Cycling and Global Fluxes of Nitrogen in Mangroves

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Abstract

Recent advances necessitate a critical reappraisal of nitrogen cycling in mangrove ecosystems. Nitrogen concentrations in soil, water and vegetation are low, but N-use and recycling efficiencies are high and N residence times are short, driven by rapid forest production and the need to conserve N. Most mangrove-associated fauna preferentially assimilate benthic algae, phytoplankton, algal detritus or complex mixtures of these forms to meet N demand. Consumer preferences, locations and types of habitat, and the relative availability of other foods determine the trophic significance of mangrove litter. A nitrogen mass balance model of the world's mangrove forests indicates that: (1) 2687 Gg N yr^{-1} is required to sustain global mangrove net primary production (NPP); (2) N burial is ≈ 25% of total N input; (3) N_2 fixation is ≤ 5% of total N input; (4) production in roots and litter account for 40% and 50% of mangrove NPP, respectively; (5) tidal export equates to ≈ 55% of N input; and (6) denitrification and N_2O effluxes account for < 10% of total N losses. Despite proportionately large tidal losses, the global flux of nitrogen in mangrove forests is roughly in balance due to multiple adaptations and strategies to efficiently use and retain nitrogen.

Key words: mangrove, nitrogen, nitrogen cycle, nitrogen retention, nutrient conservation

1. Introduction

Mangrove forests and their associated waterways constitute one of the most important aquatic environments along the world's subtropical and tropical coastlines. Mangroves inhabit over 152,000 km^2 of coastal area but occupy < 1% of global tropical forest area; they are the only woody halophytes that live in salt water. These forested wetlands serve a wide variety of economic and ecological roles: as habitat for terrestrial and marine flora and fauna; as ecosystem engineers shaping and maintaining the intertidal zone; as a renewable resource of wood and food; and as key accumulation sites for soils, sediment particles and associated elements (Van Lavieren *et al.,* 2012).

Mangroves are the most productive plants in the sea and are among the most productive forest types on earth, with average rates of gross and net primary production of 4.6 kg C ha^{-1} yr^{-1} and 1.9 kg C ha^{-1} yr^{-1}, respectively (Alongi, 2009). Most mangrove ecosystems are net autotrophic. High rates of forest primary productivity drive high requirements for nutrients and trace elements to sustain growth, production and physiological maintenance of the trees. Such large needs translate into rapid uptake of soil nutrients that are transformed by Archaea, bacteria, fungi, protozoa and microalgae, as well as dependence on the tight links between carbon fixation and nutrient cycling. While plant-soil relations in mangroves are fairly well understood, how these relationships sustain high productivity in the long term and how they impact on the linkages between mangroves and adjacent coastal environments are poorly known.

Nitrogen is one of the key essential elements for the sustenance of plant and animal life, but the dynamics of N in relation to mangrove ecosystem change and development over time is not well understood. The critical need for N in the nutrition of mangrove organisms has been confirmed repeatedly (Alongi *et al.,* 1992; Alongi, 2009). Yet no synthesis exists for mangrove N dynamics and recent advances in N cycling necessitate a critical reevaluation of how the many different forms of dissolved and particulate nitrogen (DN, PN) function in mangroves, and to what extent, in what form(s), and how much, N is exchanged between forests, the atmosphere and the tropical coastal ocean.

2. Solutes and Solids

Concentrations of dissolved inorganic and organic N in mangrove tidal water and in soil interstitial water are consistently in the μM range (Table 1). The major forms of organic N in tidal waters are complexes of particulate and dissolved organic nitrogen (PON, DON) originating from decayed vegetation and polyphenolic acids; dissolved inorganic nitrogen (DIN) consists mostly of NH_4^+ with much lower concentrations of NO_2^- and NO_3^-. Con-

centrations of DN and PN in tidal water vary in relation to the onset of the monsoon, salinity, tidal state, plankton production, organic pollution and water residence time (Bala Krishna Prasad *et al.,* 2006). Some creeks and waterways exhibit either little temporal variation or N concentration peaks that are not readily explainable (Trott & Alongi, 1999).

In interstitial water, spatial variations are more evident than temporal variations as soil nutrient pools relate closely to soil composition and grain size, pH, salinity, the presence of fine roots and degree of anoxia (Alongi, 2009). Plant uptake plays a central role in controlling soil nutrient pools, the sizes of which relate to the relative abundance of live and dead roots. In theory, dissolved nutrient concentrations should relate closely to seasonality of plant uptake and growth, with lower concentrations during periods of rapid plant growth, but rarely has this relationship been observed in nature (Boto & Wellington, 1984). That such a relationship goes unobserved is unsurprising considering that other factors regulate the size of the interstitial nutrient pools, such as rates and pathways of microbial decomposition and transformation, bioturbation, infiltration of tidal water and groundwater, faunal excreta, root decomposition and leakage, and inputs from external sources, including human wastes (Alongi, 2009).

The composition of DON in mangrove soil and in overlying water is poorly understood. The few studies that have detailed the constituents of DON (Stanley *et al.,* 1987; Maie *et al.,* 2006, 2008) found that it is composed of polyphenolic acids and lesser amounts of urea, fatty and amino acids, and proteins, plus some still unidentified inert organic matter.

Concentrations of PN in tidal waters are controlled by the same factors that regulate DN, although few studies have measured PN. The few data indicate low and variable concentrations ranging from <5 to 150 µM (Ayukai *et al.,* 2000). Tides play an important role in regulating water-column N concentrations, with large tides causing greater dilution and variation than small tides. The extent of freshwater input also plays a major role in controlling N concentrations, as rivers discharge large volumes of freshwater and suspended particles whose seasonal variability lead directly to variability in PN and DN concentrations.

Soil PN originates from dead and live roots and other tree matter, planktonic and benthic plant and animal detritus, microbial biomass, and a mixture of terrestrial and marine organic matter derived from land and sea (Alongi, 2009). PN concentrations, like those of DN, vary in relation to soil grain size and composition; as the percentage of sand increases relative to silt and clay content, N content decreases. Soil PN values can range from nearly undetectable in sandy carbonate sediments to as high as 1.7% by sediment DW in pure clay and peat deposits (Alongi *et al.,* 2004a).

PN concentrations in mangrove vegetation also vary among tree parts and species, and with tree age (Table 2). Concentrations are greatest in leaves, followed by dead and live roots, and wood. The percentage of PN tied up in living biomass increases with tree age (Table 2). On a whole-forest basis, regardless of species, most N (≈95%) is found in mangrove soils rather than in forest biomass (Table 3).

Table 1 Range of concentrations (µM) of DIN and DON in mangrove waters and in soil interstitial water. From data and references in Alongi *et al.* (1992), Trott and Alongi (1999), Ayukai *et al.* (2000), Alongi *et al.* (2002, 2004a), and Bala Krishna Prasad *et al.* (2006).

N species	Tidal water	Soil interstitial water
NH_4^+		
Unpolluted	0.05 – 15.3	0.5 – 240*
Polluted	5.3 – 75.2	3 – 1200*
$NO_2^- + NO_3^-$		
Unpolluted	0.1 – 1.2	0.1 – 15.5
Polluted	22 – 264	0 – 0.2
DON		
Unpolluted	5 – 40	<1 – 548
Polluted	5 – 80	26 – 811

*= free + exchangeable

Table 3 Mean inventory of N (kg ha^{-1}) in living tree biomass, dead fine roots, and soil in *Rhizophora stylosa* and *Avicennia marina* forests in dry tropical Australia. Values in the last row are percentage of N of total forest N pool in each forest component. Adapted from Alongi *et al.* (2003).

Rhizophora stylosa			***Avicennia marina***		
Trees	*Dead roots*	*Soil*	*Trees*	*Dead roots*	*Soil*
532	100	10,330	412	168	11,653
4.8%	1%	94.2%	3.4%	1.4%	95.2%

Table 2 Nitrogen concentrations (mg g^{-1}) in different tree parts of *Rhizophora apiculata (R.a.)*, *Rhizophora stylosa (R.s.),* and *Avicennia marina (A.m.)* in the wet and dry tropics. Adapted from Alongi *et al.* (2003, 2004b). NA = age unknown.

Spp.	Age (yr)	%N in living biomass	Leaf	Branch	Stem	Prop Root	Live Roots	Dead Roots
Wet tropics (Thailand)								
R.a.	3	2	12	3.3	2.3	2.6	6.4	6.4
R.a.	5	3	10	3.4	1.7	2.3	5.2	6.4
R.a.	25	12	13	4.0	1.4	1.8	4.1	7.8
Dry tropics (Australia)								
R.s.	NA	5	9.9	1.6	1.6	2.4	3.2	6.4
A.m.	NA	3	14.4	2.8	2.9	—	4.5	7.8

3. N Availability, Plant Nutrition and Limitation

The acquisition of nutrients is the key process sustaining growth of mangroves. Nitrogen, in addition to P and Fe, most often limits growth, but acquiring N is not a straightforward process in mangrove environments. Despite a number of ecophysiological mechanisms and strategies, mangrove trees must tolerate or avoid anoxia and salt, and balance carbon gain and water loss, while acquiring minerals to synthesize structural and reproductive tissue (Reef *et al.,* 2010).

N availability depends on environmental factors such as salinity, temperature, soil fertility and geochemical redox reactions between dissolved organic and inorganic constituents in interstitial water. In highly reducing mangrove soils, for instance, metal sulfide complexes readily bind to organic nutrients thereby limiting the amount of nutrients available to the plant (Alongi, 2009). Mangrove growth is non-linear when the supply of N increases, even when salinity is kept constant. In culture experiments, stem growth of *Rhizophora apiculata* and *Xylocarpus granatum* is enhanced to the highest rate (50 mmol m^{-2} d^{-1}) of DIN supply (Fig. 1), whereas stem growth of *Bruguiera gymnorrhiza, Avicennia marina,* and *Xylocarpus moluccensis* levels off at a DIN supply rate of 10 mmol m^{-2} d^{-1}; stem growth of *Ceriops tagal* peaks at a supply rate of ≈25 mmol N m^{-2} d^{-1} (Fig. 1).

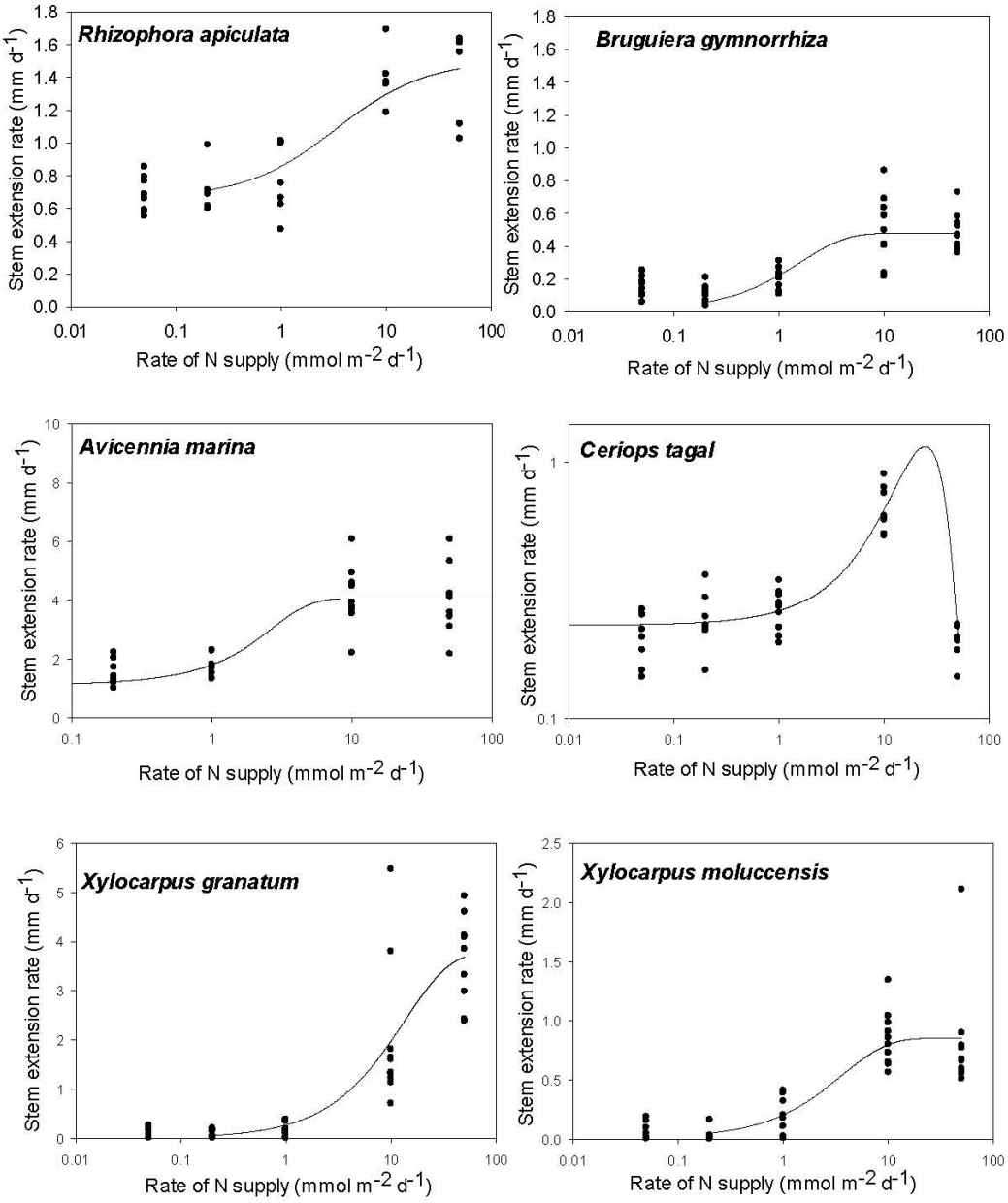

Fig. 1 Relationship between growth of saplings of the mangroves *Rhizophora apiculata* (top left panel), *Bruguiera gymnorrhiza* (top right panel), *Avicennia marina* (middle left panel), *Ceriops tagal* (middle right panel), *Xylocarpus granatum* (bottom left panel), and *Xylocarpus moluccensis* (bottom right panel) with increasing rates of DIN supply. The lines in each panel represent best-fit regressions. Adapted from Alongi (2011).

In the field, different mangrove species exhibit different growth responses to added DIN (Krauss *et al.,* 2006; Reef *et al.* 2010). N or P limitation depends greatly on the frequency of tidal inundation. For instance, in the Caribbean, fringing mangroves are N-limited, but permanently flooded forests or those deep within islands are P-limited (Feller *et al.,* 2002). In an earlier test in Australian mangroves, Boto and Wellington (1983) found N limitation from the water's edge to the high intertidal, but co-limitation of P only in the high intertidal zone.

High rates of mangrove productivity equate to high rates of N uptake, but also imply that N requirements must be met by high nutrient-use efficiencies and high rates of N resorption from leaves (Lin *et al.,* 2010). A comparison of mangrove N-use efficiencies with those measured in terrestrial evergreen and deciduous trees, and in forbs and graminoids shows a wide spread of values, with efficiencies in mangroves at the upper end of the range (Fig. 2A). The apparent strategy of using N efficiently relates well to the low N concentrations found in leaves and other mangrove tree parts (Table 2), as well as to resorption efficiencies that are at the higher end of the range for tropical trees (Fig. 2B).

Conserving N is clearly advantageous. Development of large below-ground reservoirs of dead roots and maximizing N allocation to the youngest parts of mangrove trees are efficient retention mechanisms. Also, mangroves are evergreen with sclerophyllous leaves and root/shoot biomass ratios similar to or higher than those found in other tropical trees, including desert plants (Reef *et al*., 2010). The former characteristic implies smaller nutrient investment in new leaves and lower N loss due to long tissue lifespan. Sclerophylly is linked to both low soil nutrient content and low water availability; sclerophyllous leaves are characterized by long lifespans, slow decomposition, and reduced leaf herbivory. Mangrove leaves lose a high proportion of water before wilting, having life-spans typical for tropical and subtropical broadleaved evergreens.

Recycling mechanisms are thus well-developed in mangroves, and this characteristic is reflected in residence times for total ecosystem N that, as in most marine systems, are relatively short (Galloway *et al.,* 2003). For instance, the mean residence time for ecosystem N in *Rhizophora stylosa* forests in arid Western Australia is 2-4 yr (Alongi *et al.,* 2005a) with a shorter residence time for ecosystem N of < 2 yr in *A. marina* forests. A number of factors explain the differences in nutrient-use among species, such as species-specificity in nutrient allocation and ecophysiological mechanisms, the proportion of energy and N used in chemical defences, and leaf and fine root lifespans. Another effective N conservation strategy is increasing the efficiency of various metabolic processes and in utilizing dominant soil N pools. Mangroves, like other plants, invest a large proportion of root metabolism in the uptake and assimilation of NH_4^+ which translates into a comparatively low energy investment compared with utilizing NO_3^- or possibly DON.

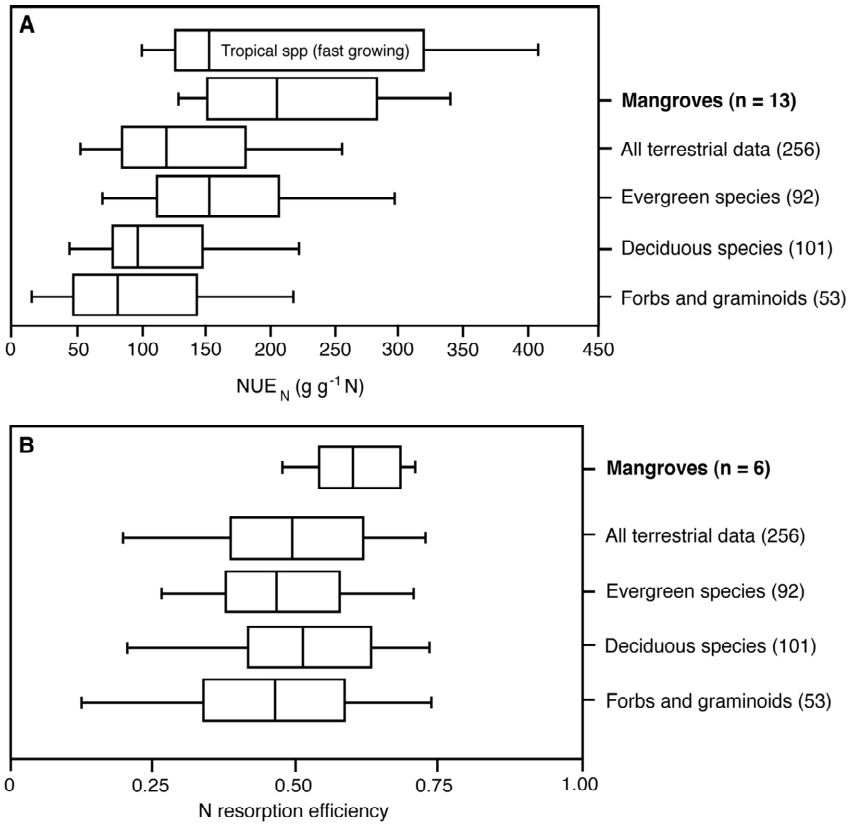

Fig. 2 Comparison of rates of (A) N-use efficiency and (B) N resorption efficiency in mangroves with tropical plantation trees and all other forest types. Adapted from Alongi (2009).

4. Soil N and Microbial Transformation Processes

The dominance of NH_4^+ in mangrove soils reflects high rates of ammonification in relation to other N transformation processes as well as plant preferences, the origin(s) of PN, other pathways of utilization (*e.g.*, microalgal uptake of NO_3^-), soil anoxia and sedimentary history. Recent genetic studies underscore the rich diversity of bacterial functional types in mangrove soils, including evidence for genetic sequences associated with dissimilatory reduction of NO_3^-, N immobilization, N_2 fixation, and denitrification (Andreote *et al.,* 2012; Liu *et al.,* 2012). A highly diverse suite of heterotrophic prokaryotes numerically and functionally dominate mangrove soils, accounting for about 80% of total living biomass (excluding trees). Knowledge of the linkages between various N transformation processes in mangrove soils is limited, but pathways such as denitrification and N_2 fixation have been measured often.

The complete soil N cycle has been deduced only in three mangrove ecosystems — on Phuket Island (Kristensen *et al.,* 2000) and in Sawi Bay in Thailand (Alongi *et al.,* 2002) and in Missionary Bay on Hinchinbrook Island in Australia (Alongi, 2009). In the soil N cycle (Fig. 3) nearly all NH_4^+ is taken up by fine roots. DN originates from the microbial decomposition of organic N found in dead plants, faeces, dead animal and microbial matter, and rich mixtures of organics transported into and onto the forest floor from rivers and adjacent coastal waters. Most of this organic N is broken down to NH_4^+ by ammonifying bacteria, with proportionally little loss to the atmosphere via anammox (anaerobic NH_4^+ oxidation) and denitrification. N_2 fixation is ordinarily not a major process within mangrove soils, although surface algal mats house large colonies of N_2 fixers that are often very important in the flux of DN across the soil-water interface. Macroalgae on aboveground roots can also utilize comparatively large amounts of DN.

About 5% of total N input is buried in mangrove soils (Table 4), but highest rates of N burial occur in forests

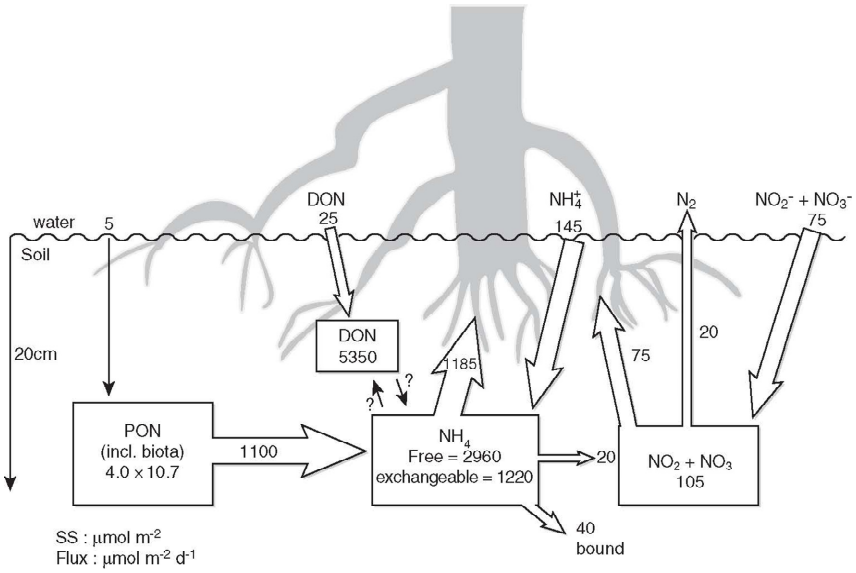

Fig. 3 Plant-soil-microbial N fluxes in the mature mixed *Rhizophora* spp. forests in Missionary Bay, Hinchinbrook Island, Australia. Adapted from Alongi (2009).

Table 4 N inputs (mmol N m^{-2} d^{-1}) to soils in Thai mangrove forests of different age and intertidal position. Adapted from Alongi *et al.* (2002).

	25-yr old, mid-intertidal *R. apiculata* forest	5-yr old, high-intertidal *R. apiculata* forest	3-yr old, mid-intertidal *R. apiculata* forest	3-yr old, high-intertidal *Ceriops decandra* forest
(A) NH_4 input from tidal water	0.5	0.05	0.01	0.04
(B) NO_3 input from tidal water	2.0	2.0	0.2	2.4
(C) DON input from tidal water	1.0	0.1	0.2	0.1
(D) Rain N	0.01	0.01	0.01	0.01
(E) N_2 fixation	0	0.06	0.2	0.05
(F) N burial	1.6	1.3	2.1	1.4
(G) Flux via NH_4 pool	32.0	7.5	19.1	8.4
Total N Input [Σ (A) to (G)]	37.1	11.0	21.8	12.4
% N buried	4%	12%	10%	11%
% total N denitrified	35	4%	6%	23%

receiving the least tidal inundation. DN uptake from the overlying tidal water accounts for only 9%-10% of N required for mangrove nutrition as most plant needs are satisfied via fine root uptake. Thus, as in most tropical terrestrial forests (Hedin *et al.*, 2009), the turnover time of the soil NH_4^+ pool is short (< 5-50 hr) reflecting rapid rates of uptake. Overall, functional differences in plant-soil-microbe relations appear to be partly a function of the interactive effects between stand age and intertidal position.

Evidence for a tight coupling between trees, microbes and soil nutrients has been obtained from studies of interstitial DON dynamics. Stanley *et al.* (1987) found that unless soils are poisoned to kill microbes and inhibit root uptake, no DON is released from the soil despite a strong concentration gradient across the soil-water interface. The non-protein amino acid, ß-glutamic acid, is a valuable biomarker as it is ordinarily immobilized in the interstitial water. Once soil microbes are poisoned, however, large amounts of this amino acid are released into the overlying water. This phenomenon suggests that DON transport is so rapid between trees, microbes and soil that there is only a small residual pool.

High rates of ammonification in mangrove soils are supported by DON released from roots. Proteins and nucleotides are hydrolyzed and catabolized by ammonifying bacteria into NH_4^+, with transformation rates partly dependent on rates of organic N input and rates of plant uptake (Alongi, 2009). In N-limited mangroves, NH_4^+ is also produced from dissimilatory NO_3^- reduction (Fernandes *et al.,* 2012a). This pathway conserves N by limiting the availability of NO_3^- for N_2O formation and denitrification.

Denitrification is usually a slow process in mangroves (Fernandes *et al.,* 2010, 2012a) as about 15% of total N input to mangrove soils is denitrified. In other coastal ecosystems, the percentage of N lost via denitrification ranges from 20%-70% (Seitzinger, 1988). Low rates of nitrification and anammox may limit denitrification in mangroves (Meyer *et al.,* 2005; Fernandes *et al.,* 2010, 2012a, b), as do low NO_3^- availability, temperature, salinity, the presence of algal mats, and soil organic matter content. NO_3^- availability is the main driver of denitrification which is often uncoupled from nitrification, implying significant N immobilization. Low rates of nitrification are associated with extensive uptake of NH_4^+ by the trees, as uptake from tidal waters is not a major source of NO_3^-. Anaerobic nitrification may be coupled to Fe reduction (Krishnan & Loka Bharathi, 2009), so NO_2^- production through nitrification in deep soils may fuel the anammox process. However, although data are scant, rates of anammox in mangroves are low (< 2 µmol N_2 m^{-2} d^{-1}) compared to other marine environments (Meyer *et al.,* 2005; Fernandes *et al.,* 2012a). Nitrification and anammox reactions may be inhibited by soluble tannins or sulfides in the interstitial water.

The fixation of atmospheric N_2 to NH_4^+ via nitrogenase activity by diazotrophic prokaryotes can counterbalance losses by denitrification. However, in many mangrove soils, N_2 fixation is low and mediated by sulfate reducers and other microbes inhabiting the rhizosphere. N_2 fixation rates range from 0-4,310 µmol m^{-2} d^{-1}, with a mean fixation rate of ≈ 620 µmol m^{-2} d^{-1} (Alongi, 2009) compared with denitrification rates of 0-11,000 µmol m^{-2} d^{-1} with a mean denitrification rate of 1,530 µmol m^{-2} d^{-1} (Alongi, 2009), roughly 2.5 times the average rate of N_2 fixation. N_2 fixers are, however, very active and diverse in the rhizosphere (Liu *et al.,* 2012), on prop roots, litter, fresh leaves, logs and bark. Further, N_2 fixation can occur deep within the rhizosphere and in extensive root systems (Naidoo *et al.,* 2008) in mutualistic relationships in which N_2-fixing bacteria provide N for immediate plant use and non N_2-fixing rhizobacteria and fungi provide metabolic by-products that benefit the growth of N_2 fixers (Holguin & Bashan, 1996).

Nitrous oxide is an important greenhouse gas and in mangroves N_2O fluxes vary greatly between seasons and forests, ranging from undetectable to release rates > 330 µmol m^{-2} d^{-1}; some forests even show net uptake of N_2O (Alongi *et al.,* 2005b; Fernandes *et al.,* 2010; Allen *et al.,* 2011; Chen *et al.,* 2012). N loading, temperature, soil redox status and the rate of nitrification and denitrification are important drivers of N_2O flux (Fernandes *et al.,* 2010).

Mangrove tidal waterways are also a source of N_2O. N_2O concentrations correspond to tidally-induced changes in DIN concentrations in mangrove waters, with peak concentrations at high tide and minima at low tide (Barnes *et al.*, 2007; Upstill-Goddard *et al*., 2007). This pattern is consistent with the idea that tidal pumping transports high interstitial concentrations of nutrients and dissolved gases into creek waters after the hydrostatic pressure gradually declines towards low tide. Very similar tidal patterns have been observed in Vietnamese and Japanese mangroves (Imamura *et al.,* 2007).

5. N Sources in Food Webs

Ubiquitous litter, rotting vegetation, and muddy turbid water create a strong impression that organic detritus and attached microbes are the main sources of N fuelling mangrove food webs. This notion was supported by work up until the early 1990s indicating that conspicuous mangrove consumers eat mostly detritus (Robertson *et al.,* 1992). The working paradigm was that attached microbes reduced complex, indigestible vascular plant detritus to simple, more readily digestible forms, with microbial enrichment itself providing sufficient N for adequate nutrition. This paradigm supported the corollary that vegetation is an important subsidy to the adjacent coastal zone.

The advent of stable isotope research ushered in a much more nuanced view, suggesting that most consumers preferentially assimilate fresh benthic microalgae and macroalgae, phytoplankton, algal detritus, or complex mixtures of these autotrophs, to meet their N requirements. Non-vascular plant material is not only more digestible, but N-rich, compared to N not readily available

in vascular plant material.

Workers have naturally focused on the diets of the most conspicuous consumers — crabs, fish, and shrimp. During the 1980s in northern Australia, and subsequently throughout the Indo-Pacific, the Caribbean, Africa and South America, sesarmid and grapsid crabs were found to be foundational ecosystem engineers in mangrove forests (Kristensen, 2008). This discovery constituted a paradigm shift from the early notions of the trophic importance of detritus transported to offshore waters, to the realization that a large (but variable) fraction of litter is consumed or hidden in crab burrows thereby reducing the amount of detritus available for export and thus also serving as a mechanism to conserve nutrients (Robertson *et al.,* 1992).

How do sesarmid and grapsid crabs meet their N requirements? It was initially thought that crabs met their needs by voraciously eating large amounts of N-poor litter and propagules, and assimilating the associated N-rich, microbial biomass. This explanation seemed reasonable considering that crabs can consume up to 100% of total litter standing stock in some forests (Robertson *et al.,* 1992), and that they paste fragments of litter onto their burrow walls facilitating fungal and bacterial colonization to make the litter more palpable and nutritious over time.

This notion presented a paradox in that mangrove leaves, even aged ones, have both high tannin content and C/N ratios that are too high to sustain adequate nutrition, even with high consumption rates. Some workers suggested that crabs supplement their diet by ingesting sediment and associated bacteria and microalgae (Bouillon *et al.,* 2002), but sediment consumption would have to be inordinately high to meet N demands (Thongham & Kristensen, 2005), so crabs may obtain sufficient N from supplementary consumption of animal tissue, such as carcasses of fish and crustaceans, and meiofauna (Kristensen *et al.,* 2010). For example, in laboratory experiments the sesarmid *Neoepisarma veriscolor* preferentially eats fish meat, which contributes up to 50% of the crab's dietary N (Kristensen *et al.*, 2010).

Like most higher organisms, crabs need to consume a variety of foods to maintain a balanced diet. This idea is supported by feeding experiments and biochemical analyses of grapsid crabs from Indonesia (Nordhaus *et al.,* 2011) where *Episesarma* spp. and *Perisesarma* spp. are omnivorous, feeding mainly on detritus, mangrove litter and bark, and on lesser amounts of roots, algae and animal tissue; chemical analyses indicate that bacteria contribute significantly to the amount of N available for these crabs. As found by Gatune *et al.* (2012) for penaeid shrimp post larvae, the nutritive value of mangrove litter can be further enhanced by consumption of surface microbial biofilms. Other means to acquire dietary N exist. For example, Caribbean sponges living as epibionts on *Rhizophora mangle* roots have bacterial endobionts capable of degrading and assimilating mangrove-derived dissolved organic matter; the endobionts in turn transfer N-rich compounds back to the sponges to nourish growth (Hunting *et al.,* 2010).

Mangrove-associated fish, shrimp, and zooplankton also have varied diets with many, but not all, species having a clear preference for phytoplankton or benthic algae rather than mangrove detritus (Thimdee *et al.,* 2008; Giarrizzo *et al.,* 2011; Chew *et al.,* 2012; Vaslet *et al.,* 2012). But within a mangrove estuary or forest, multiple food webs partitioned by dietary preferences can exist. In the Klong Ngao mangroves of Thailand, for example, four trophic levels exist with at least two fish species capable of dietary switching; extremely turbid water limits phytoplankton production in these Thai waters such that litter is the main source of nutrition (Thimdee *et al.,* 2008). In northern Brazil, C and N stable isotope analyses indicate three distinct food webs: (1) a mangrove food web, consisting of epibenthos and zooplanktivorous food chains; (2) an algal food web where fiddler crabs, polychaetes, mullets and several other fish species directly consume benthic algae; and (3) a mixed food web of mainly benthivorous fishes that consume a wide variety of foods (Giarrizzo *et al.,* 2011).

If other significant primary producers such as seagrass meadows are nearby, the dietary sources are even more complex. In Florida and Belize, for example, the contribution of mangroves and seagrasses to predatory fishes varies by type of mangrove habitat (*i.e.*, fringe versus basin mangroves) and fish residency status (Vaslet *et al.,* 2012). Residents show a stronger mangrove signal than transients that actively forage in nearby seagrass beds. In overwash mangroves, most fish show a stronger seagrass signal, especially juvenile reef fish that shelter in mangroves but feed in adjacent seagrass beds. The trophic significance of mangrove N to consumers thus depends on location and type of habitat, relative availability of other primary producers, species dietary preferences and the universal need to secure a balanced diet.

6. Ecosystem and Global N Budgets

Only one complete N budget exists for a mangrove ecosystem — the Missionary Bay mangroves at the northern end of Hinchinbrook Island in Australia (Alongi *et al.,* 1992; Alongi, 2009). The budget shows two main N inputs to the ecosystem (Table 5): (1) N_2 fixation by microbes living on logs and other pieces of fallen timber, surface soils, live tree stems and above-ground prop roots, and (2) incoming tides. Net tidal exchange represents the largest loss of N, as litter is exported via mangrove waterways. Secondary N losses are denitrification and sedimentation. There are likely other sources and sinks for N in this ecosystem, but these are probably small. Overall, the N cycle in the Missionary Bay ecosystem is in balance considering the many extrapolations and systematic and relative errors involved in a large number of individual measurements made over time. Of course, other mangrove ecosystems show net N export (Kurosawa *et al*., 2003; Silva *et al*., 2007), and some systems even show a net loss due to NH_3 degassing (Biswas *et al*., 2005).

Table 5 N fluxes (kmol N yr^{-1}) in the mangrove ecosystem of Missionary Bay, Australia. The budget was constructed using data from papers cited on page 279 in Alongi *et al.* (1992).

Process	Input	Output	Net exchange
Precipitation			
NO_2+NO_3	0.7		
NH_4^+	0.5		
DON	1.3		
PN	0.1		
			subtotal = 2.6
Groundwater			
	2.4		
			subtotal = 2.4
N_2 fixation			
Saltpan	466.2		
Soil Surface	479.7		
Prop roots	1192.7		
Logs/timber	930.7		
Stems	376.7		
			subtotal = 3446
Tidal exchange			
NO_2+NO_3	437.5	525.0	-87.5
NH_4^+	928.0	696.8	231.2
DON	12684.3	8821.4	3862.9
PN		6360.8	-6360.8
			subtotal = - 2354.2
Denitrification			
		658.4	-658.4
Sedimentation			
		342.5	-342.5
Total	**17501**	**17405**	**95.9**

Table 6 A nitrogen mass balance of the world's mangrove ecosystems. The model assumes a global mangrove area of 152,000 km^2 (Spalding *et al.,* 2010).

Pathway	C flux (Tg C yr^{-1})[1]	C:N ratio (weight: weight)	N flux (Gg N yr^{-1})
	Inputs		
Net primary production	309	115[2]	2687
Wood	67	220[2]	305
Litter	68	52[3]	1307
Roots			1075[4]
N_2 fixation			100[5]
			Total Inputs =2787
	Outputs		
Burial	29	40[7]	740
Export	29 (POC) + 14 (DOC)	3.5 (P), 16 (D)[8]	1496
Denitrification			180[9]
Soil N_2O release			10[9]
Water N_2O release			10[9]
			Total Outputs =2436
			Net Gain = 351

[1] from Alongi (2009)
[2] from Alongi *et al.* (2003)
[3] from Robertson *et al.* (1992)
[4] determined by the difference between total NPP and wood + litter production
[5] median rates for soil, logs and prop roots in Alongi (2009) multiplied by global area
[7] median C: N ratio (wt: wt) at 1m soil depth (Alongi *et al.,* 2004a, 2005b)
[8] median POC: PON and DOC: DON ratios from Alongi (2009)
[9] median rates in Alongi (2009) multiplied by global area

The Hinchinbrook work (Fig. 3, Table 3) suggests that a number of mechanisms operate to conserve N in mangroves: (1) very high rates of soil N recycling to the extent that most DN is taken up by the trees; (2) crabs retaining litter N in the soil; (3) tree stems, roots, logs, and other timber providing maximum surface area to facilitate microbial colonization and maximize N_2 fixation; (4) large pools of below-ground dead roots acting as nutrient reservoirs; and (5) most N exported being highly refractory, not labile, and high in concentrations of humic and fulvic acids and polyphenolics.

The importance of these retention mechanisms can also be discerned from an estimate of the main N flows in the world's mangrove ecosystems (Table 6). This global mass balance is only indicative, but is instructive in pinpointing the magnitude of global sinks and sources of mangrove N. Derived from C:N stoichiometry (see Table 6 footnotes), the mass balance indicates that: (1) 2687 Gg N yr^{-1} is required to sustain global mangrove net primary production; (2) N burial is ≈ 25% of total N input; (3) N_2 fixation is ≤ 5% of total N input; (4) ≈ 40% of N input required for total mangrove NPP is vested in below-ground root production; (5) ≈ 50% of N required for mangrove NPP is vested in litter; (6) tidal export equates to ≈ 55% of N vested in mangrove NPP; (7) < 10% of mangrove N is lost via denitrification and N_2O emissions;and (8) N fluxes are in net balance as the net gain (351 Gg N yr^{-1}) is very small compared to the total inputs, outputs and sources of error.

Most N needed to support mangrove primary production must eventually come from net tidal import of sediment particles from upstream or from the coastal ocean or both, given the relatively small amounts of N fixed within forests. Much of this allochthonous N is efficiently recycled via plant-soil-microbe pathways as 75% of mangrove N is vested in litter fall, exported by tides and buried in sediments. This notion is supported by the fact that a large proportion of N is vested in producing fine roots below ground. Of course, this preliminary global budget is crude and does not include minor pathways that may be important in some forests, but it does suggest that despite large tidal losses, N fluxes in the world's mangrove forests are roughly in balance due to the evolution of a number of highly efficient N conservation strategies and adaptations.

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