Sig. of F
Intercept	1	8749.44	0.00
Species	13	1897.13	0.00

B. Test involving DISTANCE Within-subject effect

Mauchy's sphericity test, W	0.00
Chi-square approx.	0.00 with 65 DF
Significance	0.00
Greenhouse-Geisser Epsilon	0.212
Huynh-Feldt Epsilon	0.339
Lower-Bound Epsilon	0.090

C. Multivariate test of significance for different effects

Tests name	Value	Approx. F	Hypoth. DF	Error df	Sig. of F
Distance					
Pillai's Trace	1.00	41340046 [#]	8.00	21.00	0.00
Hotteling's Trace	15748589	41340046 [#]	8.00	21.00	0.00
Roy's Largest root	15748589	41340046 [#]	8.00	21.00	0.00
Wilk's Lambada	0.00	41340046 [#]	8.00	21.00	0.00
Distance by species					
Pillai's Trace	4.005	2.160	104.00	224.00	0.00
Hotteling's Trace	0.00	0.00	104.00	154.00	0.00
Roy's Largest root	0.00	0.00	13.00	28.00	0.00
Wilk's Lambada	0.00	306.81	104.00	155.59	0.00

D. Test involving "Distance" Within – Subject effect and averaged tests of significance for distance using UNIQUE sums of squares

Source	DF	Mean square	Sig. of F
Distance	11	108.44	0.00
Distance by species	143	253.09	0.00

[#] F statistics are exact

Appendix VIII

Abstracts of repeated measure analysis (MANOVA) for density of the species along the distance from the sea – land interface to the land interior transect.

A. Tests of Between-Subjects effects and tests of significance for T_1 using UNIQUE sums of square

Source	DF	Mean square	Sig. of F
Intercept	1	89351515	0.00
Species	13	23754511	0.00

B. Test involving DISTANCE Within-subject effect

Mauchy's sphericity test, W	0.00
Chi-square approx. Significance	0.00 with 65 DF
Greenhouse-Geisser Epsilon	0.206
Huynh-Feldt Epsilon	0.329
Lower-Bound Epsilon	0.09091

C. Multivariate test of significance for different effects

Tests name	Value	Approx. F	Hypoth. DF	Error df	Sig. of F
Distance					
Pillai's Trace	1.00	119496.5 [#]	9.00	20.00	0.00
Hotteling's Trace	53773.44	119496.5 [#]	9.00	20.00	0.00
Roy's Largest root	53773.44	119496.5 [#]	9.00	20.00	0.00
Wilk's Lambada	0.00	119496.5 [#]	9.00	20.00	0.00
Distance by species					
Pillai's Trace	4.098	1.801	117.00	252.00	0.00
Hotteling's Trace	2594661	404106.7	117.00	164.00	0.00
Roy's Largest root	2582638	5562604 ^{##}	13.00	28.00	0.00
Wilk's Lambada	0.00	107.58	117.00	162.98	0.00

D. Test involving "Distance" Within – Subject effect and averaged tests of significance for distance using UNIQUE sums of squares .

Source	DF	Mean square	Sig. of F
Distance	11	1544666	0.00
Distance by species	143	2822350	0.00

[#] F statistics are exact

^{##} The statistic is an upper bound on F that yields a lower bound on the significance level

Appendix IX

Abstracts of repeated measure analysis (MANOVA) for regeneration (seedling height <50 cm) of the species along the distance from the sea – land interface to the land interior transect.

A. Tests of Between-Subjects effects and tests of significance for T₁ using UNIQUE sums of square

Source	DF	Mean square	Sig. of F
Intercept	1	913.91	0.00
Species	6	1.96	0.00

B. Test involving DISTANCE Within-subject effect

Mauchy's sphericity test, W	0.00
Chi-square approx.	735.28 at DF 65
Significance	0.00
Greenhouse-Geisser Epsilon	0.276
Huynh-Feldt Epsilon	0.325
Lower-Bound Epsilon	0.091

C. Multivariate test of significance for different effects

Tests name	Value	Approx. F	Hypoth. DF	Error df	Sig. of F
Distance					
Pillai's Trace	0.645	7.594 [#]	11	46	0.00
Hotteling's Trace	1.816	7.594 [#]	11	46	0.00
Roy's Largest root	1.816	7.954 [#]	11	46	0.00
Wilk's Lambada	0.355	7.594 [#]	11	46	0.00
Distance by species					
Pillai's Trace	2.580	3.498	66	306	0.00
Hotteling's Trace	9.580	6.435	66	266	0.00
Roy's Largest root	5.126	23.768 ^{##}	11	51	0.00
Wilk's Lambada	0.012	4.873	66	251.595	0.00

D. Test involving "Distance" Within – Subject effect and averaged tests of significance for distance using UNIQUE sums of squares

Source	DF	Mean square	Sig. of F
Distance	11	0.152	0.003
Distance by species	66	0.106	0.00

[#] F statistics are exact

^{##} The statistic is an upper bound on F that yields a lower bound on the significance level

Appendix X

Abstracts of repeated measure analysis (MANOVA) for regeneration (seedling height 50-100 cm) of the species along the distance from the sea – land interface to the land interior transect.

A. Tests of Between-Subjects effects and tests of significance for T_1 using UNIQUE sums of square

Source	DF	Mean square	Sig. of F
Intercept	1	838.22	0.00
Species	6	0.415	0.00

B. Test involving DISTANCE Within-subject effect

Mauchy's sphericity test, W	0.00
Chi-square approx.	0.00 at DF 65
Significance	0.00
Greenhouse-Geisser Epsilon	0.332
Huynh-Feldt Epsilon	0.396
Lower-Bound Epsilon	0.091

C. Multivariate test of significance for different effects

Tests name	Value	Approx. F	Hypoth. DF	Error df	Sig. of F
Distance					
Pillai's Trace	0.962	154.88 [#]	8	49	0.00
Hotteling's Trace	25.296	154.88 [#]	8	49	0.00
Roy's Largest root	25.286	154.88 [#]	8	49	0.00
Wilk's Lambada	0.038	154.88 [#]	8	49	0.00
Distance by species					
Pillai's Trace	2.063	3.538	48	324	0.00
Hotteling's Trace	147.302	145.256	48	284	0.00
Roy's Largest root	145.41	981.484 ^{##}	8	54	0.00
Wilk's Lambada	0.002	13.563	48	245.163	0.00

D. Test involving "Distance" Within – Subject effect and averaged tests of significance for distance using UNIQUE sums of squares

Source	DF	Mean square	Sig. of F
Distance	11	0.159	0.00
Distance by species	66	0.118	0.00

[#] F statistics are exact

^{##} The statistic is an upper bound on F that yields a lower bound on the significance level

Appendix XI

Abstracts of repeated measure analysis (MANOVA) for regeneration (seedling height > 100 cm) along the distance from the sea – land interface to the land interior transect.

A. Tests of Between-Subjects effects and tests of significance for T₁ using UNIQUE sums of square

Source	DF	Mean square	Sig. of F
Intercept	1	800.848	0.00
Species	6	0.439	0.00

B. Test involving DISTANCE Within-subject effect

Mauchy's sphericity test, W	0.00
Chi-square approx.	0.00 at DF 65
Significance	0.00
Greenhouse-Geisser Epsilon	0.224
Huynh-Feldt Epsilon	0.260
Lower-Bound Epsilon	0.090

C. Multivariate test of significance for different effects

Tests name	Value	Approx. F	Hypoth. DF	Error df	Sig. of F
Distance					
Pillai's Trace	0.881	62.829 [#]	6	51	0.00
Hotteling's Trace	7.392	62.829 [#]	6	51	0.00
Roy's Largest root	7.392	62.829 [#]	6	51	0.00
Wilk's Lambada	0.119	62.829 [#]	6	51	0.00
Distance by species					
Pillai's Trace	1.228	2.403	36	336	0.00
Hotteling's Trace	43.283	59.314	36	296	0.00
Roy's Largest root	42.947	400.84 ^{##}	6	56	0.00
Wilk's Lambada	0.017	9.622	36	226.718	0.00

D. Test involving "Distance" Within – Subject effect and averaged tests of significance for distance using UNIQUE sums of squares

Source	DF	Mean square	Sig. of F
Distance	11	0.086	0.00
Distance by species	66	0.087	0.00

[#] F statistics are exact

^{##} The statistic is an upper bound on F that yields a lower bound on the significance level

Appendix XII

Abstracts of ANOVA tables for nutrients (NPK) remaining in the decomposing leaf litter during 12 months in three zones of mangrove forest at Pudukkottai.

Sources	df.	Mean square		
		Nitrogen	Phosphorus	Potassium
Between zones	2	5066.53**	2503.80	846.12
Between species	5	94519.61**	19104.74**	8558.26**
Between months	11	26356.96**	38773.27**	498.36*

* indicates significant at 5% level

** indicates significant at 1% level

Appendix XIII

Abstracts of ANOVA tables for leaf phenology of *Rhizophora mucronata* during 12 months.

Source	df	Mean square			
		Old leaves	New leaves	Leaf scars	Total leaves
Between months	11	15.71**	13.75**	0.856**	20.17**

** indicates significant at 1% level

Appendix XIV
Abstracts of ANOVA tables for leaf phenology of *Bruguiera cylindrica* during 12 months.

Source	df	Mean square			
		Old leaves	New leaves	Leaf scars	Total leaves
Between months	11	231.29**	1.519**	5.27**	249.82**

** indicates significant at 1% level

Appendix XV
Abstracts of ANOVA tables for leaf phenology of *Avicennia officinalis* during 12 months.

Source	df	Mean square			
		Old leaves	New leaves	Leaf scars	Total leaves
Between months	11	160.45**	176.67**	18.29**	288.99**

** indicates significant at 1% level

Appendix XVI
Abstracts of ANOVA tables for leaf phenology of *Sonneratia caseolaris* during 12 months.

Source	df	Mean square			
		Old leaves	New leaves	Leaf scars	Total leaves
Between months	11	59.21**	14.95**	20.28**	62.17**

** indicates significant at 1% level

Appendix XVII

Abstracts of ANOVA tables for leaf phenology of *Excoecaria caseolaris* during 12 months.

Source	df	Mean square			
		Old leaves	New leaves	Leaf scars	Total leaves
Between months	11	742.75**	54.87**	40.63**	606.15**

** indicates significant at 1% level

Appendix XVIII

Abstracts of ANOVA tables soil chemical attributes along the distance from the sea-land interface to the land interior

Source	df	Mean square
Between distances		
pH	11	6.31**
Electrical conductivity	11	121.57**
Nitrogen	11	12645**
Phosphorus	11	53619.65**
Potassium	11	48652.21**
Sodium	11	68745.54**
<i>In situ</i> redox potential	11	0.217**

** indicates significant at 1% level

**ZONATION, LEAF PHENOLOGY AND LITTER
DYNAMICS OF MANGROVE FOREST
AT PUDUVYPPU**

By
AJAY DATTARAM RANE

ABSTRACT OF THE THESIS

Submitted in partial fulfilment of the
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ABSTRACT

As species distribution along the sea-land interface to the land interior is attributed to gradients in soil electro-chemical properties and tidal frequency and nutrient cycling in a system is dependent on litterfall and decay dynamics. Hence, the study for estimating zonation pattern and regeneration status of species along the ocean-land interior transects, along with litter dynamics (litterfall and litter decay) was carried out at Pudukkottai mangrove forest. Zonation pattern of species was revealed by carrying out phytosociological analysis along the land-ocean transect and correlating with gradients in electro-chemical properties of soil. Litterfall was studied by evaluating interzonal and monthly variations in litterfall between species for one year. Leaf fall and production was in turn correlated with weather parameters. Decay dynamics was studied by involving six predominant species of the forest namely, *Avicennia officinalis*, *Bruguiera cylindrica*, *Rhizophora mucronata*, *Sonneratia caseolaris*, *Acanthus ilicifolius* and *Excoecaria agallocha* and by estimating interzonal and monthly variations in mass loss and nutrient concentrations of decomposing leaf samples for 12 months.

Results show that the area can be divided into three zones (zone I: 0-300 m, zone II: 301-800 m, zone III: 801-1200 m from the sea) based on species distribution pattern. Species diversity along the zones decreased from zone I to zone II, whereas, phytosociological parameters of species increased. It was also observed that species like *R. mucronata* and *S. caseolaris* were restricted in zone I, whereas, *A. officinalis* and *B. cylindrica* were abundant towards the landward side, due to the tidal sorting of the species.

Electrical conductivity and soil nutrient (N, K, Na) concentrations increased towards the landward side, whereas, pH decreased. Furthermore, soil P concentrations and *in situ* redox potential positively affected stand density and *E. agallocha* stand density respectively.

Regeneration was profuse in the central zone of the forest (700-800 m from the sea) and decreased towards the landward side and the seaward side, implying that monospecificity and tidal inundation affected regeneration. Among the species, *A. officinalis* seedlings were abundant in the lower height class (<50 cm) and *B.*

cylindrica in upper height class (>50 cm), implying that shade tolerance of the species decided its establishment potential.

Litterfall did not vary among the zones suggesting that the dominant *A. officinalis* determined litterfall of the forest. Leaf fall peaked during winter season (November-December), whereas, leaf production was initiated by rainfall, implying that rainfall and temperature controlled phenological cycles in species.

Mass loss followed an exponential pattern in *A. ilicifolius*, *A. officinalis*, *E. agallocha* and *S. caseolaris*, whereas, it followed a linear pattern in *B. cylindrica* and *R. mucronata*. Similarly decay rates were inversely related with initial lignin and lignin: nitrogen ratio of the decomposing leaves. And also, interzonal variations in decay rates were observed, implying that site and species affected decay rates. Nutrient concentrations decreased with N and K concentrations decreasing and P moderately increasing in the litter bags during the course of decomposition, implying that tidal frequency and mineralization-immobilization frequencies decided nutrient release patterns in these species. In general this is a low diversified, juvenile with an efficient nutrient input-output mechanism.