

# Nutrient Dynamics and Productivity in Mangrove Ecosystems



Literature Review – Submitted in partial fulfilment of assessment for the  
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## **1. Productivity, Biomass and Nutrient Cycling**

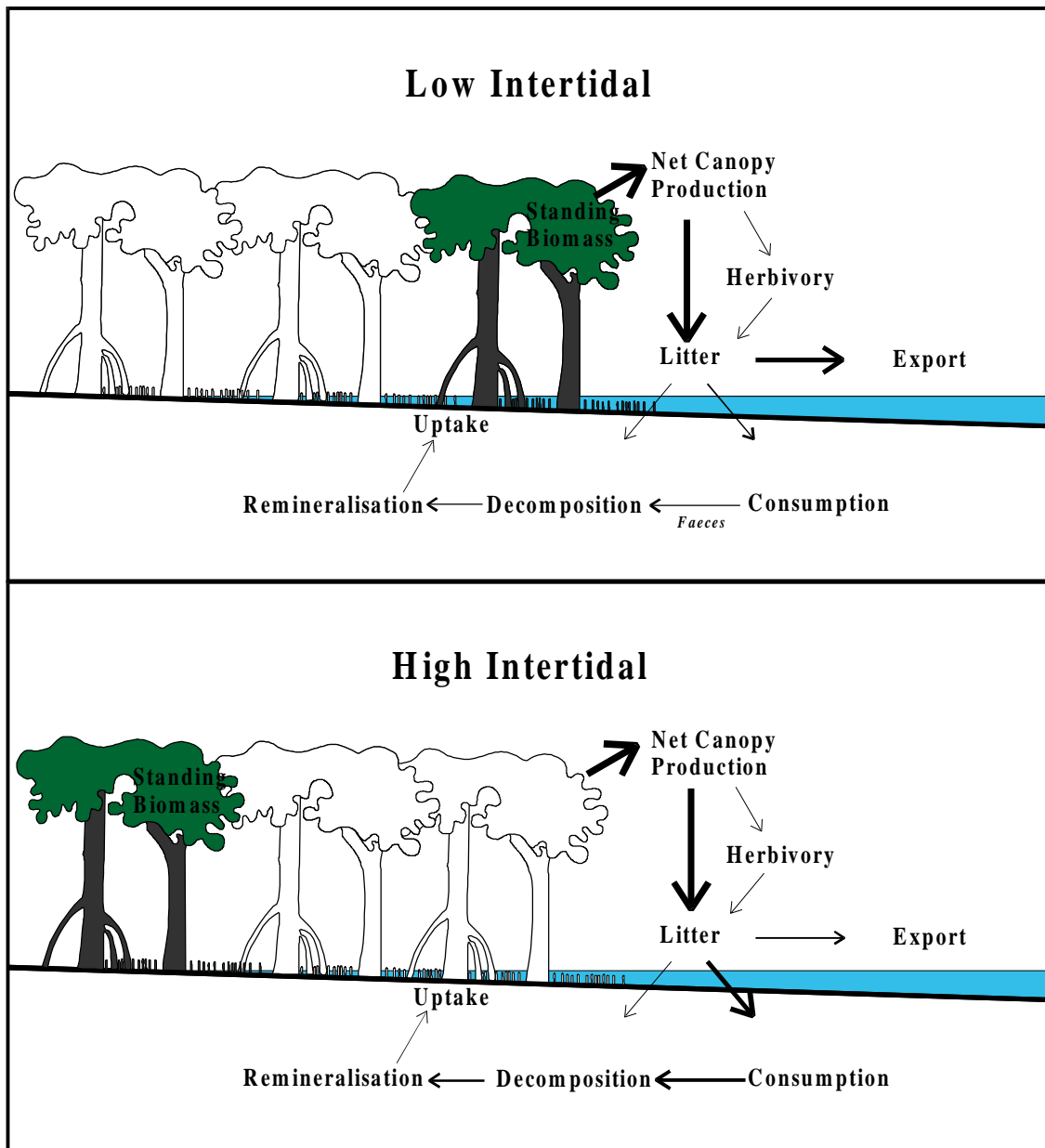
Mangroves are tropical and subtropical marine plants and can cover up to 75% of coastlines (Pernetta, 1993). Two centres of diversity exist: the Indo-West Pacific, with the highest diversity and the Caribbean/Florida region with low generic diversity (Tomlinson, 1995). Although there is an extensive body of research from the Caribbean region (Pernetta, 1993), mangroves in the Indo-West Pacific have only recently been studied. It is in the latter region where mangrove forests are most under threat from over-exploitation, destruction and environmental degradation (Pernetta, 1993; Ong et al., 1995; Tomlinson, 1995). Human communities in these developing countries have traditionally used mangroves for wood and tannin products on a sustainable level (Tomlinson, 1995), but now large tracts of mangrove forest are being 'reclaimed' for aquaculture and industrial development (Ong et al., 1995).

Until recently mangrove forests, particularly in developed nations, have been considered wastelands. Recognition by governments and the general public of the value of mangrove forests has been slow and is still limited. It is the 'ecosystem products' of mangrove forests which are most significant (Pernetta, 1995), but which are rarely recognised. These include: coastal protection from tidal erosion and storm surges, sediment trapping for land accretion (Pernetta, 1995) and use of mangrove habitats by juvenile fish and prawns (Robertson and Blaber, 1992).

It may be that current problems in coastal marine systems provide the opportunity for utilisation and protection of mangrove ecosystems. Eutrophication, the increase in nutrient (carbon, nitrogen and phosphorous) loads to coastal systems by human activities, is an increasing problem (Valiela, 1995; Richardson and Jorgenson, 1996).

The potential utilisation of mangroves as sewage ‘filters’, converting dissolved inorganic nutrients to particulate matter, has been largely neglected because of the lack of information on nutrient dynamics in mangrove ecosystems (Robertson, 1992). Before this can occur, a more comprehensive understanding of nutrient cycles within mangrove systems and their interactions with offshore ecosystems is required.

**Figure 1:** Productivity and nutrient cycles in mangrove forests



Understanding of productivity and nutrient cycling within mangrove forests has been revolutionised by research in North Queensland over the last 20 years. Aspects of productivity, cycling of nutrients within the forest and links with coastal marine ecosystems (Figure 1) are discussed in Section 1. Section 2 and 3 focus on the pools and cycling of nitrogen and phosphorous, the primary nutrients limiting productivity in marine systems. Results from nutrient enrichment experiments are discussed in Section 4, with reference to the potential use of mangrove ecosystems as sewage filters.

### **1.1 Standing biomass**

Reliable biomass measurements provide the basis for comparisons of potential primary production, estimations of the potential yield of commercial products and understanding of long term changes in forest structure (Clough and Scott, 1989). Estimates of mangrove biomass, particularly below ground biomass are few (Clough, 1992). Initial estimates of biomass in Florida (Lugo and Snedaker, 1974) suggested that compared to other tropical forests the biomass of mangroves was low. However more recent measures in Indo-West Pacific and African mangrove forests (Putz and Chan, 1986; Komiyama et al., 1988 as cited in Saenger and Snedaker, 1993; Amarasinghe & Balasubramanian, 1992; Slim et al., 1996) have reported much higher biomass (Saenger and Snedaker, 1993). Mangrove biomass in these regions can reach up to 460 t DW ha<sup>-1</sup> (Putz and Chan, 1986) and in North Queensland may be as high as 700 t DW ha<sup>-1</sup> (Clough, 1992).

Mangrove forest biomass consists of two components: above and below ground biomass. Both components are subject to high variability.

#### 1.1.1 Above-ground

Above ground biomass (AGB) includes the trunk, branches, stems and leaves. In mature trees of all species the trunk constitutes the largest component of the AGB (Ong et al., 1995). AGB is site and species dependent, affected by forest age, history and morphology (Lugo and Snedaker, 1974), species composition (Tam et al., 1995) and local sediment characteristics (eg. nutrient availability, salinity and temperature) (Clough, 1992).

Saenger and Snedaker (1993) reported a general latitudinal trend of increasing AGB with decreasing latitude (Table 1). *Rhizophora* species had generally higher AGB than all other species (Saenger and Snedaker, 1993) but this may result from their dominance of forests at low latitudes. Some is also evidence for within species variation in AGB exists (Woodroffe, 1985). Woodroffe (1993) reported the occurrence of two distinct growth forms of *Avicennia marina*: taller forests at the creek bank had an AGB more than ten times that of stunted forests on the mudflat. This is most likely a result of sub-optimal growth conditions. Despite the differences in AGB between stunted and taller mangrove forests, forest productivity and leaf turnover rates were similar in the two forest types (Saenger and Snedaker, 1993).

**Table 1:** Biomass estimates for mangrove species by component

Latitude	Forest type	Biomass component	Biomass (t DW.ha <sup>-1</sup> )
1° - 10°	<i>Rhizophora</i> .	AG <sup>1</sup>	96.7 – 460.0
		BG <sup>2</sup>	509.5
22° – 36°	<i>Avicennia</i> .	AG <sup>3</sup>	19.4 – 140.4
		BG <sup>4</sup>	153.8
	<i>Aegicerus</i>	AG <sup>5</sup>	67.1
		BG <sup>5</sup>	95.5

AG – above ground biomass

BG – below ground biomass

#### References

<sup>1</sup> Putz and Chan (1986); Komiyama et al. (1988 as cited in Saenger and Snedaker, 1993); Ong et al. (1995); Slim et al. (1996)

<sup>2</sup> Komiyama et al., 1987

<sup>3</sup> Brigg et al. (1977); Wood et al. (1985); Steinke et al. (1995)

<sup>4</sup> Tam et al. (1995)

#### 1.1.2 Below-ground

In terrestrial forests, below ground biomass (BGB) represents approximately 30% of total forest biomass (Ulrich et al., 1974, as cited in Clough, 1992). The proportion of total biomass as BGB in mangroves varies with species (Briggs, 1977; Komiyama et al., 1987; Tam et al., 1995). Estimates of BGB are 54% and 58% for *A. marina* and *A. corniculatum* respectively (Briggs, 1977; Tam et al., 1995) and only 15% of *R. stylosa* (Ong et al., 1995). These may in fact be underestimates of root biomass given the difficulty of removing all the fine root materials (Komiyama et al., 1987). Gill and Tomlinson (1977) attributed the difference in BGB between the species to the primarily above-ground cable system of *Rhizophora* species.

The considerable size of the root biomass of mangroves suggests they are important in nutrient cycling of organic and inorganic materials (Clough & Attiwill, 1982).

## 1.2 Primary Production

Net primary production consists of gross primary production less that lost through respiration of the whole plant (Clough & Attiwill, 1982). Measurement of mangrove net primary production is difficult as quantification of respiratory losses from all components of the biomass are problematic (Clough, 1992). Respiratory losses from branches and the trunk are often overestimated due to the presence of non-photosynthetic organisms on the surface of these components. Additionally, the high concentrations of bacteria in mangrove sediments (Alongi, 1989, 1990) make accurate measurements of respiratory losses from roots difficult (Clough, 1992).

Bunt et al. (1979) developed a 'light transmission method' for the measurement of potential net primary production in mangrove forests. The procedure measures the light attenuation through the forest canopy attributable to plant utilisation.

Standardisation is accomplished through leaf pigment assays from leaves throughout the canopy (Bunt et al., 1979). Although this method provides information on trends in potential production, Clough (1992) suggested that it provides conservative estimates of net primary production which are too low to account for biomass accumulation.

An alternative to these techniques to obtain more accurate measurement of net primary production is to estimate biomass accumulation (eg. Wium-Anderson and Christensen, 1978) and losses of dry matter (Clough, 1992). Net primary production could then be calculated by summing above ground biomass accumulation and litter loss (Clough, 1992). Because of the ease of measurement of above ground dry matter losses and its importance to coastal ecosystems, a large body of data exists on

temporal and spatial variation of this loss (Table 2). However, there is no available data on losses of below ground matter, and only one study has combined measurements of biomass accumulation and above ground dry matter lost (Clough, 1992).

Day et al. (1987) combined estimates of woody above ground growth with litterfall data and obtained estimates of net primary production of 16.1 - 24.6 t DW ha<sup>-1</sup> y<sup>-1</sup> (Day et al., 1987). These values fall within the range expected for woody plants (Day et al., 1987). This is despite the loss of up to 70% of litter as export to offshore communities compared to much tighter recycling of nutrients and organic matter in many terrestrial forests.

It is most convenient to discuss trends in mangrove primary production in terms of litterfall because of the dearth of literature available on this aspect of production.

Litterfall rates vary with latitude (Saenger and Snedaker, 1991), season (Williams et al., 1981), species (Slim et al., 1996), structural morphology of the forest (Woodroffe, 1982) and sediment nutrient availability (Saenger and Snedaker, 1991). Litterfall is higher in tropical mangrove forests (eg. Putz and Chan, 1986; Slim et al., 1996) than sub-tropical (Rogers, unpubl. data) and temperate forests (Table 2) (Goulter & Allaway, 1979; Woodroffe, 1982). This trend may be related to species differences, as tropical forests (for which litterfall has been measured) are dominated by species of *Rhizophoraceae* (eg. Leach and Burgin, 1985; Putz & Chan, 1986) while *A. marina* dominates subtropical and temperate forests (eg. Goulter & Allaway, 1979; Woodroffe, 1982). Within these latitudinal groupings litterfall rates are fairly similar despite differences in geographical location. Woodroffe (1982) reported differences

in rates of litterfall in *A. marina* forests of different morphologies. In ‘tall’ forests, estimated litterfall was more than twice that of ‘low’ mangroves (Woodroffe, 1982).

Seasonal fluctuations exist for all components of the litter (Williams et al., 1981). Leaf fall peaks during the wet season for most species (Williams et al., 1981; Woodroffe, 1988). Amount of reproductive material in the litter is also cyclic, dependent on the peak flowering times (Williams et al., 1981), which can show variation with latitude (Duke, pers.comm.).

**Table 2:** Annual total litterfall for various mangrove forests

<b>Latitude</b>	<b>Forest type</b>	<b>Litterfall</b> (t DW ha <sup>-1</sup> yr <sup>-1</sup> )
2° - 18°	<i>Rhizophora</i> <sup>1</sup>	5.6 – 19.6
26° - 36°	<i>Avicennia</i> <sup>2</sup>	3.7 – 18.0

#### References

<sup>1</sup> Duke et al. (1981); Leach and Burgin (1985); Putz and Chan (1986); Slim et al. (1996); Twilley et al. (1997)

<sup>2</sup> Goulter and Allaway (1979); Woodroffe (1982); Twilley et al. (1986); Steinke and Ward (1990); Rogers (unpubl.data)

### 1.3 Nutrient Transformation Processes

#### 1.2.1 Consumption

##### 1.2.1.1 Leaves

Mangrove leaves are grazed predominantly by insects, but they are also a food source for one species of crab (Beaver et al., 1979) and monkeys (Duke, pers.comm).

Herbivory by monkeys and crabs is geographically restricted, however.

Direct grazing on mangrove leaves accounts for only a small proportion of total leaf production (Heald, 1971; Onuf et al., 1977; Johnstone, 1981; Robertson and Duke, 1987; Farnsworth and Ellison, 1991; Robertson, 1991). Robertson & Duke (1987) estimated that only 6.5% of total leaf area for North Queensland mangrove forests is lost to insect herbivores. This does not constitute a significant loss of nutrients from the system, particularly if much of this is returned to the sediment as frass (insect faeces) (Duke, pers.comm.).

The percentage leaf area consumed is highly variable between mangrove species, sites and individual trees (Johnstone, 1981; Robertson & Duke, 1987). Interspecific differences in susceptibility to insect damage are also important.

The 25 mangrove species in North Queensland, Australia, exhibited greater than two orders of magnitude difference between species in percentage leaf area lost to insects (Robertson & Duke, 1987). These differences in percentage loss can be attributed to a variety of leaf characteristics (Robertson & Duke, 1987). *Excoecaria agallocha*, often referred to as “blind-your-eye” mangrove, produces a milky, toxic exudate when leaves are damaged (Tomlinson, 1994). Given the low rates of insect damage to this species, it has been hypothesised that this exudate may be a deterrent to insects (Robertson & Duke, 1987). Leaves of species of the *Rhizophoraceae* have high concentrations of soluble tannins, low % nitrogen content and high C:N ratios which would decrease palatability of the leaves, while *Avicennia marina* leaves have low tannin concentrations, high % nitrogen content and low C:N ratios (Lacerda et al., 1986), making these leaves more favourable and energy efficient insect food (Robertson & Duke, 1987; Rao et al., 1994). This trend is evident in Moreton Bay,

where *A. marina* the dominant mangrove, has a higher incidence of gall and leaf miner damage than other species including *R. stylosa* (Law, 1995).

Given that C:N ratios of leaves may be an important determinant of leaf area loss to insects, several studies have considered the impact of nitrogen enrichment of forests on herbivory. The earliest of these was conducted in Florida mangroves in areas receiving high natural inputs of guano (Onuf et al., 1977). The authors reported a significantly greater loss to insect herbivory in the nitrogen-enriched forests, which they attributed to an improvement in the plant tissues as a nutritive source. An increased percentage leaf area lost to insects was observed in dwarf *Rhizophora mangle* trees enriched with phosphorous and nitrogen and phosphorous fertilisers (Feller, 1995), while no differences in insect damage were detected between enriched and non-enriched trees in Papua New Guinea (Johnstone, 1981). As neither study quantified changes in nutritive quality of the leaves, these differences provide no conclusive evidence of the importance of total N content to insect damage. Clearly this relationship requires further investigation.

Despite low figures for total leaf production loss, cyclic events (eg. the population explosion of a lepidopteran larvae in mangrove forests in China (Anderson & Lee, 1995) can result in complete defoliation of large areas and may have more impact on reproduction and nutrient cycling in the forest than constant low level insect damage. Anderson & Lee (1995) removed populations of a lepidopteran larva from plots within the *A. marina* forests and found that insect damage was significantly higher (55% of leaf area) in control plots (no insects removed) than in treatment plots (5% of leaf area) (insecticide applied). As trees 'drop' leaves that have been damaged, these

seasonal changes to litterfall will have flow-on effects to organic matter flux (Anderson & Lee, 1995). This event also has a significant impact on reproductive output. Production of both flowers and propagules was significantly higher in treatment plots resulting in a much greater input of propagules to the detritus food chain (Anderson & Lee, 1995).

#### 2.2.1.2 Litter

Until recently understanding of food web dynamics in mangrove forests was based on research by Odum and Heald (1972, 1975) which suggested that the majority of the litter was exported to adjacent waterways where the initial fragmentation and decomposition occurred. Recent work in Australia (Robertson, 1986, 1991; Robertson and Daniel, 1989; Smith et.al., 1991; Micheli, 1993) and Africa (Steinke et al., 1993) has shown that in the Indo-Pacific mangrove forests 20-70% of litter is recycled within the forest by crabs which remove the litter to burrows or consume it directly from the forest floor.

Robertson (1986) provided the first estimates of litter removal by crabs, although the importance of crabs in litter dynamics had been suggested as early as 1968 (Macnae, 1968). *Sesarmid* crabs, which are often highly abundant in forests in the Indo-Pacific region retain and consume a significant proportion of mangrove leaf litter (Robertson, 1986). The rates of removal varied within forests: crabs in high intertidal *Bruguiera gymnorhiza/ Ceriops tagal* forests removed up to 79% of litter (Robertson & Daniel, 1989) while in mid and low intertidal *R. stylosa* forests crabs removed only 28% of fallen litter (Figure 1) (Robertson, 1986). Litter removal rates also suggest that the role of crabs and microbial communities in nutrient cycling may differ with the

amount of tidal influence on the forest (Robertson & Daniel, 1989). However in the high intertidal *A. marina* forests processing of litter by microbial decay and removal by crabs were of equal importance, accounting for 32% and 33% of litter removal respectively (Robertson & Daniel, 1989). Robertson & Daniel (1989) attributed this variation in the importance of the crabs to differences in species composition of crab communities. The crab communities of *A. marina* forests were dominated by microphagus oypodid species (species that feed on detrital particles) rather than the leaf-eating *Sesarmid* crabs found in the other forest types (Robertson & Daniel, 1989).

The existence of fundamental differences in leaf litter processing between Caribbean and Indo-West Pacific mangrove forests was recently confirmed by McIvor & Smith (1995). Although crab abundance was greater in the Caribbean, there was significantly lower species diversity in the Caribbean crab communities. The *Sesarmid* family of crabs, the primary consumers of litter in Indo-West Pacific mangroves, are rarely found in the Florida mangroves, where communities are dominated by non-leaf eating species (McIvor & Smith, 1995).

Of the litter removed by crabs, some is consumed on the forest floor, while much more is removed to burrows (Micheli, 1993). Crabs consumed greater than 78% of the buried litter within 6 hours. However, crabs are often referred to as ‘sloppy feeders’ and it has been estimated that 20% of leaf material is lost from the mandibles on to the floor of the burrow (Camilleri, 1989). Of the 80% of leaf material ingested, an estimated 68% is egested as faeces (Camilleri, 1989). So, of the leaf material removed to the burrow, approximately 20% enters the nutrient cycle as organic matter and 68% enters as ammonium (faeces) via ammonification (see Section 2.2.1.4). The

retention and rapid breakdown of such a large portion of the litter produced, particularly in the mid and high intertidal forests where up to 75% of litter is retained, represents a significant influence on the recycling of leaf litter nutrients (Robertson & Daniel, 1989; Robertson, et.al., 1992). The consumption of approximately 75% of propagules, which have high % nitrogen content, by crabs may also have a significant influence on nutrient cycling (Smith, 1987; Robertson, et.al., 1992).

Crabs also influence nutrient cycling within mangrove forests by their burrowing activities (Smith, et al., 1991). When crabs were removed, higher sulphide and ammonium concentrations were recorded in sediments and the reproductive output of trees decreased (Smith, et al., 1991).

The influence of *Sesarmid* crabs on mangrove forest nutrient dynamics is thus two-fold. The removal of 22 – 83% of litter and a proportion of propagules contributes significantly to nutrient retention and cycling within the forest (Robertson, 1986; Robertson & Daniel, 1989) and the burrowing activities of the crabs stimulates sediment turnover affecting nutrient transformation (Smith, et al., 1991).

### 1.3.2 Export of particulate matter

Heald (1971, as cited in Robertson et al., 1992) and Lugo and Snedaker (1974) first suggested that mangroves play an important functional role in offshore nutrient cycles as exporters of large amounts of plant detritus. This outwelling characteristic, involving the tidal export of leaves, reproductive parts, wood and frass (Lee, 1995) with subsequent offshore decomposition, was thought to provide a source of carbon, nitrogen and phosphorous to offshore systems (Lugo and Snedaker, 1974). Despite

these early indications, there have been few attempts to quantify the importance of mangrove outwelling (Robertson et al., 1992). Recent studies of leaf removal rates by macro-invertebrates (Robertson, 1986, 1991) and decomposition rates (Robertson et al., 1992) suggest that export and offshore decomposition account for a much smaller proportion of litterfall than previously thought (Robertson and Daniel, 1989).

Consumption and decomposition have been shown to account for up to 70% of litterfall, with frequency of tidal inundation an important determinant (Figure 1) (Robertson and Daniel, 1989). Export dynamics are relatively site specific, however, and depend on the geomorphology and tidal regimes of the different regions (Odum and Heald, 1975; Twilley, 1988) as well as the structural characteristics of the vegetation.

Boto and Bunt (1981) developed a detailed hydrodynamic model for Coral Creek, Hinchinbrook Island, North Queensland. Based on litterfall data and detailed topographical studies estimating forest area inundation at various tidal heights, they estimated that 3560 tonnes (dry weight) of mangrove litter ( $10.5 \text{ kg C ha}^{-1} \text{ d}^{-1}$ ) was exported from the bay annually (Boto and Bunt, 1981). These estimates were based on the assumption that all litter from the low and mid intertidal forest was exported. However, Robertson (1986) reported that removal of litter by crabs accounted for 28% of annual leaf litterfall in low and mid intertidal mixed *Rhizophora* forests and decreased Boto & Bunt's (1981) original export estimate by 22% to account for removal, burial and consumption by sesarmid crabs. This revised export figure does not include consumption of other components of the litter (eg. propagules and flowers which crabs have been observed to consume) and therefore is likely to be an overestimate (Robertson et al., 1992).

### 1.3.3 Decomposition

Decomposition involves three processes: fragmentation, leaching and decay (Robertson et al., 1992). Fragmentation is the breaking up of leaf and other litter by tidal action, water currents or macrofauna (Camilleri, 1992). Leaching is the loss of the chemical structure and decay is the breakdown of the structural component by bacteria and fungi. Rates of decay are extremely site and species dependent and are affected by tidal inundation frequency (Rice & Tenore, 1981; Twilley et al., 1986; Flores-Verdugo et al., 1987; Mackey & Smail, 1996; Twilley et al., 1997), air and water temperature (Mackey & Smail, 1996), chemical and nutritional content of leaf material (Melillo et al., 1984; Steinke et al., 1983; Robertson, 1988; Lacerda et al., 1995), oxygen availability for root decomposition (Albright, 1976) and decomposer species composition (Reice et al., 1984).

Leaf litter decomposition rates were higher in forests in the lower latitudes (Table 3). This has been attributed to the influence of air and water temperatures on decomposition rates (Mackey & Smail, 1996). Consistently higher temperatures throughout the year in the lower latitudes resulted in increased decomposition process rates (Mackey & Smail, 1996). This effect of temperature can be seen on a local scale with comparison of decomposition rates in summer and winter in a south east Queensland forest (Mackey & Smail, 1996). Leaves and twigs placed at both high and low intertidal regions decomposed up to six times faster (twigs, low intertidal) during summer (Mackey & Smail, 1996).

Fragmentation of leaf litter by macroinvertebrates in the initial stages of decomposition increased rates of leaf litter decomposition (Robertson, 1986;

Camilleri, 1992). Leaf shredders decrease the size of particulate matter, resulting in more rapid colonisation and greater microbial populations, but also digest material which is then rapidly broken down by microbes once it has passed through the animals gut (Camilleri, 1992).

The degree of submersion of leaves and twigs influences speed of leaching and hence affected decomposition rates. Leaves suspended within creeks decomposed at a much greater rate than leaves in the forest (Woodroffe, 1982; Flores-Verdugo et al., 1987; Robertson, 1988). Within the forest, leaves in low intertidal regions which were inundated by tides daily decomposed at a much greater rate than leaves in high intertidal forests inundated by tides less frequently (Reice et al., 1984; Twilley et al., 1986; Mackey & Smail, 1996). The more rapid decomposition rate for submerged leaves was attributed to more rapid leaching of tannins from submerged leaves and greater stability and predictability of the environmental conditions (Cundell, 1979; Melillo et al., 1984; Robertson, 1988). Bacterial and fungal colonisation will be much more rapid under these conditions (Cundell, 1979).

The high initial lignin concentrations in wood, roots and pneumatophores results in much slower decay rates for these components of the litter compared to leaves (Albright, 1976; Steinke et al., 1983; Melillo et al., 1984; Mackey & Smail, 1996). Lignin is resistant to microbial attack and is rich in compounds that inhibit decay (Melillo et al., 1984). Wood decay rates were much lower than rates for pneumatophores and roots (Albright, 1976; Steinke et al., 1983; Mackey & Smail, 1996) and decay for buried material was much slower than for material at the

sediment surface (Table 3) (Albright, 1976). This was attributed to the slower decomposition rates under anaerobic conditions (Albright, 1976).

Generally, plant litter decomposition rates of terrestrial and aquatic plants have been shown to decrease with increasing biochemical complexity and increase with increasing element concentrations, particularly nitrogen (Melillo et al., 1984).

Comparative litter decomposition rates for the mangrove species studied are generally in agreement with these trends. Leaves of species of *Rhizophoraceae* and *C. tagal* with very high tannin concentrations, high C:N ratios and a thick relatively impervious cuticle decomposed much slower than leaves of *A. marina* and *Ae. corniculatum* which have high initial nitrogen concentration, low C:N ratios and low concentrations of tannins (Steinke, 1983; Robertson, 1988; Tam, 1990). High tannin concentrations inhibit microbial activity (Lacerda et al., 1995) and the thick cuticle would impede entry of degradative organisms (Steinke et al., 1983).

Decomposition and subsequent remineralisation of mangrove detritus is important in nutrient dynamics within the forest as well as in off shore systems (Reice et al., 1984; Mackey and Smail 1996; Twilley et al., 1997). Decomposition within the forest accounts for 20-70% of litterfall, depending on frequency of tidal inundation (Robertson et al., 1992). In high intertidal forests, decomposition accounts for a greater percentage of total litterfall than in low intertidal forests, as litter remains on the forest floor for sufficient time to allow for degradation (Robertson et al., 1992). The removal of leaves by crabs also contributes to retention and decomposition of litterfall (Camilleri, 1992). Although most authors have considered only leaf decomposition, little information exists on decomposition of fallen logs, dead roots

(Mackey & Smail, 1996) and reproductive material (Steinke et al., 1983).

Understanding of decomposition rates for roots and woody material is important in nutrient dynamics research as virtually all woody material remains in the forest, contributing significantly to nutrient recycling.



## **2. Nitrogen Dynamics**

Productivity in marine and coastal ecosystems is influenced by availability of nutrients, particularly nitrogen (Valiela and Teal, 1974). Limitation of growth and productivity by nitrogen (N) availability has been reported for saltmarsh (Valiela and Teal, 1974) and mangrove ecosystems (Boto and Wellington, 1983). Availability of N to the plant is determined by nitrogen content in the sediment (Boto and Wellington, 1983), but also a range of sediment processes (eg N fixation and denitrification) and sediment-water column exchange (Figure 2).

### **2.1 Nitrogen Pools**

#### **2.1.1 Vegetation**

Nutrient uptake by mangrove forests leads to the immobilisation of significant amounts of N as plant tissues (Clough et al., 1983). Mangrove leaf N content, which averages 1-1.5%, is low compared to N contents of a range of Australian plant species (Turnball et al., 1996).

N content of mangrove leaves and other structural components have been found to vary with species (Lacerda et al., 1986; Sah et al, 1989) position within the forest (Wong et al., 1995), nutrient status of the sediment (Table 4) (Boto & Wellington, 1983), structural component of the forest (Gong & Ong, 1990; Rao et .al., 1994) and leaf age (Clough & Attiwill, 1975; Clough et al., 1983).

Of the structural components of mangroves, leaves had the highest N content (Clough & Attiwill, 1975; Gong & Ong, 1990). Fruit (propagules), small fibrous roots and small branches also had relatively high N content (Clough & Attiwill, 1975; Gong &

Ong, 1990). Propagules represent a massive investment of N in reproduction for the trees, and a large outwelling of N to coastal waters.

Considerable difference in N status of leaves exists between species (Lacerda et al., 1986; Sah et al., 1989; Rao et al., 1994). Except for *Rhizophora mangle* in Brasil, with N concentrations of 4.5% (Lacerda et al., 1986), species of the *Rhizophoraceae* had consistently lower leaf N status than other mangrove species including *Heritiera littoralis* and *A. marina* (Rao et al., 1994). This was attributed to morphological differences of the leaves of the two groups of species (Rao et al., 1994). Leaves of the *Rhizophoraceae* have a thick leathery cuticle which has a higher carbon and lower N composition (Rao et al., 1994).

Leaf N status was found to correlate with soil nitrogen status, with higher N content in leaves in low intertidal regions than high intertidal regions (Boto & Wellington, 1983). When these forests were exposed to additional nutrient loads, the response to enrichment differed with tidal inundation (Table 5). N content in leaves in low intertidal increased following N and phosphorous enrichment, while in high intertidal regions, N content did not increase following phosphorous enrichment (Boto & Wellington, 1983). No response was observed in leaf N status in forests receiving sewage in China and Brasil (Lacerda et al., 1986; Wong et al., 1995). This may be a result of low nutrient loading in the sewage the forests received.

**Table 4:** Nitrogen content of different structural components of several mangrove species

Location	Species	Structural component	Nitrogen content (% dry wt.)	Reference
Westenport Bay, Australia	<i>A. marina</i>	Leaves	2.11	Clough & Attiwill (1975)
		Branches	0.61 – 1.43	
		Trunk	0.49	
		Roots	0.68 – 1.20	
		Fruit	1.60	
Sundurbans, India	<i>A. marina</i>		1.64	Sah et al. (1989)
	<i>A. alba</i>		1.55	
	<i>E. agallocha</i>		1.12	
Matang Reserve, Malaysia	<i>R. apiculata</i>	Leaves	1.64	Gong & Ong (1990)
		Branch	0.55	
		Trunk	0.40	
		Roots	0.43 – 0.76	
Gazi Bay, Kenya	<i>A. marina</i>	Leaves	1.90	Rao et al. (1994)
	<i>R. mucronata</i>		0.70	
	<i>B. gymnorrhiza</i>		0.80	
	<i>C. tagal</i>		0.80	

N status of the leaves, particularly senescent leaves will determine the contribution of mangroves to offshore nutrient cycles but is also important to internal nutrient cycling of the mangrove forest (Rao et al., 1994). It was suggested mangroves were generally efficient at retaining N during senescence of leaves, with up to 69% of nitrogen being removed prior to abscission (Clough & Attiwill, 1975; Rao et al., 1994). Species with high leaf nitrogen content had the highest rates of resorption of nitrogen (~69% resorbed), while *Rhizophora* species resorbed only around 53-60% (Rao et al., 1994).

**Table 5:** Literature review of N content of mangrove leaves following nutrient enrichment

Location	Species	Treatment	Nitrogen content (% dry wt.)	Reference
Hinchinbrook Island, Australia	<i>Rhizophora</i>	Low intertidal		Boto & Wellington (1983)
		C	1.17 – 1.20	
		N	1.35	
		P	1.43	
		High intertidal		
		C	0.95 – 1.17	
Sepetida Bay, Brasil	<i>A. schaueriana</i>	C	2.30	Lacerda et al. (1986)
		S	1.90	
	<i>R. mangle</i>	C	4.50	
Futian Nature Reserve, China	<i>Kandelia candel</i>	C	1.13	Wong et al. (1995)
		S	1.07	
	<i>A. corniculatum</i>	C	1.08	
		S	1.09	

C – control plots  
N – nitrogen enriched  
P – phosphorous enriched  
S – sewage enrichment

### 2.1.2 Sediment

N occurs in marine sediments in various forms: dissolved in the porewaters, adsorbed or bound to sediment particles or as particulate organic N (Nixon and Pilson, 1983).

In mangroves the sediment N pool is composed largely of the organic N form (Clarke, 1985). These are not readily available for plant uptake (Clarke, 1985).

Concentrations of dissolved inorganic forms, particularly nitrate (NO<sub>3</sub>), are low compared to concentrations in other marine sediments (Clarke, 1985; Alongi et al., 1992). Of the dissolved inorganic nitrogen (DIN) forms, ammonium (NH<sub>4</sub><sup>+</sup>) was the most abundant, but detectable levels of NO<sub>3</sub><sup>-</sup> and nitrite (NO<sub>2</sub><sup>-</sup>) were consistently

found in mangrove sediments (Table 6) (Boto & Wellington, 1984; Clarke, 1985; Alongi et al., 1992; Morell & Corredor, 1993; Alongi, 1996)

Comparison of DIN concentrations in mangrove and mudflat sediments revealed that in mangrove sediments DIN concentrations were consistent to 20 cm depth, while concentrations in mudflat sediments were higher at the surface than mangrove sediments and increased with increasing depth (Alongi, et al., 1992; Alongi, 1996). Sediment depth profiles in North Queensland showed depletion of  $\text{NH}_4$  to a depth of 100 cm. This reduction reflects uptake of DIN by the plants (Alongi, et al., 1992).

Sediment N varies with distance from the forest fringe (Clark, 1985). Total N content in sediments in North Queensland mangroves decreased along a transect from the forest fringe to high intertidal regions (Robertson, 1996).  $\text{NO}_3^-$ , and to a lesser degree  $\text{NH}_4^+$ , decreased with increasing tidal elevation (Clarke, 1985). These changes reflect the influence of frequency of tidal inundation; regular tidal incursions and denitrification in the sediment surface would result in the removal of  $\text{NO}_3^-$  at a greater rate than  $\text{NH}_4^+$  (Clarke, 1985).

Sediment N concentrations were also influenced by mangrove forest species composition. The comparison of the soil chemistry of sediments of *Rhizophora* dominated and *Avicennia* dominated forests revealed the *Avicennia* forest sediment had a total %N (TN) concentration of 0.35% at the surface, more than twice that of *Rhizophora* forest sediment (Lacerda, et.al., 1995). This difference was attributed to differences in the composition of the organic matter (eg. leaf material) of the two species. Tannins, which occur in high concentrations in *Rhizophora* leaves compared

to *Avicennia* leaves (Lacerda, et.al., 1995), are reported to decrease the activity of benthic organisms such as the bacteria involved in N cycling (Alongi, et.al., 1989).

A high degree of spatial heterogeneity was observed in porewater nutrient concentrations in mangrove ecosystem (Alongi, 1996). This heterogeneity was attributed to 'micro-oxic' zones resulting from oxygen translocation via plant roots to surrounding sediments and the influence of crabs on sediment turnover (see Section 1.4) (Alongi, et al., 1996). These 'micro-oxic' zones contain populations of nitrifying bacteria, which supply  $\text{NO}_3^-$  to roots (Boto et al., 1985). However, the role of  $\text{NO}_3^-$  in mangrove nutrition is still debated. Boto et al (1985) suggested  $\text{NO}_3^-$  was the primary source of N nutrition to *A. marina* seedlings as when seedlings were supplied with only  $\text{NH}_4^+$  and nitrate reductase activity was blocked, growth was inhibited compared to a  $\text{NO}_3^-$  treatment. Stewart and Orebamjo (1984) found that although mangrove species were able to utilise  $\text{NO}_3^-$  when roots were incubated in  $\text{NO}_3^-$ , mangrove soils



had generally low nitrate reductase activity and therefore  $\text{NH}_4^+$  was the primary source of N.

## **2.2 Nitrogen cycling**

The nitrogen cycle within mangrove forests is mediated predominantly by microbial rather than chemical processes (Alongi et al., 1992). The major transformations in the nitrogen cycle discussed are shown diagrammatically (Figure 2). The relative importance of the various transformations within the forests are dependent on the forms of N pools present within the forest. The rate at which these transformations can occur will also be affected by a wide range of physical characteristics of the soil, however, determining the relative importance of the processes of the N cycle by comparison of process rates is difficult because there is little consistency in the units rate values are presented in.

### 2.2.1 Biotic Processes

#### 2.2.1.1 Nitrogen Fixation

Biological N fixation, the reduction of nitrogen gas to  $\text{NH}_4^+$ , occurs in a diverse array of Eubacteria and Archaea that have the required enzyme, nitrogenase (Postgate, 1978; Capone, 1997). N fixation may be a key process in ecosystems where N is limiting productivity because of its potential to provide N in a usable form to plants (Capone, 1997).

It has been hypothesized that N inputs from N fixation by both heterocystous and non-heterocystous forms of cyanobacteria may have a significant effect on the overall productivity of mangrove forests (Potts, 1979, 1984; Mann and Steinke, 1989).

Ambient levels of N fixation in mangrove sediments were considerably lower than rates in seagrass and saltmarsh communities (Valiela, 1995). Rates varied from 0.7 to 3974.4 mg N m<sup>-2</sup> d<sup>-1</sup> with a great deal of spatial and temporal variation (Table 7) (Zuberer & Silver, 1979; Potts, 1984; Hicks & Silvester, 1985; Mann & Steinke, 1989). N fixation rates in sediments in North Queensland forests were considerably lower (Boto and Robertson, 1990) than in sediments in Florida (Zuberer and Silver, 1978) and New Zealand (Hicks and Silvester, 1985). This is surprising, because these forests are both located in bays near to high population regions and therefore nutrient inputs would be higher than the relatively pristine region in North Queensland.

**Table 7:** Literature review of nitrogen fixation rates in mangrove sediments and structural components of mangrove trees

Location	Environment	N fixation rate (mg N m <sup>-2</sup> d <sup>-1</sup> )	Reference
Tampa Bay, Florida	Anoxic mud	38.4 – 283.2	Zuberer and Silver (1978)
	Tidal sediment	28.8	
	Prop-root assoc. sediment	40.8 – 81.6	
	Pneumatophore assoc. sediment	14.4	
	Litter	3974.4	
Whangateau Harbour, New Zealand	<i>A.marina</i> forest	470.4 - 962.4	Hicks and Silvester (1985)
Missionary Bay, Australia	<i>Rhizophora</i> forest		Boto and Robertson (1990)
	Sediments		
	Mid intertidal	0	
	High intertidal	1.0 – 3.3	
	Algal mats	2.9 – 3.9	
	Prop roots		
	Low intertidal	22.0	
	Mid intertidal	34.9 – 72.7	
High intertidal	8.3		
	On logs	0.7 – 1.5	

The available dissolved organic carbon (DOC) in sediments may also influence N fixation rates in mangrove ecosystems. Higher rates of N fixation were reported in sediments associated with roots (Zuberer & Silver, 1979; Boto and Robertson, 1990) and decaying organic matter (Hicks & Silvester, 1985). However, Mann & Steinke (1989) reported that higher concentrations of organic carbon did not stimulate N fixation, rather the extent of desiccation was the principle factor influencing N fixation. This result is contrary to that found in seagrass sediments, where DOC exudations from seagrass roots stimulate N fixation, which suggests that the N fixing communities of seagrass and mangroves may be dominated by different bacterial groups (Perry, pers.comm.).

#### 2.2.1.2 Nitrification

Nitrification is the oxidation of  $\text{NH}_4^+$  to  $\text{NO}_2^-$  nitrite, which in turn is oxidised to  $\text{NO}_3^-$  (Figure 2) (Kaplan, 1983). Nitrifying bacteria are chemolithotrophic (Kelly, 1971), with different genera mediating the two steps of the nitrification process (Kaplan, 1983). Most nitrifying activity in marine systems occurs in sediments where dissolved oxygen concentrations are low (Kaplan, 1983). Therefore in mangrove forests nitrification occurs predominantly close to the sediment surface (Kaplan, 1983) in micro-oxic zones (Figure 2). These zones are created by the oxygen pumping activity of mangrove roots (Boto et al., 1985) and in the oxidised lining of animal burrows (Boto, 1982).

Despite the possible importance of nitrate in nitrogen nutrition (Boto, et al., 1985), rates of nitrification in mangrove sediments have rarely been quantified (Alongi et al., 1992). Nitrification is very difficult to measure (Kaplan, 1983) the end product,

nitrate, is rapidly taken up by plants and denitrified (Boto et al., 1985). Nitrification rates at least an order of magnitude lower (Table 8) were measured in sediments in North Queensland (Iizumi 1986, as cited in Alongi et al., 1992) compared to sediments in Malaysia (Shaiful, 1986). This is potentially due to tannins, which occur in much higher concentrations in leaves of *Rhizophoraceae* than in leaves of *Avicennia*, and subsequently would be higher in sediments and porewaters in the North Queensland forest (Lacerda et al., 1986). Tannins are known to inhibit microbial activity (Kimball & Teas 1975)

Tidal inundation is also suggested to influence nitrification rates in mangrove sediments (Kristensen et al., 1988). Higher nitrate concentrations at the end of the high tide period (compared to during the low tide), suggest nitrification rates are higher during the high tide (Kristensen et al., 1988). Other abiotic factors including air and water temperatures, salinity and organic matter concentrations which have been shown to influence rates of nitrification in marine sediments (Kaplan, 1983) may also be influencing nitrification in mangrove sediments.

**Table 8:** Literature review of nitrification rates in mangrove forest sediments

<b>Location</b>	<b>Forest type</b>	<b>Rate</b> ( $\mu\text{gN g}^{-1} \text{d}^{-1}$ )	<b>Reference</b>
Missionary Bay, Australia	<i>Rhizophoraceae</i>	0.014	Iizumi (1986 As cited in Alongi et al., 1992)
Sementa, Malaysia	<i>Avicennia</i>	0 – 0.220	Shaiful et al. (1986)

### 2.2.1.3 Denitrification

Biological denitrification is the reduction of  $\text{NO}_3^-$  or  $\text{NO}_2^-$  by facultative anaerobes to the gaseous end products of  $\text{N}_2$  or  $\text{N}_2\text{O}$  (Capone, 1997). Given that mangrove sediments are largely anaerobic,  $\text{NO}_3^-$  availability is the factor controlling denitrification rates (Seitzinger, 1990). In marine sediments, denitrification rates increase as a function of  $\text{NO}_3^-$  concentration (Seitzinger, 1990), so there is potential for the removal of additional  $\text{NO}_3^-$  (eg. sewage) in mangrove sediments.

There are two types of denitrification: direct and coupled. Differentiation between the two types depends on the source of  $\text{NO}_3^-$ : direct denitrification in mangrove systems is fuelled by  $\text{NO}_3^-$  diffused into the sediment and coupled denitrification is supported by nitrate products of nitrification (Rivera-Monroy et al., 1995). Denitrification rates reported in mangroves (Table 9) are generally much lower than reported for estuarine sediments, despite the suitability of mangrove sediments (ie. with alternating anoxic and oxic conditions with tidal inundation) to the coupling of mineralization – nitrification – denitrification processes (Rivera-Monroy and Twilley, 1996).

Experimental manipulation has shown that denitrification rates are generally limited by the supply of  $\text{NO}_3^-$ , either from nitrification or diffusion from the overlying water (Morell and Corredor, 1993; Corredor and Morell, 1994; Rivera-Monroy and Twilley, 1996).

Research on denitrification in mangrove ecosystems has focussed on the measurement of direct rates of denitrification. It is important that both types of denitrification be measured, however, given that the relative importance of the two may vary in different forests and that fluxes of N into sediments are low (Boto & Wellington,

1988; Alongi, 1996), coupled denitrification is more likely to be the dominant type (Seitzinger, 1987; Morell and Corredor, 1993; Corredor and Morell, 1994; Rivera-Monroy et al., 1995; Rivera-Monroy and Twilley, 1996).

In unpolluted mangrove stands in North Queensland, low rates of direct and indirect denitrification have been reported (Iizumi 1986 as cited in Alongi, et al., 1992). The authors hypothesized that low indirect denitrification rates may be due to inhibition of nitrifying bacteria by high tannin levels and low  $\text{NO}_3^-$  concentrations in porewaters (Iizumi, 1986 as cited in Alongi, et al., 1992). Low rates of denitrification, with the majority of denitrification capacity supported by coupled nitrification-denitrification are generally reported in unpolluted systems (Seitzinger, 1987; Morell and Corredor, 1993). A switch in the predominant denitrification pathway was observed when a source rich in  $\text{NO}_3^-$  and  $\text{NO}_2^-$  was added (eg. sewage effluent) with denitrification rates responding sufficiently to balance the entire input of  $\text{NO}_3^-$  and  $\text{NO}_2^-$  (Corredor and Morell, 1994). The rate of denitrification following addition of filtered sewage was approximately nine times that observed in nearby mangrove forests not receiving sewage (Table X). This suggests that in unpolluted mangrove systems denitrification is  $\text{NO}_3^-$  limited and that coupled denitrification is the primary pathway for denitrification. This work also supports the potential use of mangrove ecosystems as tertiary treatment sites for well nitrified sewage effluent (Corredor and Morell, 1994).

**Table 9:** Literature review of denitrification rates in mangrove forest sediments under ambient and nitrogen enriched conditions

Location	Forest type	Treatment	Rate ( $\mu\text{g N m}^{-2} \text{d}^{-1}$ )	Reference
Missionary Bay, Australia	<i>Rhizophora</i>	A	4320	Iizumi (1986)
Joyuda Lagoon, Puerto Rico	Top 2cm 2cm – 8cm	A A	71 – 7526 235 – 54062	Morell and Corredor, (1993)
La Parguera, Puerto Rico	<i>Rhizophora</i> fringe Transition zone <i>Avicennia</i> landward	C N C N C N	16700 – 34171 65520 – 587664 3259 – 61488 14246 – 437808 5846 – 52550 139675 – 362880	Corredor and Morell (1994)
Falmouth Harbour, Jamaica	<i>Rhizophora</i> and <i>Avicennia</i>	A	116200 – 1166200	Nedwell et al. (1994)
Terminos Lagoon, Mexico	Mixed spp. Fringe forest Basin forest	A NH <sub>4</sub> NO <sub>3</sub> A	0 – 3158 840 - 9408 1344 – 73920 0 – 1512	Rivera- Monroy, et al. (1995); Rivera- Monroy and Twilley (1996)

A – ambient

C - control

N – nitrogen enriched

NH<sub>4</sub> – ammonium enriched

NO<sub>3</sub> – nitrate enriched

#### 2.2.1.4 Ammonification

Ammonification is the breakdown of organic N resulting in the release of NH<sub>4</sub><sup>+</sup>

(Alongi et al., 1992). Organic N mineralisation occurs in a range of organisms from

microbes to vertebrates in which NH<sub>4</sub><sup>+</sup> is the end product of excretion (Alongi et al.,

1992). Net estimates of ammonification rates have been made for mangrove

sediments (Hesse, 1961; Rosenfeld, 1979; Hines and Lyons, 1982; Iizumi 1986 as

cited in Alongi et al., 1992; Shaiful et al., 1986), however, NH<sub>4</sub><sup>+</sup> excretion rates for

the various infaunal groups (eg. bacteria, meiofauna and macrofauna) are largely unknown (Alongi et al., 1992). Knowledge of these rates at different depths would enable determination of which organisms are regulating the regeneration of the  $\text{NH}_4^+$  pool.

In North Queensland mangroves, the presence of nematodes, which are among the dominant taxa in Florida mangrove forests (Fell et al., 1975), was not found to affect  $\text{NH}_4^+$  regeneration rates (Tietjen and Alongi, 1990). The relatively insignificant contribution of nematodes to  $\text{NH}_4^+$  regeneration and the low and erratic  $\text{NH}_4^+$  excretion rates for *Sesarma spp.* was attributed to the poor nutritional quality of *Rhizophora* leaf litter (Tietjen and Alongi, 1990; Gissler, unpublished data, as cited in Alongi et al., 1992). Given that ammonification rates similar to those recorded for saltmarshes have been measured in mangrove sediments, microbial activity must be regulating the available  $\text{NH}_4^+$  pool (Alongi et al., 1992).

**Table 10:** Literature review of ammonification rates reported in mangrove forest sediments

<b>Location</b>	<b>Forest type</b>	<b>Rate</b> ( $\mu\text{g N g}^{-1} \text{d}^{-1}$ )	<b>Reference</b>
Florida Bay	<i>Avicennia</i>	1.06	Rosenfeld (1979)
Missionary Bay, North Queensland	<i>Rhizophora</i>	0.42 – 1.82	Iizumi (1986)
Selangor, Malaysia	<i>Avicennia</i>	0.06 – 0.38	Shaiful et al. (1986)

$\text{NH}_4^+$  release is highly dependent on the C:N ratio of the sediments and decomposing organic matter (Shaiful et al., 1986; Alongi et al., 1992). Net mineralisation will occur when a substrate has a low C:N ratio and high N concentrations as available

$\text{NH}_4^+$  is in excess of microbial needs, while substrates with high C:N ratios will favour net immobilisation (Shaiful et al., 1986 Alongi et al., 1992). The C:N ratio in mangrove litter is species dependent, but for species of *Rhizophoraceae* which dominate forests throughout the Indo-West Pacific, C:N ratios are high. This, combined with low flux rates for  $\text{NH}_4^+$  across the sediment-water interface throughout the tidal cycle (Kristensen et al., 1988) and high rates of bacterial cell production (Alongi, 1988) suggest rates of immobilisation may be high in mangrove forests (Alongi et al., 1992).

## 2.2.2 Abiotic Processes

### 2.2.2.1 Sediment-Water Column Exchange

Direct measurements of N fluxes within mangrove sediments are few (Alongi et al., 1992). Those available suggest flux rates are low, from  $-104$  to  $-29 \mu\text{mol m}^{-2} \text{h}^{-1}$  for  $\text{NH}_4$  and  $-51$  to  $-30 \mu\text{mol m}^{-2} \text{h}^{-1}$  for  $\text{NO}_3$  (Boto & Wellington, 1988; Alongi, 1996). Although a concentration gradient exists between sediment porewaters and overlying tidal water, the direction of nutrient flux is into the sediment (Kristensen et al., 1988). It appears mangrove forests act as a source of dissolved and particulate organic nitrogen and a sink for dissolved inorganic nitrogen (Rivera-Monroy et al., 1995).

Flux rates can vary depending on local physical characteristics such as geomorphology, tidal regime, climate and groundwater inputs (Twilley, 1988; Alongi, 1996) and sediment biological characteristics such as bacterial activity (Alongi, 1989, 1990, 1996). Data on the effect of season on nutrient fluxes is contrary. In North Queensland, seasonal differences in nitrogen flux were low, probably a result of low

variation in temperatures throughout the year (Boto & Wellington, 1988; Alongi, 1990), while in Florida tidal nutrient exchange to mangroves exhibited a distinct seasonal pattern, with greatest export in late summer (Twilley, 1985).

The most comprehensive study of benthic N dynamics to date was carried out on Hinchinbrook Island, North Queensland (Alongi, 1996). Import of inorganic N was higher in low intertidal areas than in mid intertidal areas and sediments accounted for 84% and 36% of uptake respectively. In mid intertidal forests, prop roots were responsible for 62% of uptake. Sediment and prop root N uptake accounted for 6% and 2% of forest primary productivity requirements respectively. Thus although concentrations of nutrients imported to mangrove forests via tidal exchange were low, they constitute a significant portion of nutrients available in the creek. The mangrove forests lining Coral Creek, Hinchinbrook Island import approximately 95% of dissolved N that is imported to coastal waters (Alongi, 1996).

Tidal exchange of nutrients appears not to contribute significantly to nutrient cycling within this forest in areas where water column nutrient concentrations are low compared to recycling within the forest by decomposition (Robertson et al., 1992) and crab ingestion (Robertson and Daniel, 1989). The influence of tidal exchange requires further investigation, particularly in waters with high nutrient loads.

In the same way nutrients may be deposited to mangrove sediments from tidal waters, sediment particles with adsorbed nutrients may also be deposited. This type of deposition has not been studied in relation to mangrove forest nutrient dynamics, but

may represent a fairly significant input in mangroves adjacent to waterways with high nutrient concentrations.

### **3. Phosphorous Dynamics**

Although it has been suggested that phosphorous (P) may be limiting productivity in high intertidal regions of mangrove forests (Boto & Wellington, 1983), little data is available on P concentrations and transformations in sediments of mangrove forests. The available data suggest P pools are predominantly in the organic form and are largely unavailable for plant uptake (Hesse, 1963; Boto and Wellington, 1984). Of the inorganic pool, a large proportion is bound as salts or oxides (Hesse, 1963; Alongi et al., 1992).

The transformations of P are illustrated in Figure 3, but identification of the relative importance of each process to the P cycle and to P availability is difficult as little data is available.

#### **3.1 Phosphorous pools**

##### **3.1.1 Vegetation**

P status also varies between the different structural components having different P concentrations (Table 11) (Clough & Attiwill, 1975; Gong & Ong, 1990). P concentrations in mangrove leaves range from 0.02 – 0.167. Concentrations vary with species (Sah et al., 1989; Clough & Attiwill, 1975), position within the forest relative to tidal inundation (Wong et al., 1995) and sediment nutrient status (Boto & Wellington, 1983; Clough et al., 1983).



**Table 11:** Phosphorous content of different structural components of several mangrove species

Location	Species	Structural component	Phosphorous content (% dry wt.)	Reference
Westenport Bay, Australia	<i>A. marina</i>	Leaves	0.12	Clough & Attiwill (1975)
		Branches	0.04 – 0.11	
		Trunk	0.03	
		Roots	0.03 – 0.08	
		Pneumatophore	0.03	
		Fruit	0.16	
Sundurbans, India	<i>A. marina</i>	Leaves	0.16	Sah et al. (1989)
	<i>A. alba</i>	Leaves	0.15	
	<i>E. agallocha</i>	Leaves	0.30	
Matang Reserve, Malaysia	<i>R. apiculata</i>	Leaves	0.02	Gong & Ong (1990)
		Branch	0.03	
		Trunk	0.03	
		Roots	0.02 – 0.03	

Different responses in leaf % P were found following enrichment in the various forests (Table 12). In Darwin, following enrichment with sewage over a 20 year period, P concentrations in leaves were elevated (Clough et al., 1983). A slight stimulation of leaf %P was observed following treatment with wastewater in China (Gong & Ong, 1990), but no stimulation of leaf %P was observed in a North Queensland *Rhizophora* forest following P additions (Boto & Wellington, 1983).

From comparison of %P in fresh and senescent leaves it is clear that P is less efficiently resorbed from senescent leaves than nitrogen (Clough & Attiwill, 1975). The absence of a stimulation following P enrichment in North Queensland (Boto & Wellington, 1983) and China (Chiu et al., 1996) and low resorption rates of P

compared to N (Clough & Attiwill, 1975), suggest P may not be limiting mangrove growth in the forests studied.

**Table 12:** Literature review of P content of mangrove leaves following nutrient enrichment

Location	Species nutrient treatment	Treatment	P content (% dry wt.)	Reference
Hinchinbrook Island, Australia	<i>Rhizophora</i> Low intertidal	C	0.10 – 0.11	Boto & Wellington (1983)
		N	0.12	
		P	0.10	
	High intertidal	C	0.09 – 0.11	
		P	0.09	
Futian Nature Reserve, China	<i>K. candel</i>	C	0.11	Wong et al. (1995)
		S	0.12	
	<i>Ae. corniculatum</i>	C	0.12	
		S	0.13	

### 3.1.2 Sediment

Total P concentrations in mangrove sediments are low, between 0.15% and 0.129% (Table 13) reflecting the low ambient P status of many Australian soils (Boto & Wellington, 1984).

Within the top 25cm of mangrove soils, 75-80% of total P is in an organic form (Hesse, 1963; Boto & Wellington, 1984). Below this, inorganic phosphate concentrations increase with depth, due to increasing anoxia (Hesse, 1963). Inorganic P is present as dissolved phosphate  $PO_4^-$ , or in one of two forms which plants cannot assimilate: chemically bound to calcium, iron and aluminium and as soluble reactive P adsorbed onto or incorporated into hydrated iron or aluminium oxides (Sahoo et.al.,

1988; Alongi, 1992). Extractable P was also found to decrease with increased tidal elevation (Boto & Wellington, 1984; Mackey et al., 1992), suggesting a tidal influence in the deposition of P (Mackey et al., 1992). Other factors including seasonal changes in plant growth and microbial activity, temperature, rainfall and sediment type have been suggested to influence P concentrations in sediments over time (Boto, 1982).

Although organic P concentrations are high within mangrove sediments, much of this P is chemically bound to humic compounds and is not biologically available (Boto, 1988, as cited in Alongi, et.al., 1992). The inorganic forms, although a much smaller component of the P pools, are the most readily available to plants and microbes (Boto, 1988, as cited in Alongi, et.al., 1992).

**Table 13:** Literature review of phosphorous concentrations in mangrove forest sediments

Location	Forest type	Total P (% dry wt.)	Extractable P ( $\mu\text{g}\cdot\text{g}^{-1}$ )	Reference
Wellington, Sierra Leone	<i>Rhizophora</i> <i>Avicennia</i>	0.151 0.129	- -	Hesse (1961)
Hinchinbrook Island, Australia	<i>Rhizophora</i> dominated Below MHW Above MHW	0.45 - 0.54 0.34 - 0.37	10.2 - 20.1 5.0 - 12.1	Boto and Wellington (1984)
Boggy Creek, Australia	<i>Avicennia</i> dominated High intertidal Low intertidal	- -	20.4 - 30.5 12.1 - 17.8	Mackey et al. (1992)

MHW – mean high water level

## 3.2 Phosphorous Cycling

In sediments, most P transformations involve abiotic processes (Figure 3). Those that are mediated by organisms are direct uptake by plants and uptake and excretion by organisms (Alongi et al., 1992).

### 3.2.1 Biotic Processes

Infauna (ie. bacteria, meiofauna and macrofauna) take up and assimilate both organic and inorganic forms of P (Alongi et al., 1992). The turnover time of P by organisms is short compared to the remobilisation of P from phosphate salts and oxides, and therefore may be important in providing inorganic P for plant uptake (Alongi et al., 1992).

There is little data available on P uptake and excretion rates for mangrove forest infauna groups (Alongi, et al., 1992). P excretion by nematodes did not raise organic or inorganic P concentrations above those resulting from leaching and bacterial decomposition in North Queensland mangrove forests (Tietjen and Alongi, 1990).

The low abundances of nematodes and their relatively insignificant contribution to P regeneration in the *Rhizophora* dominated forests of North Queensland was attributed to the poor nutritional quality of the mangrove litter (Tietjen & Alongi, 1990).

Phosphorous regeneration by meio- and macrofaunal groups is therefore dependent on litter quality (Alongi et al., 1992), so *Avicennia* dominated forests may have greater P regeneration rates than *Rhizophoraceae* dominated forests. Clearly, the dynamics of the P cycle require further investigation.

### 3.2.2 Abiotic processes

#### 3.2.2.1 Chemical Processes

The abiotic processes in the phosphorous cycle (Figure 3) involve the transformations of dissolved inorganic phosphates (DIP) (Alongi, et al., 1992). Immobilisation of DIP occurs, by precipitation to form Ca, Al and Fe salts or by adsorption to form Al and Fe oxides (Hesse, 1963; Alongi et al., 1992). These processes influence phosphorous availability to mangroves by further reducing the already small pool of available P (Alongi, et al., 1992).

Phosphate immobilisation occurs rapidly following the addition of inorganic phosphorous to sediments (Hesse, 1963; Boto & Wellington, 1983). In Sierra Leone, approximately 90% of P was adsorbed within 5 minutes of addition, with equilibrium reached within an hour (Hesse, 1963). In North Queensland, however, mangrove sediment P concentrations did not increase significantly following addition of 400 kg P ha<sup>-1</sup> over a twelve-month period (Boto & Wellington, 1983). These results suggest mangrove soils have a high capacity for immobilisation of additional inputs of P.

No measurements of dissolution and resorption of phosphate salts and oxides are available for mangrove sediments, but rates are hypothesized to depend on physiochemical characteristics of the soil (eg. pH, redox state and available sulfides) (Boto 1988, cited in Alongi, et al., 1992). Biotic processes may play a greater role than dissolution and resorption in regeneration of P pools to forms available for plant uptake (Alongi, et al., 1992).

### 3.2.2.2 Sediment-water column exchange

P fluxes between porewaters and tidal waters have been measured in mangroves on Hinchinbrook Island, Australia (Boto & Wellington, 1988; Alongi et al., 1992) and in Florida (Rosenfeld, 1979). Both studies suggest that the flux of P to mangrove sediments relative to the requirement for forest productivity may be greater than the equivalent N fluxes (Alongi, 1996). This may be a result of sediment concentration gradients, especially as P is rapidly bound to form oxides or salts in the sediment (Rosenfeld, 1979) and is therefore removed from the dissolved P pool.

Fluxes of P are subject to the same physical and biological influences as N fluxes (see Section 2.3) and therefore P fluxes vary considerably (Rosenfeld, 1979; Alongi, 1996). In the most comprehensive study of sediment P dynamics within mangrove ecosystems to date (Alongi, 1996), more than four times as much P was imported and taken up by low intertidal than mid intertidal sediments, 28% and 5% of forest productivity requirements respectively (Alongi, 1996).

## 4: Nutrient Enrichment Experiments

Many factors may control rates of productivity in mangrove ecosystems (eg sediment anoxia and water availability) (Boto and Wellington, 1983, 1984). However, substrate characteristics, particularly nutrient availability, are considered to exert the most direct control on productivity (Boto and Wellington, 1984).

### 4.1 Mangrove forests

#### 4.1.1 Experimental nutrient enrichment

There has only been one ecosystem level experimental manipulation of sediment nutrient concentrations within mangrove forests. Boto and Wellington (1983) examined the response of a mixed *Rhizophora* forest to increased levels of nitrogen and phosphorous in North Queensland. At the site closest to the creek, growth (as stipule fall rate) increased significantly following  $\text{NH}_4^+$  ( $100 \text{ kg N ha}^{-1}$ ) but not phosphorous ( $100 \text{ kg P ha}^{-1}$ ) enrichment. At the higher intertidal site, a significant increase in growth was observed following phosphorous enrichment. Leaf % P increased significantly following P enrichment, indicating P deficiency may be limiting growth at the high intertidal site (Table 12). Following ammonium enrichment, %N and %P of leaves increased significantly. While P enrichment at the edge site had no effect on leaf %P, but did result in increased leaf %N (Table 5) (Boto and Wellington, 1983). It is possible this increase in leaf %N resulted from increased nitrogen fixation activity, a trend that has been observed in seagrass sediments following P enrichment (O'Donohue, pers. comm.). This supports the suggestion that nitrogen is limiting growth at the edge site.

Boto and Wellington (1983) concluded that mangrove growth in Missionary Bay, Australia was primarily N limited, although for those sites at higher elevations P may also be limiting (Boto and Wellington, 1983). Interactions between soil nutrient status, soil redox potential and salinity were also suggested to influence nutrient availability to the plants and control mangrove growth.

Feller (1995) carried out nutrient enrichment experiments on *Rhizophora mangle* trees in Central America focussing on the relationship between the dwarf condition and nutrient limitation. Dwarf trees along a gradient of tidal inundation were enriched with nitrogen and phosphorous. Phosphorous availability was the primary factor limiting growth (resulting in the dwarf character) and small increases in insect herbivory were also reported for enriched trees (Feller, 1995).

Nutrient enrichment experiments have also been performed on seedlings in a laboratory setting. *Rhizophora mangle* and *Avicennia germinans* seedlings were exposed to one of two nutrient treatments for 2 months: High N ( $5 \text{ mol m}^{-3}$ ) and P ( $4 \text{ mol m}^{-3}$ ) and low N ( $2.5 \text{ mol m}^{-3}$ ) and P ( $2 \text{ mol m}^{-3}$ ) (McKee, 1995). Seedlings treated with the low nutrient concentrations had greater investment in root biomass compared to seedlings exposed to high nutrient concentrations, while investment in shoot biomass was greater in seedlings treated with higher nutrient concentrations (McKee, 1995). Response of leaf C:N ratio to N and P enrichment also differed with level of enrichment. For both species the leaf C:N ratio in seedlings exposed to higher nutrient concentrations was approximately twice that of seedlings exposed to low nutrient concentrations (McKee, 1995).

Similar experiments were conducted with *A. marina*, examining the response of seedlings to different nutrient and salinity regimes (Naidoo, 1987). Increased investment in shoot biomass and higher concentrations of nitrogen in shoots than roots in seedlings exposed to higher nutrients were also reported in this study, but this was dependent on salinity (Naidoo, 1987). The results of these experiments suggest seedling growth is dependent on sediment nutrient availability (Naidoo, 1987; McKee, 1995).

#### 4.1.2 Enriched nutrients

Mangrove forests receiving significant nutrient inputs from bird guano and sewage enriched mangrove forests also provide unique opportunities to study enrichment effects.

##### 4.1.2.1 Sewage

Studies of a mangrove forest receiving sewage effluent were carried out by Wong, et.al. (1995) in the People's Republic of China. No significant difference between control and sewage enriched total and available N and P in the sediments or leaf N and P in the two dominant species were found. The lack of response over the 12 month period was attributed to low concentrations of organic matter, nitrogen and P in the wastewater and the large capacity for mangrove swamps and soils to assimilate additional nutrients (Wong et al, 1995).

#### 4.1.2.2 Guano

Onuf, Teal and Valiela (1977) compared mangrove material from forests receiving high natural guano inputs from large bird colonies and forests nearby not inhabited by bird colonies. They reported stimulated plant growth and increased percent nitrogen concentrations in forests receiving guano inputs. The most significant difference was in the amount of insect herbivory to the leaves of plants: much higher insect herbivory rates were found at the guano-enriched sites. They suggested changes to nutritive values of the leaves may have had important consequences for community dynamics.

The response of mangrove forests to nutrient enrichment appears largely site dependent. Initial sediment and vegetation nutrient concentrations compared to forests in other parts of the world should be given more consideration as forests with high ambient nutrient pools may not have the capacity to assimilate additional nutrients. However, the high capacity for denitrification, immobilisation of inorganic P in mangrove sediments and uptake of N and P by plants suggests mangrove forests may be suitable as sewage filters. The lack of a cohesive literature base on mangrove nutrient dynamics suitable must be addressed while there is still potential for policy changes in developing countries.

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