Nitrogen cycling: A review of the processes, transformations and fluxes in coastal ecosystems

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The coastal and marine nitrogen cycle occupies a complex, central role within the biogeochemical cycles. Human interventions in the earth system have risen to unprecedented levels, strongly influencing the global nitrogen cycle. The nitrogen cycle in the open ocean compared to coastal ecosystems appears to have remained unharmed, although recent observations have shown increasing anthropogenic influence. Projections suggest that global nitrogen cycle is being altered either directly by the continued addition of anthropogenically created fixed nitrogen to the earth system and its cascading effects, or indirectly through anthropogenically induced climate change. These alterations have the potential to cause positive feedbacks in the climate system, but they are neither well understood nor quantified. In the atmosphere, concentrations of the greenhouse gas, nitrous oxide and of the nitrogen-precursors of smog and acid rain are increasing. This unprecedented nitrogen loading has contributed to long-term decline in coastal fisheries. This article reviews some of the major processes, transformations and fluxes of nitrogen in the coastal ecosystems with reference to mangroves, occurring naturally and also due to human perturbations.

Keywords: Coastal ecosystem, nitrogen cycling, processes, transformations.

NITROGEN (N) is an extremely essential element, existing in both inorganic and organic forms as well as many different oxidation states. Typically five main processes cycle N through the biosphere, atmosphere and geosphere: N-fixation, N-uptake, N-mineralization (decay), nitrification and denitrification. Microorganisms, particularly bacteria, play major roles in all of the principal N-transformations. Its rates are affected by environmental factors that influence microbial activity, such as temperature, moisture, and resource availability[1]. Recent work[2–4] in diverse areas of the coasts and oceans has produced strong evidence that the marine nitrogen cycle is both more dynamic and less well understood than previously thought of. Application of new experimental methods and the extension of fieldwork to previously un- or under-sampled regions of the ocean support the notion that the major inputs (e.g. N_2-fixation) and outputs (e.g. denitrification) of the nitrogen cycle are both acting at high enough rates to turn over nitrogen on a timescale of several millennia. The best current estimates of the global N cycle suggest that the oceans are currently well out of steady state and are losing substantially more nitrogen through denitrification than they are gaining via transport from land and *in situ* N_2-fixation[5].

Major nitrogen sources to coastal ecosystems include atmospheric deposition onto land, freshwaters and estuary, fertilizers from agriculture and wastewater from sewage. Tidal exchange can introduce marine nitrogen, but this source is relatively unimportant in embayments receiving high nitrogen loads from the riverine systems and estuaries. N exists in the surface ocean mostly as dissolved organic nitrogen (DON), but despite decades of research, only a small fraction of the DON in surface ocean waters has been chemically characterized.

Estuaries and shallow lagoons are the link between terrestrial and oceanic ecosystems and receive considerable external inputs of nutrients and organic matter. Excess inorganic nutrient loading from coastal watersheds has been directly related to increases in primary production, changes in habitat structure and trophic dynamics of the receiving waters. Coastal ecosystems and bays constitute a major type of land margin ecosystem on most continents and a major difference in the nitrogen cycling processes between these systems is the large influence that benthic primary producers have on nutrient transformations in shallow coastal lagoons and bays. Exchanges across the sediment–water interface play a key role in nutrient cycling in coastal systems because the water column is well-mixed and small in volume relative to the large sediment surface area. It is this coastal-margin interface that makes the biogeochemical cycles complex as also challenging to our understanding of these complexities.

Atmospheric sources of N to coastal and marine systems

Atmospheric deposition is currently a major source of N to many aquatic and terrestrial ecosystems[6–8]. The global

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nitrogen cycle has been massively perturbed by human activity[9] and this includes the atmospheric component. Not only have total atmospheric nitrogen emissions changed over the last few hundred years associated with a doubling of overall global nitrogen fluxes[10], but the nature of sources continues to change as global patterns of agriculture and industry evolve[9,11]. Because N is the primary nutrient-limiting plant, algal and microbial production in many terrestrial and marine environments, as well as some freshwater environments, increases in N inputs can markedly alter the ecosystems[12–14].

The current fixed N inputs to the world's oceans (Table 1) as given by Jickells[15], emphasizes the contribution of the atmospheric and riverine sources, which have probably doubled due to human activities.

Atmospheric deposition rates of nutrients, including nitrogen and contaminants are in general higher into coastal waters than to open ocean areas because these are closer to the sources. The higher NH_3 concentrations in the atmosphere and complex ammonia cycling in the atmosphere and nutrient-rich waters indicate that air–sea exchange fluxes for ammonia can be particularly complex[16,17]. Assessing the impacts of atmospheric deposition to coastal waters is complicated by the importance of other inputs such as rivers and groundwater[18–20]. These are not completely independent because a significant component of the fluvial nitrogen input may be derived from atmospheric inputs to the catchment. For instance, the contribution[21] of atmospheric inputs to the total fluvial nitrogen input ranges from 7 to 61%. Thus atmospheric nitrogen sources are clearly significant compared to other terrestrial nitrogen sources, and these inputs have been significantly increased by human impact. In addition, responses can be anticipated from different coastal biogeochemical communities in response to nutrient loadings depending on the hydrography of each coastal area (e.g. refs 11 and 18).

Riverine nitrogen inputs

River discharge is a major source of nutrients (Table 1) to coastal waters and river inputs are important both in terms of the physical structure of the systems and as a source of N[22]. Inputs of N to rivers arise primarily from fertilizers, atmospheric deposition to the catchment, and to a lesser extent, direct discharges. Following discharge to a river system, denitrification, photosynthesis and particle–water interactions can modify N and P fluxes. The balance of inputs and river processing of nutrients is such that river fluxes have not only increased in absolute magnitude, but the N : P ratio of those inputs has increased to a value greater than that required for optimal plant growth (16 : 1 on an atomic basis[7,23–25]). This has led to a pressure to reduce inputs, which has met with some success for P, but less for N[22,26]. Rivers of the humid tropics, which drain about one-fifth of the exoreic drainage area and carry about half of the river water to the oceans, transport about 55% of the dissolved organic carbon, nitrogen and total dissolved phosphorus[27–29].

Table 1. Current fixed nitrogen inputs to the world's oceans[15]

Source	Flux (10^{12} mol yr^{-1})
Atmospheric	3.1–7.9
Biological N_2-fixation	5.7
Rivers	5.4
Lightning	0.6

Riverine discharge injects both soluble and particulate N to the ocean, which has substantial impact on the coastal regions of Asia[30,31]. Anthropogenic and natural inputs of reactive nitrogen (N) to terrestrial landscapes and the associated riverine N fluxes have been quantified[32] (Figure 3 *a*) using an empirical model relating total N inputs per landscape area to the total flux of N discharged in rivers based on watershed data from contrasting ecosystems spanning multiple spatial scales. Anthropogenic N sources were greater than natural sources in Asia (74%), North America (61%) and Europe (59%). A direct linear relationship between total net nitrogen inputs (TNNI) and the total N fluxes in these watersheds was observed, which suggests that on average 75% of the N inputs is retained in the landscape (that is stored in soils and vegetation or lost via volatilization and denitrification), while 25% of the N inputs is exported to rivers. Rates of riverine N export vary greatly among the continents, reflecting the regional differences in N inputs. This significantly affects water quality, as riverine N fluxes from Asia to the coastal zone (16.7 Tg N yr^{-1}) and to inland waters (5.1 Tg N yr^{-1}) are the largest in the world. Model studies on the fate of N from Asian rivers[33] show that about 12 Tg N yr^{-1} of dissolved inorganic N is discharged annually from Asian rivers into adjacent coastal seas (Figure 3 *b*). This value is about 20% of the anthropogenic N mobilized within Asia[34].

In developing nations, wastewater inputs can be an additional major source of nitrogen to an estuary or coastal system[35]. Human sewage and wastewaters are obvious sources of nitrogen to rivers. An analysis[36] of 42 major world rivers concluded that sewage inputs alone are sufficient to account for the increased flux of nitrate observed in rivers whose watersheds have a higher population density. Other factors that contribute significantly to nitrogen export from rivers are deforestation, atmospheric deposition and fertilizer application.

Coastal ecosystems of India

The Indian sub-continent has an area of 3.28 million km^2 (329 million hectares) and a coastline of 7516.5 km. The

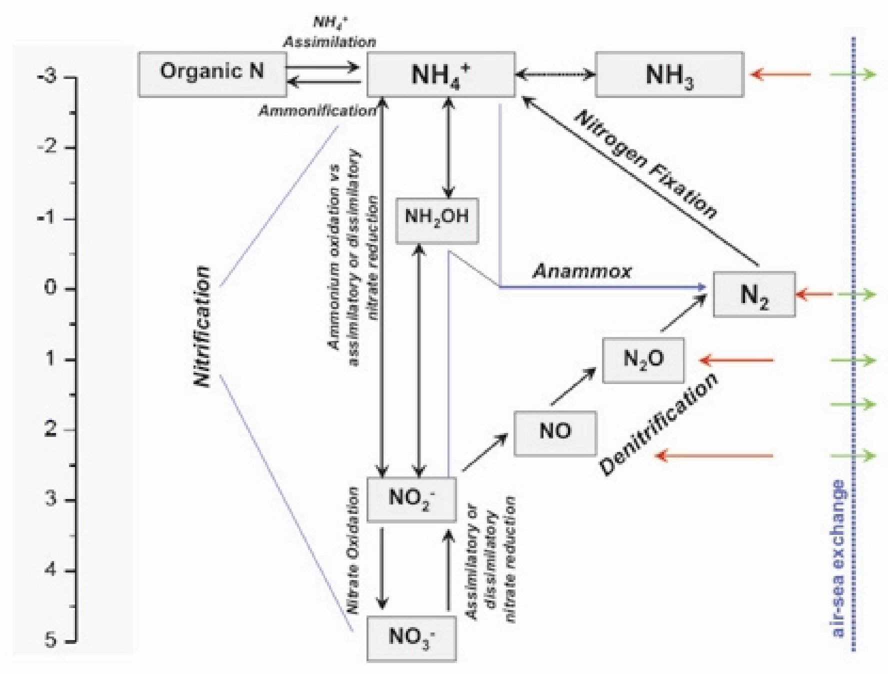

Figure 1. Major chemical forms and transformations of nitrogen in the coastal and marine environment[188]. The various chemical forms of nitrogen are plotted against their oxidation states.

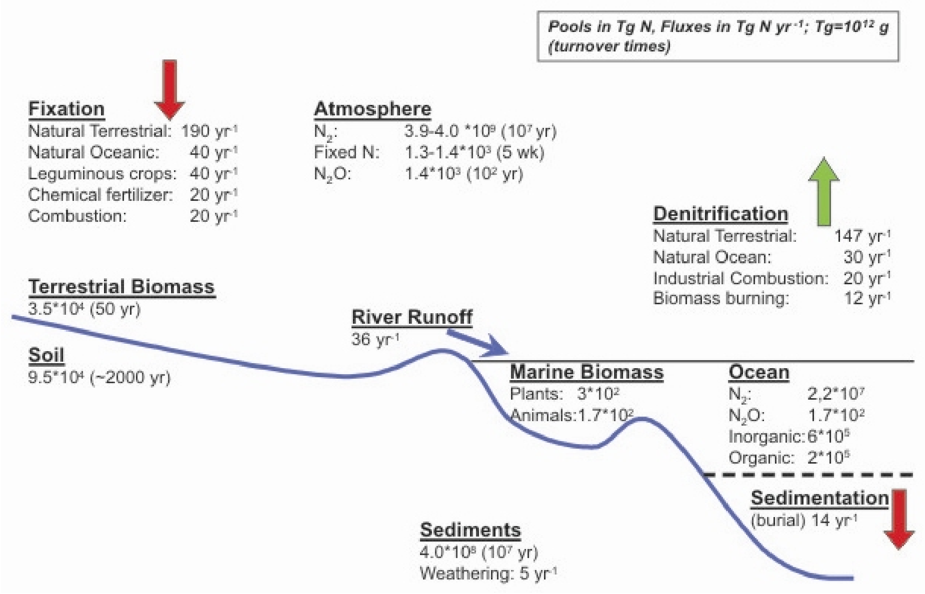

Figure 2. Global nitrogen reservoirs, fluxes and turnover times[189]. Major reservoirs are underlined; pool sizes and fluxes are given in Tg (10^{12} g) N and Tg N yr^{-1}. Turnover times (reservoir divided by largest flux to or from reservoir) are in parentheses.

nearshore coastal waters of India are extremely rich fishing grounds and the rich biodiversity of the wetlands is seriously threatened due to human pressures. The dissimilarities of marine biodiversity between the west and east coasts are remarkable. The west coast is generally exposed with heavy surf and rocky shores and headlands, whereas the east coast is generally shelving with beaches, lagoons, deltas and marshes. The west coast is a region of intense upwelling associated with the southwest monsoon (May–September), whereas the east coast experiences

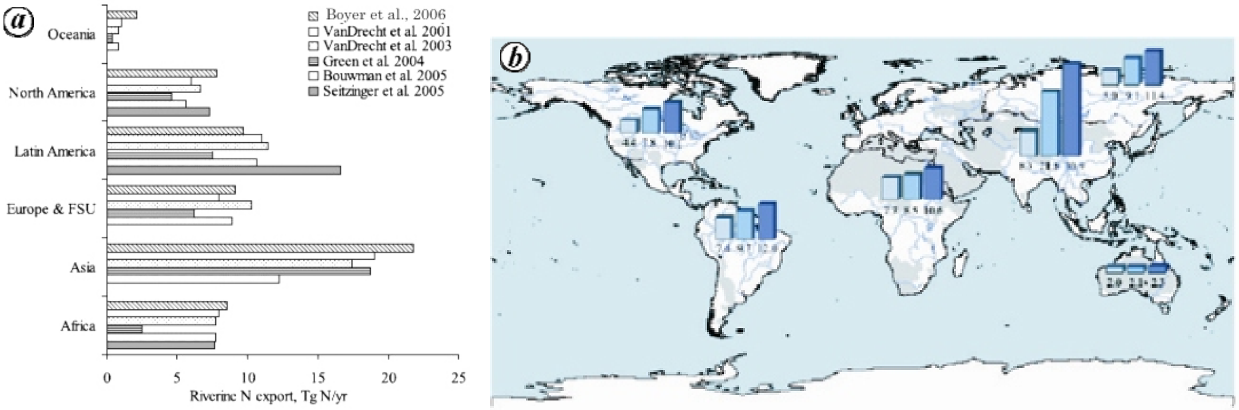

Figure 3. ***a***, Total riverine export by region (adapted from Boyer *et al.*[32]). ***b***, Riverine Nr export to the coastal zone (Tg N yr^{-1}) in the past (1860), present (1990) and future (2050). Dry and inland watershed regions that do not transmit to coastal areas are shown in grey (adapted from Galloway[34]).

only a weak upwelling associated with the northeast monsoon (October–January), resulting in marked differences in hydrographic regimes, productivity patterns and qualitative and quantitative composition of fisheries. All islands on the east coast are continental islands, whereas the major island formations in the west coast are oceanic atolls. India has a wide range of coastal ecosystems such as estuaries, lagoons, seagrass, mangroves, backwaters, salt marshes, rocky coasts, sandy stretches and coral reefs, which are characterized by unique biotic and abiotic properties and processes. The nitrogen cycle in the mangrove ecosystem is discussed in detail below.

Nitrogen cycle in mangrove ecosystem

Mangrove wetlands are present both along the east and west coast of the mainland of India and in the coastal zone of Andaman and Nicobar Islands. According to the estimates[37], the total area of the Indian mangrove forest is 487,100 ha, out of which nearly 56.7% (275,800 ha) is present along the east coast, 23.5% (114,700 ha) along the west coast and the remaining 19.8% (96,600 ha) is found in the Andaman and Nicobar Islands. Mangrove wetlands of the west coast of India are small in size, less in diversity and less complicated in terms of tidal creek network. This is mainly because the costal zone of the west coast is narrow and steep in slope due to the presence of the Western Ghats and there is no major west-flowing river. On the other hand, mangrove wetlands of the east coast are larger in area, high in biodiversity and the water bodies associated with mangroves are characterized by the presence of nutrient-rich, large brackish waterbodies and a complex network of tidal creeks and canals. This is mainly due to the presence of the larger delta created by east-flowing rivers and gentle slope of the coast.

Nitrogen cycle within mangrove forests is mediated predominantly by microbial rather than chemical processes[38]. The major transformations in the nitrogen cycle are summarized schematically (Figure 4) and the rates of these transformations are detailed in Table 2. The relative importance of the various transformations within the mangroves is 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.

Nitrogen pools

Vegetation

Nutrient uptake by mangrove forests leads to the immobilization of significant amounts of N as plant tissues[39]. N content of mangrove leaves and other structural components has been found to vary with species[40–42], position within the forest[43], nutrient status of the sediment[44], structural component of the forest[31,45] and leaf age[39,46]. Among the structural components of mangroves, leaves had the highest N content[45,46]. Fruit (propagules), small fibrous roots and small branches also had relatively high N content[45,46]. Propagules represent a massive investment of N in reproduction for the trees, and a large outwelling of N to coastal waters. It has been estimated[47] that the total N pool (within 1 m soil depth) in a mangrove stand of *Kandelia obovata* was 2.73 mg ha^{-1}. The contributions of leaf, stem bark, stem wood, root bark, root wood and soil in the N pool are as shown in Figure 5. The authors reported that the N pool in aboveground biomass (0.442 mg ha^{-1}) was 1.4 times as large as that in belowground biomass (0.312 mg ha^{-1}) and the soil N stock was 3.3 times as large as the biomass N stock (0.754 mg ha^{-1}).

Sediment

The sediment N pool in mangroves is composed largely of the organic N form and is not readily available for

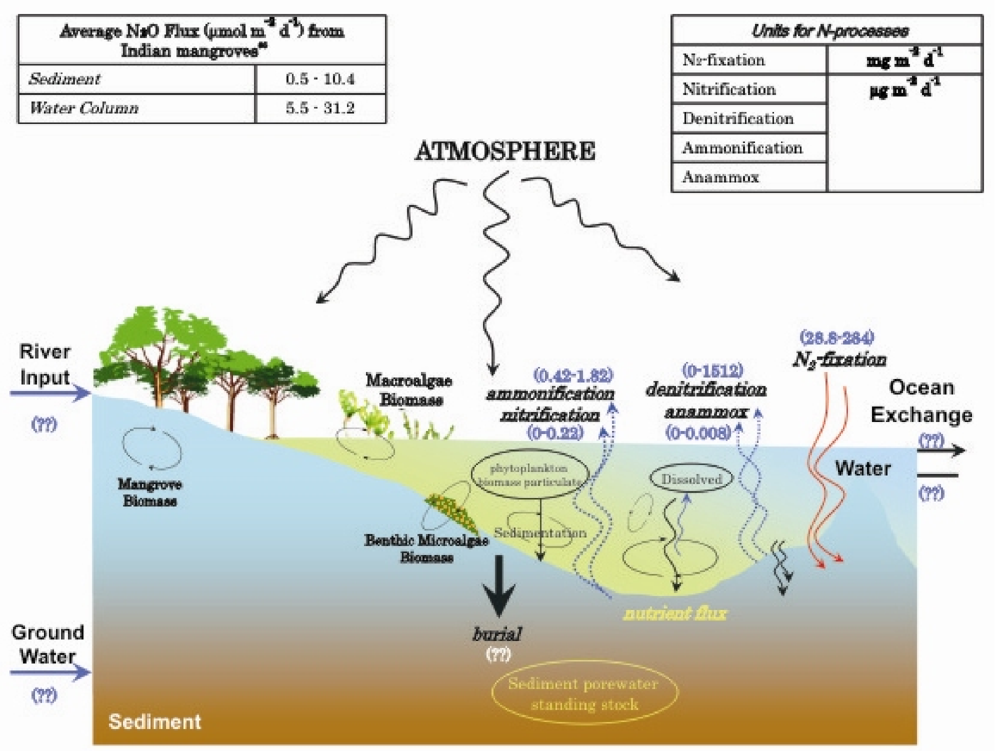

Figure 4. Major processes and transformation rates in the N-cycle of mangrove ecosystems.

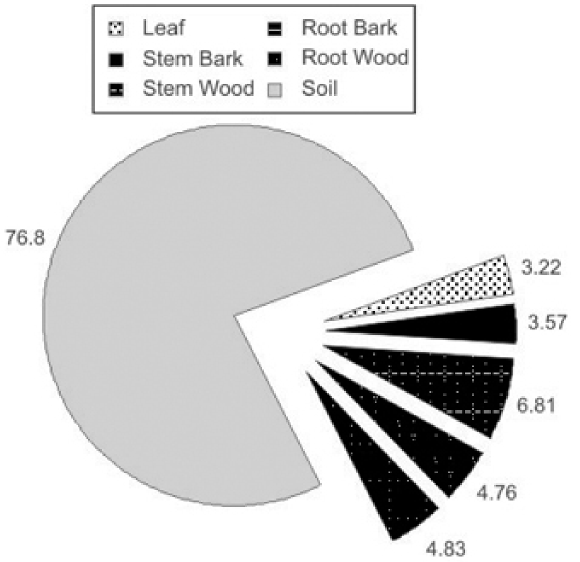

Figure 5. Nitrogen pool in mangroves.

plant uptake[48]. Concentrations of dissolved inorganic forms, particularly nitrate (NO_3^-), are low compared to those in other marine sediments[38,48]. Among the dissolved inorganic nitrogen (DIN) forms, ammonium (NH_4^+) is the most abundant, but only barely detectable levels of NO_3^- and NO_2^- (Table 2) is consistently found in mangrove sediments[38,48–52]. Also, a high degree of spatial heterogeneity was observed in porewater nutrient concentrations in mangrove ecosystems[52]. This heterogeneity was attributed to the presence of 'micro-oxic' zones resulting from oxygen translocation via plant roots to surrounding sediments and the influence of mangrove crabs on sediment turnover[52]. These 'micro-oxic' zones contain populations of nitrifying bacteria, which supply NO_3^- to the roots[53].

N_2-fixation

Biological N fixation, the reduction of nitrogen gas to NH_4^+, occurs in a diverse array of Eubacteria and Archaea that have the required enzyme, nitrogenase[54,55]. It is generally believed that N fixation is a key process in ecosystems, where N is limiting productivity because of its potential to provide N in usable form to plants[55]. Low levels of ambient N fixation in mangrove sediments were reported[56] than those in seagrass and salt marsh communities. Rates varied between 0.7 and 3974 mg N m^{-2} d^{-1}, with a large degree of spatial and temporal variation[57–60]. Literature suggests that the availability of dissolved organic carbon (DOC) in sediments may influence N fixation rates in mangrove ecosystems. Higher rates of N fixation were reported in sediments associated with

Table 2. Nitrogen budget for various mangrove ecosystems based on inputs–outputs

Budget components	Location	Species	Biomass	Source
Standing stocks				
Aboveground biomass (t ha^{-1})	Sunderbans, India	*Avicennia* sp.: Total	147.7	166
		Bruguiera gymnorhiza	11.2	
		Soneratia apetala	34.5	
		Ceriops tagal	4.8	
	Tritih, Java, Indonesia	Mixed forest	93.7	167
	Matang Mangroves, Malaysia	Mixed forest	202.4	45
	Hainan Island, China: Total	Mixed forest	9.6–14.2	168
	Hainan Island, China	*Soneratia caseolaris*	47.2	168
	Near Brisbane, Australia:	*A. marina*		
		Aboveground	110–340	169
		Belowground	109–126	
	Mary River, Australia	*A. corniculatum*		
		Aboveground	40	170
		Belowground	50	
		A. marina		
		Aboveground	150	
		Belowground	80	
		E. agalocha		
		Aboveground	140	
		Belowground	40	
		R. stylosa		
		Aboveground	70	
		Belowground	100	
		C. australis		
		Aboveground	110	
		Belowground	50	

Budget component	Location	Species/structural component	N–content (% DW)	Source
N-content: Mangrove structural components	Sunderbans, India	*A. marina*	1.64	42
		A. alba	1.55	
		Excoecaria agalocha	1.12	
	Westernport Bay, Australia	*A. marina*		
		Leaves	2.11	46
		Branches	0.61–1.43	
		Trunk	0.49	
		Roots	0.68–1.20	
		Fruit	1.6	
	Matang Mangroves, Malaysia	*R. apiculata*		
		Leaves	1.64	45
		Branches	0.55	
		Trunk	0.4	
		Roots	0.43–0.76	
	Gazi Bay, Kenya	*A. marina*: leaves	1.9	41
		R. mucronata: leaves	0.7	
		B. gymnorhiza: leaves	0.8	
		Ceriops tagal: leaves	0.8	
	Samana Bay, Domican Republic	*R. mangale*		
		Leaves	2.9	171
		Branches	10.4	
		Trunk	63.1	
		Prop Roots	17.2	
		Twigs	6.4	
		L. racemosa		
		Leaves	1.8	
		Branches	12.5	
		Trunk	81	
		Prop Roots	–	
		Twigs	4.7	

(*Contd*)

Table 2. (*Contd*)

Budget component	Location	Species/structural component	N–content (% DW)	Source
		A. germinans		
		Leaves	3	
		Branches	11.3	
		Trunk	82.8	
		Prop Roots	–	
		Twigs	2.9	
N-content (mg ha^{-1}): mangrove sediments	Okinawa Island, Japan	Litter	0.754	47
Inputs	**Location**	**Sediment/litter**	**Rate**	**Source**
1. N_2-fixation	Gazi Bay, Kenya	Sediment + mangrove leaf litter	1.87–9.36	64
µmol g^{-1} N_2 d^{-1}	Tampa Bay, Florida	Anoxic mud	1.37–10.11	172
		Tidal sediment	1.03	
		Prop root-associated sediment	1.46–2.91	
		Pneumatophore-associated sediment	0.51	
	Shark River Estuary, Florida	Mangrove sediments	0–0.75	63
		Mangrove pneumatophore	0–0.12	
		Avicennia germinans aged leaf litter	0.6–12.96	
		R. mangale: aged leaf litter	0.17–5.36	
		L. racemosa: aged leaf litter	0.81–80.3	
	Mangroves of Southern Florida	*R. mangale*: 14 day leaf litter	3.6–10.8	173
µmol N_2 m^{-2} d^{-1}	Whangateau Harbour, New Zealand	*A. marina*: Forest	16.8–34.4	174
	Missionary Bay, Australia	*Rhizophora* forest: high inter-tidal sediments	0.04–0.12	
		Algal mats	0.10–0.13	
		Prop roots: low inter-tidal	0.79	
		Mid inter-tidal	1.24–2.60	
		High inter-tidal	0.29	
		On logs	0.03–0.05	
	Mangroves of southern Thailand	Mangrove sediments	48–576	85
Aerobic N_2-fixing heterotroph population (per dry matter)	Ganges delta, India	Plant-associated mangrove swamp sediment	0.57–0.63*10^5	65
		Plant-associated dryland ridge soil	1.55–2.61*10^5	
		Avicennia sp. Roots from swamp bed	16.4–20.8*10^6	
Other inputs (t yr^{-1})				
Point source	Moreton Bay, Australia	–	3383	175
Non-point source		–	571	
Atmosphere		–	1692	
Groundwater		–	120	
Primary production		–	–	
N_2-fixation		–	9177	
Outputs	**Location**	**Species/sediment**	**Rate**	**Source**
1. Nitrification				
µmol g^{-1} N_2 d^{-1}	Missionary Bay, Australia	*Rhizophora* sp.	0.014	83
	Semanta, Malaysia	*Avicennia*	0–0.22	84
µmol N_2 m^{-2} d^{-1}	Bangrong Mangrove, Pukhet, Thailand	Mangrove sediment	12–74	79
	Mangroves of southern Thailand	Mangrove sediment	120–690	85
	Acahra River Mangrove, India	Mangrove sediment	1.65	176
	Ria Lagartos Lagoon, Yucatan, Gulf of Mexico	Mangrove sediment	3612	177
2. Denitrification				
µmol m^{-2} d^{-1}	Missionary Bay, Australia	*Rhizophora* sp: ambient	154.3	83
	Joyuda Lagoon, Puerto Rico	Upper 2 cm sediment: ambient	2.5–268.8	50
		2–8 cm sediment: ambient	8.4–1931	
	La Parguera, Purerto Rico	*Rhizophora* fringe: control	596.4–1220.4	91

(*Contd*)

Table 2. (*Contd*)

Outputs	Location	Species/sediment	Rate	Source
		Rhizophora fringe: nitrogen enriched	2340–20988	
		Transition zone: control	116.4–2196	
		Avicennia landward: control	208–1877	
		Avicennia landward: nitrogen enriched	4988–12960	
	Oyster Bay, Falmouth Harbour, Jamaica	*Rhizophora* and *Avicennia*	4150–41650	102
	Terminos Lagoon, Mexico	Mixed species: fringe forest	0–113	88
		Mixed species: NH_4^+ enriched	30–336	
		Mixed species: NO_3^- enriched	48–2640	
		Basin dorest: ambient	0–54	86
	Fiji	Not reported	78–261	90
	Australia	Basin mangrove	0.53	83
	Puerto Rico	Fringe mangrove	9.7–183	91
	Terminos Lagoon, Mexico	Fringe mangrove	0.08–9.4	86
		Basin mangrove	1.9–4.5	
		Riverine: enrichment <200 μmol core-1	–	
		Riverine: enrichment >200 μmol core-2	3.7–221.1	
	Ria Lagartos Lagoon, Yucatan, Gulf of Mexico	Mangrove sediment	1137.6	177
	Mangroves of Southern Thailand	Mangrove sediment	40–100	85
nmol g^{-1} h^{-1}	Tamshui Estuary, Taipei	*Rhizospheric* sediment: planted	120.6	178
		Rhizospheric sediment: unplanted	80.2	
		Non-*rhizospheric* sediment: planted	101.8	
		Non-*rhizospheric* sediment: unplanted	93.8	
3. Amonification				
μmol g^{-1} N_2 d^{-1}	Missionary Bay, Australia	*Rhizophora* sediment	0.015–0.065	174
	Selangor, Malaysia	*Avicennia* sediment	0.002–0.014	84
	Florida Bay	*Avicennia* sediment	0.038	179
	Marica Beach, Rio de Janeiro, Brazil	Mangrove sediment	0.17	180
	Oyster Bay, Falmouth Harbour, Jamaica	Mangrove sediment	6.54–21.81	102
mmol m^{-2} d^{-1}	Shark River Estuary, Florida	*Rhizophora* mangale mangrove sediment	1.25–8.50	120
	Mangrove of Southern Thailand	Surface sediments	0.30–2.30	85
4. Anammox				
nmol N m^{-2} h^{-1}	Logan River sediments, Queensland, Australia	Mangrove sediments	0.5–8.0	116
	Skagerrak	Marine sediments	0.08–11	117
5. Mineralization				
mmol m^{-2} d^{-1}	Pukhet Island, Thailand	Mangrove sediments	4.3–18	100
	Oyster Bay, Falmouth Harbour, Jamaica	Mangrove sediments	3.3–21.8	102
	Gazi Bay, Kenya	Mangrove sediments	0.30–1.10	181
	Bangrong Mangrove, Pukhet, Thailand	Mangrove surface sediments	0.008–0.024	103
		Mangrove deeper sediments	0.02–0.06	
Other outputs				
6. N-Immobilization (%)	Terminos Lagoon, Mexico	Mangrove fringe sediments	3.0–60.0	86
		Mangrove basin sediments	0.0–29.0	
		Mangrove riverine sediments	9.0–15.0	
		Overlying water	>0.1	
7. N-Burial (%)	Mangrove of southern Thailand	Surface sediments	4.0–12.0	85
8. Ocean exchange	Location	Export: species of N	Rate	Source
mol yr^{-1}	Malaysian mangroves	Particulate organic nitrogen	–	182
	Eastern Australia	Organic and inorganic nitrogen	–	183
	Mangroves of North Brazil	Dissolved organic nitrogen	2×10^9	150
	Mangrove dominated lagoon, Yucatan Peninsula, Mexico	DIN: (NO_3^- + NO_2^-)	34.9×10^6	71
		NH_4^+	15×10^6	
		Particulate organic nitrogen	93.9×10^6	
		Total nitrogen	128.8×10^6	

roots[57,61] and decaying organic matter[59]. However, it has been reported[60] that higher concentrations of organic carbon did not stimulate N-fixation; rather the extent of desiccation was the principal 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[62].

Assays were made[63] of nitrogen fixation (acetylene reduction method) on fresh leaf litter (yellow leaves recently fallen from trees), aged leaf litter (brown leaves on the forest floor) of *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*. In addition, rates were measured on pneumatophores of *A. germinans* and mangrove sediments from two different sites along the Shark River estuary in the Everglades National Park (South Florida, USA). Fresh leaf litter, sediments and pneumatophores showed low ethylene production rates, ranging from 0 to 31.3 nmol C_2H_4 g dry wt^{-1} h^{-1} (Table 2). Aged leaf litter showed the highest ethylene production rates, ranging from 7.3 to 538.8 nmol C_2H_4 g dry wt^{-1} h^{-1}. Ethylene production rates showed no apparent differences in species composition but there was an effect during each stage of decomposition of the leaves. Fresh leaf litter and mangrove sediments represent initial and final stages in decomposition respectively, and both have minimum rates of nitrogen fixation in the forest floor. Thus it was inferred that new nitrogen to this forest by fixation in leaf litter is associated with the intermediate stages of litter decomposition.

Enrichment of nitrogen was observed[64], as well as the activity of N_2-fixing bacteria during decomposition both during the rainy and dry seasons in a tropical coastal lagoon (Gazi, Kenya) in two mangrove species (*Rhizophora mucronata* and *Ceriops tagal*). Maximum rates of nitrogen fixation were recorded for *C. tagal* (380 nmol g^{-1} N_2 h^{-1}) during the rainy season, in contrast to 78 nmol g^{-1} N_2 h^{-1}, about one-fifth lower in the dry season. N_2-fixation rate for *R. mucronata* was only slightly higher (390 nmol g^{-1} N_2 h^{-1}) in the rainy season, but was nearly half (189 nmol g^{-1} N_2 h^{-1}) in the dry season. However, total nitrogen immobilized in the leaves was highest during the dry season. Biological N_2-fixation accounts for between 13 and 21% of the maximum nitrogen immobilized in the decaying mangrove leaves.

Higher rates of N fixation in sediments associated with roots and decaying organic matter were reported[61], suggesting that the available DOC in sediments influences N fixation rates in mangrove ecosystems[57,59]. DOC exudations from seagrass roots stimulate N fixation, which suggests that the N-fixing communities of seagrass and mangroves are dominated by different bacterial groups[62]. By contrast, it is argued[60] that the extent of desiccation was the principal factor influencing N fixation. High to very high rates of nitrogenase activity (64–130 nmol C_2H_4 g^{-1} dry root h^{-1}) were shown[65] to be associated with roots of seven common early-succession mangrove species from inundated swamps.

Dissolved inorganic nitrogen in mangroves and tidal variations

Dissolved inorganic nitrogen (DIN) was examined[66] from four Indian mangrove ecosystems experiencing varying levels of anthropogenic impact. It has been reported that the total DIN at four mangrove sites was dominated by NH_4^+ (Table 3), as in similar mangrove environments[67]. The highest DIN loading of 265 μM was observed at the Sundarbans. However, this mangrove system is river-dominated and N concentrations are heavily influenced by inputs from the adjacent Hooghly estuary, which drains the Ganges; mean freshwater discharge is 1000 m^3 s^{-1} during the dry season (November–May). The pristine Andaman Islands had the lowest DIN concentrations (~15 μM); higher levels were recorded at the Muthupet and Pichavaram (DIN ~ 30–95 μM) mangroves, reflecting anthropogenic inputs, the latter being consistent with local eutrophication.

Diel variations of DIN

Most of the diel nutrient oscillations in the mangrove creek are due to dilution of the nutrient-rich groundwater input by a variable volume of estuarine water with a lower nutrient concentration[67–70]. Groundwater is the major source of DIN in the Celestun Lagoon[71] mangroves (Yucatan Peninsula, Mexico), the majority of which is recycled within the lagoon, with only a small fraction exported to the coastal ocean (10%). Seasonal differences in DIN were seen[66,72] with a strong tidal signal in the mangroves of Andaman Islands. NH_4^+ accounted for ~90% of DIN during the dry season (January), but only 33–85% during the wet season (July). This is consistent with an increased freshwater NO_3^- input during the wet season, and/or increased nitrification following periods of rainfall. During both seasons, DIN was maximal at low tide irrespective of salinity (wet season salinity 0–28; dry season salinity 24–32). These data are consistent with ‘tidal pumping’, in which pore waters containing elevated concentrations of nutrients seep into creek waters from surrounding mangrove sediments following the gradual release of hydrostatic pressure towards low water[73].

The N flux was determined[74] in Chaliyar river and estuary, where the major source of N to the estuary was river discharge. The study indicated the predominance of DIN during monsoon, which otherwise contained organic nitrogen in its surface waters. Thus, N was not a limiting nutrient for primary production in this mangrove system. When the monsoon discharges were maximum, 80–90%

Table 3. Sediment denitrification rate (μmol m^{-2} d^{-1}), N_2O flux (μmol m^{-2} d^{-1}) and associated parameters in four Indian mangrove ecosystems. All fluxes were determined using static chambers[72]

Site	Date	Water column DIN (μM)	N_2O flux	Denitrification rate	Sediment organic carbon (%)
Wright Myo Andaman Islands	July 2003	20	2.9	7.6	2.4
Muthupet	June 2003	66	3.8	10.2	3.0
	September 2003	27	6.5	13.5	2.9
	December 2003	35	5.5	17.4	3.1
	April 2004	ND	7	10.5	3.0
	August 2004	ND	5.4	6.4	3.2
Pichavaram	April 2004	78	9.7	23	4.5
	August 2004	94	10.4	22	ND
Sunderbans	December 2004	265	0.5	11.2	1.2

ND, Not determined.

contribution to the total nitrogen pool is almost entirely dominated by NO_3^--N, while in the pre-monsoon season 75–85% of total nitrogen pool is from organic-N. Similarly mangrove surface waters from the Gautami–Godavari (GG) river estuary and Kakinada Bay, high concentration of nutrients in the mangrove ecosystem was reported[75] in comparison to the bay and estuarine ecosystems, which reveals the importance of mangroves as a source of nutrients to the adjacent coastal ecosystems.

Nitrification in mangroves

Near-shore tropical marine ecosystems are more susceptible to nitrogen loading as depurative capacity of the microbial communities is limited by the fragility of the nitrification link[76]. Most nitrifying activity in marine systems occurs in sediments where dissolved oxygen concentrations are low[77]. Therefore, in mangrove forests nitrification occurs predominantly close to the sediment surface in micro-oxic zones[77]. These zones are created by the oxygen-pumping activity of mangrove roots[53] and in the oxidized lining of animal burrows[78].

Active subsurface nitrification associated with roots of aquatic macrophytes due to downward translocation and release of O_2 by roots, comparable to earlier studies has been reported[79–81]. Nitrification rates increase generally with depth at the vegetated site, reflecting a higher population density or enzyme activity of nitrifying bacteria and that nitrifiers are subject to more oxic conditions compared with the non-vegetated sediments. Numerous studies listed in Table 2 confirm that potential nitrification in sediments is only an indicator of nitrifiers being present and not a measure of actual nitrification[82]. The potential nitrification rates of 12 and 74 μmol m^{-2} d^{-1} reported[79] are in the low range of previously published rates from tropical mangrove sediments (0 to 300 nmol cm^{-3} d^{-1})[83,84], and more than an order of magnitude lower than that usually found in temperate coastal sediments[82]. Nitrification is an aerobic process and the depth of oxygen penetration at the sediment surface is an indicator of the nitrification zone and can be used to provide a maximum estimate of the surficial nitrification rate[79]. Also, presence of NO_3^- in the porewater down to at least 30 cm depth in the vegetated sediment indicates active nitrification below the oxic surface layer. Active subsurface nitrification associated with roots of aquatic macrophytes has been observed in a number of cases[80,81] and is due to downward translocation and release of O_2 by the roots. Nitrification rates were measured[85] (Table 2) in the mangrove ecosystems of southern Thailand using the C_2H_2 block method. The study determined that nitrification rates were significantly large during the dry season, with values varying between 0 and 690 μmol N m^{-2} d^{-1}. Slow rates of nitrification in mangrove forests are associated with the extensive uptake of ammonium by the mangrove trees and microbes.

Denitrification in mangroves

Denitrification rates (Table 2) reported for mangroves are generally much lower than those reported for estuarine sediments, despite the suitability of mangrove sediments (i.e. with alternating anoxic and oxic conditions with tidal inundation) to the coupling of mineralization – nitrification–denitrification processes[86]. In marine sediments, denitrification rates increase as a function of NO_3^- concentration[87], so there is potential for the removal of additional NO_3^- (e.g. sewage) in mangrove sediments. There are two types of denitrification: direct and coupled. Differentiation between the two types depends on the source of NO_3^-: direct denitrification in mangrove systems is fuelled by NO_3^- diffused into the sediment and coupled denitrification is supported by nitrate products of nitrification[88]. In accordance with the low NO_3^- levels, denitrification rates in the Ao Nam Bor mangrove forest were low. Use of the ^{15}N enrichment technique confirms[86,89] the low rates as denitrification was barely detectable at *in situ* NO_3^- concentrations and only ranged between 40 and

Table 4. Contribution of coastal systems to global N_2O production

Coastal/marine system	Percentage of world's ocean area[a]	N_2O emission ($Tg\ yr^{-1}$)	Percentage of global oceanic N_2O emission[$]	Source
Estuaries	0.4	0.2^b–1.5^c	10	184^b 185^c
Coastal upwelling	0.2	3.0^a–4.7^d	35	186^a 187^d
Continental shelves	17.9	0.6^b–2.7^a	15^b	184^b 186^a
Open ocean	81.5	4.2^a–5.8^d	40	186^a 187^d

[$] Percentage of global oceanic N_2O emission from estuaries + coastal upwelling + continental shelves is 60, which demonstrates high production per unit area related to the open ocean.

Table 5. N_2O (% saturation) and fluxes ($\mu mol\ m^{-2}\ d^{-1}$) in water bodies surrounding four Indian mangrove ecosystems[72]. Numbers in parentheses refer to individual estimates

Site	Date	Water column N_2O (range)	Water column N_2O (mean)	Water to air flux N_2O	Comments
Wright Myo, Andaman Islands	Jan–2004	103–208 (24)	153	5.8^a	Tidal fixed station sampling
	Jul–2004	127–166 (24)	148	5.5^a	Tidal fixed station sampling
	Jul–2004			28.8^b (8)	Free-floating exchange chamber deployed at low tide
Muthupet, South India	Jun–2003	90–189 (19)	125	ND	Axial transect from mangrove to sea (10 km)
	Dec–2003	113 –180 (19)	150	ND	Axial transect from mangrove to sea (10 km)
	Apr–2004	80–170 (17)	134	3.5^b (5)	Axial transect from mangrove to sea (10 km)
	Aug–2004	109–140 (15)	121	2.9^b (5)	Axial transect from mangrove to sea (10 km)
Pichavaram, South India	Jan–2004	90–221 (19)	112	ND	Axial transect from mangrove to sea (10 km)
	Apr–2004	96–210 (18)	157	ND	Axial transect from mangrove to sea (10 km)
	Aug–2004	ND	ND	31.2^b (5)	Free-floating chamber deployed during heavy rain
Sunderbans	Dec–2004	97–134 (42)	116	ND	Axial transect (50 km)

[a] Estimated using an air–sea gas exchange model; [b] Estimated using a free-floating chamber.

200 $\mu mol\ m^{-2}\ d^{-1}$ in sediments amended up to 200 mmol NO_3^-. This substantiated the fact that the capacity for denitrification in mangrove sediments is generally low and not only related to NO_3^- availability. Mangrove forests receiving large NO_3^- discharges from sewage treatments plants[90,91] show relatively high denitrification rates, between one and two orders of magnitude higher than that usually observed[79]. In unpolluted mangrove stands in North Queensland, low rates of direct and indirect denitrification have been reported[38], which may be due to inhibition of nitrifying bacteria by high tannin levels and low NO_3^- concentrations in porewaters[38,50,83,92].

Sediment denitrification and N_2O fluxes in mangroves

Rates of microbial N transformations in natural systems are a function of substrate availability and NO_3^- concentrations[93]. The response of N_2O sediment/air flux to N addition was assessed in *Rhizophora mangle* sediments; N_2O fluxes increased with enhanced NH_4^+ or NO_3^- loadings[94]. Denitrification rates at the mangrove ecosystems of Andaman Islands and along the southeast coast of India (Table 3) were generally up to three orders of magnitude lower[72] than in typical temperate settings[95], consistent with low concentrations of NO_3^- in the mangrove surrounding waters.

Studies[76,96] have indicated that nitrification was the major N_2O source and this is supported by the results of Barnes *et al.*[72]. The estimated N_2O emissions[97] generally far exceed the reported maximum denitrification N_2O yield of 6%. Given that the energy yield for organic C oxidation by reduction of N_2O to N_2 is high in most mangrove sediments, denitrification is likely to be a sink for N_2O rather than a source[66]. Table 4 provides an insight into the contribution of coastal ecosystems to global N_2O production.

N_2O fluxes from mangrove surrounding waters

Table 5 provides estimates of the contribution made by coastal systems to the global N_2O production. It is clear that the combined N_2O emission from coastal systems (i.e. estuaries + coastal upwelling + continental shelves) to the global oceanic N_2O is as high as 60%, compared to the open oceans. This demonstrates the high production per unit area of the coastal systems related to the open ocean surface water[66,72,94]. N_2O saturations and water-to-air fluxes from Indian mangrove surrounding waters are shown in Table 5 based on measurements[66] of direct emissions using floating chambers; always higher than those estimated using a transfer velocity–wind speed relationship (Table 3). N_2O produced by nitrification and denitrification seems to be driven principally by oxygen and nitrogen substrates. Extrapolating the data using mangrove forest and creek water areas of 0.2×10^6 km^2 and 0.36×10^6 km^2 respectively, Barnes *et al*. provide a global atmospheric source N_2O strength from mangroves of 0.01–0.1 Tg yr^{-1}. The upper value of this range exceeds the lower estimate of 0.07 Tg yr^{-1} based on an N model for global estuarine N_2O emissions[98], suggesting that mangroves are small but significant sources of atmospheric N_2O.

Ammonification and anammox in mangroves

Ammonification may be an important nitrogen transformation in mangrove ecosystems due to their generally low NO_3^- sediment concentrations (porewaters = 0–21 μM[38,99] and high C : N ratios >20). Despite the potential key role NO_3^--ammonification might have in the nitrogen cycle in mangrove ecosystems (Table 2), there are no published references on this process from Indian mangroves. Most accurate measurements of ammonification in mangrove sediments have been made using ^{15}N in surface sediments in other Rhizophora forests in Thailand[79,100,101] and Jamaica[102]. Later, the net ammonium production rate was quantified[85] to be 490–2260 μmol N m^{-2} day^{-1} during the northeast monsoon and from 280 to 1505 μmol N m^{-2} day^{-1} during the southwest monsoon in four mangrove forests of different ages and types in southern Thailand, in relation to forest net canopy production.

The ammonium pool in the mangroves of southern Thailand is mainly by ammonification and/or nitrogen fixation in deep sediments, whereas most other inputs were found to be small[85]. Most of the nitrogen required to sustain net production in mixed Rhizophora forests in northern Australia is derived from the ammonium pool via ammonification, with much less flow via the nitrate pool by nitrification, or by nitrogen fixation. In Thai forests at Ao Nam Bor, it was found[101] that nearly all of the nitrogen required for low- and mid-intertidal *R. apiculata* forests (Table 2) was derived from belowground mineralization processes. Ammonification rates observed[103] are within the range of those measured using a similar method in mangroves further south of Sawi Bay. An imbalance between rates of ammonium production and sediment–water exchange was also observed, which was attributed to rapid and efficient assimilation by sediment microbes, rather than to uptake by fine mangrove roots. In an Indian mangrove ecosystem, the bacteria involved in nitrogen transformations (ammonification, nitrification and denitrification) were in greater numbers in soils with plants than soils without plants[104].

Anammox

Anammox (anaerobic ammonium oxidation) is the anaerobic conversion of NO_2^- and NH_4^+ to N_2. Although its existence was suggested[105,106] as early as 1965, the first direct evidence for this process came from studies of activated sludge from a wastewater treatment plant in The Netherlands only a decade ago[107]. Recent studies[3,4] (Table 2) have reported the presence of anammox in estuarine and offshore sediments[108–111], permanently anoxic bodies of water[112,113] and multiyear sea ice[114]. Anammox may be an important pathway in global N cycling, since it can account for as much as 67% of benthic N_2 production[108–110,115], the remainder being produced by denitrification. However, characterization of the biogeography of anammox, its significance compared to denitrification, and its regulation in nature are still incomplete, since the methods used to detect the presence and activity of anammox bacteria have become available only recently.

The occurrence and significance of the anammox process was investigated[116] (Table 2) relative to denitrification and the process correlated to the availability of NO_2^- in sediments from four locations in an Australian subtropical tidal river fringed by mangrove vegetation. Porewater profiles of NO_x^- ($NO_2^- + NO_3^-$) and NO_2^- were measured with microscale biosensors and the availability of NO_2^- was compared with the potential for anammox activity; the study indicates ubiquitous nature of the process. Potential rates of anammox in the Logan River sediments (0.5–8 nmol N m^{-2} h^{-1}) were within the range reported for other sediments investigated for anammox thus far, such as temperate estuaries and offshore marine sediments[117]. The contribution of anammox to sediment N_2 production in the Logan River system (0–9%) was relatively low and within the range reported previously for temperate estuaries such as the Thames estuary in the United Kingdom[110] and the Danish estuary, Randers Fjord[108]. Thus, both in temperate and subtropical estuaries, denitrification governs benthic N_2 production, in contrast to offshore sediments, where anammox has been found to dominate[109]. Reports[117] suggest that variables such as NO_3^- availability, local gradients in sediment organic content or the presence of microphytobenthos may regulate anammox within the overall frame defined by the organic loading of the sediment. The anammox process is also important in anoxic water columns where it may account for 35% of the nitrogen removal. It is argued that anammox in sediments and anoxic water bodies may amount to 1/3–1/2 of the global marine nitrogen removal.

Mineralization of N in mangrove sediments

Relative N mineralization (N mineralization per unit of total N) is a useful index to compare overall soil quality[118]. Nitrogen immobilization is mediated by microbial conversion of inorganic N (NH_4^+ and NO_3^-) into organic forms during decomposition of organic matter[119]. The relative N mineralization was observed to decrease exponentially[120] with distance from the mouth of the estuary (Table 2). This indicates that the proportion of recalcitrant organic N in mangrove soils increases rapidly with distance from the Gulf of Mexico towards the upstream mangrove marsh ecotone. The C : N ratio of soil organic matter is influenced by the presence of leaf litter, such that the litter horizon of soils low in nitrogen will have higher C : N ratios than litter in N-rich sites[121,122]. Decomposing macrophyte litter with high C : N ratios tends to favour net immobilization of N during decomposition, whereas N-rich litter (low C : N) favours net mineralization[38,123,124].

Mangrove leaf litter, such as the genus *Rhizophora*, is characterized by low concentrations of N, and C : N ratios of leaf litter from the canopy have been reported[125,126] as >90. During the initial stages of decomposition, concentrations of N increase in the leaf litter[127,128], resulting in immobilization of N and reduction of C : N to 40. The accumulation of ^{15}N in mangrove sediments[86] suggests that nitrogen limitation in leaf litter leads to immobilization of inorganic N supplied by tidal waters. Immobilization of inorganic N may account for the low loss of N_2.

A distinct loss of added ^{15}N in the sediment pool was reported[86] in the mangroves of Terminos Lagoon due to uptake by pneumatophores and algae attached to these aerial roots, which were present in the experimental cores. The fate of inorganic N is different among fringe, basin and riverine mangroves, given their differences in fertility and supply of inorganic N to leaf litter. Also, it was found that NH_4^+ uptake by mangroves exceeds regeneration rates[129] and that fine root development in mangrove seedlings is extensive[130], when the seedlings were supplied with NO_3^-. Thus, organic matter in wetland sediments accumulates on decadal timescales, and N immobilization in sediments can eventually contribute to the burial of N in mangrove ecosystems. However, some of this immobilized N (Table 2) in the early stages of litter decomposition may be recycled by ammonification and used in plant uptake.

Internal recycling and export of nitrogen in mangroves

Mangroves receive dissolved nutrients from land and sea; however, these inputs are not sufficient to maintain their high productivity[38,73,131], which can exceed 7000 mg C m^{-2} day^{-1}. Internal recycling of organic matter is a major factor in meeting this high nutrient demand[132]. Mangrove leaves play a key role as they contain up to 40% water-soluble components, which can be converted into bacterial biomass in less than 8 h after falling into mangrove waters[133]. In addition, crabs recycle and bury mangrove leaves[134]. As a consequence of this strong internal recycling, large amounts of macro-detritus and dissolved substances can be exported to the adjacent coastal waters. Material exchange occurs in dissolved as well as particulate forms and is temporally and spatially highly variable[135–138]. The nutrients and organic detritus potentially enrich the coastal sea and ultimately support fishery resources. Bacteria and fungi contribute to decomposition of the mangrove material and to the transformation and cycling of nutrients. Fungi are the primary litter invaders, reaching their peak in the early phases of decomposition[139]. Rapid nitrogen increase in leaves was measured[140] after six weeks of decomposition. It has been suggested that the litter provides a surface for microbial nitrogen synthesis and acts as a nitrogen reservoir. The C : N ratio of decomposing *Avicennia marina* leaves drops dramatically from approximately 1432 to 28, primarily due to a large increase in the nitrogen content[141,142]. The contribution of mangroves could be particularly important in clear tropical waters, where nutrient concentrations are normally low[143].

Export/outwelling of N from mangroves

Earlier studies on mangrove outwelling were conducted in macro-tidal, ‘typical’ mangrove communities, which were found to be the net exporters of organic carbon and nutrients[149]. Salt marsh outwelling was discussed in detail[144], and it focused[145] mainly on the relationship between mangrove occurrence and offshore fisheries production. Experiments show[146] that outwelling from estuarine wetlands depends on the physical characteristics of the wetland[147]. Mangrove mass balance studies indicate that net export of organic matter is a common feature of most mangroves, because stronger tidal exchange, regular rainstorms and floating and non-retained litter (standing dead litter in the salt marsh) are all conducive to this difference from the salt marsh wetlands[148]. The literature suggests that export is a feature of most tidally inundated mangroves[149]. The annual export was calculated[150] from mangroves on a regional scale from the North Brazilian mangroves. This indicates that DIN was exported (Table 2) almost completely in ammonium form. This is reasonable, since the flux of ammonium-rich porewater from the reducing mangrove sediments is considered to be the principal source of DIN in the tidal creek[67]. The nutrient-rich water at low tide is not immediately exported from the mangroves, but transported back at the beginning of the flood tide. In the course of the flood tide, it is mixed with nutrient-poor estuarine water and spread out in the mangrove at high tide. During the ebb tide, a comparatively well-mixed water-body leaves the mangrove. Only when most water has already flowed out and the water-body almost stagnates does the influence of porewater lead to elevated nutrient concentrations. Thus, a net export of DON ($\approx 2 \times 10^9$ mol yr^{-1} and, ammonium $\approx 0.4 \times 10^9$ mol yr^{-1}) was observed[150] from the mangroves to the ocean. However, when export from mangroves was compared with the Amazon River discharge, the fluxes were low (1–3% of the Amazon fluxes). Reports[71] exist of similar exports of DIN and particulate organic nitrogen (PON) (Table 2) from the mangrove-dominated lagoon of Yucatan, Mexico. According to these reports, PON accounted for between 65 and 85% of the net export from the mangroves. Majority of the DIN from groundwater (a significant source of N to the mangrove) was recycled within the mangrove system, with only 10% exported to the coastal ocean.

Productivity of the Indian coastal systems

The productivity of coastal margin waters is largely controlled by the availability of either nitrogen or phosphate nutrients. A number of anthropogenic sources often contribute via point-source pollution of streams and rivers or through urban and agricultural run-offs[151]. The additional nutrients have impacts well beyond just increasing net productivity. For example, increased plankton in the water can severely reduce the water depth at which light penetrates to the bottom in sufficient amounts for seagrasses and other benthic flora to grow. This can then have major consequences on other parts of the ecosystem, such as fisheries that depend on seagrass beds or causes algal blooms.

Significance of the N-cycle in coastal ecosystems

As demonstrated in this article, biologically available nitrogen tends to be in short supply in coastal marine environments. Over the last 20 years, there has been growing awareness that coastal ecosystems have been experiencing a number of environmental problems that can be attributed to the introduction of excess nitrogen. In coastal ecosystems, eutrophication can lead to excessive and sometimes toxic production of algal biomass (including red and brown tides), loss of important nearshore habitats such as seagrass beds (caused by light reduction), changes in marine biodiversity and species distribution, increased sedimentation of organic particles and depletion of dissolved oxygen (hypoxia and anoxia).

It has been estimated that the total amount of N in the atmosphere, soils and waters of the earth is approximately 4×10^{21} g – more than the mass of other elements (C, H, O) combined[152]. However, more than 99% of this N is not available to more than 99% of living organisms. The reason for this seeming contradiction is that while there is an abundance of N in nature, it is almost entirely in the form of molecular nitrogen, a chemical form that is not usable by most organisms. Breaking the triple bond holding the two N atoms together requires a significant amount of energy that can be mustered only in high-temperature processes or by a small number of specialized N-fixing microbes[153]. N compounds in nature can be divided into two groups: non-reactive and reactive. Non-reactive N is N_2; reactive N (Nr) includes all biologically, photochemically and radiatively active N compounds in the earth's atmosphere and biosphere. Thus, Nr includes inorganic reduced forms of N (e.g. ammonia [NH_3] and ammonium [NH_4^+]), inorganic oxidized forms (e.g., nitrogen oxide [NO_x], nitric acid [HNO_3], nitrous oxide [N_2O], and nitrate [NO_3^-]), and organic compounds (e.g. urea, amines, proteins and nucleic acids).

The creation of Nr from N_2 occurred primarily through two processes[153]: lightning and biological nitrogen fixation in the pre-human world. Reactive N did not accumulate in environmental reservoirs because the microbial N_2-fixation and denitrification processes were approximately equal[154]. Now, reactive N is accumulating in the environment at all spatial scales – local, regional, and global[10]. During the last few decades, production of Nr by humans has been greater than that from all natural systems. Coastal ecosystems (e.g. estuaries) receive most of their Nr from riverine and groundwater inputs; direct atmospheric deposition is an important source in some systems, and inputs from the ocean are important in others. These inputs have increased several fold as a consequence of human activities[7,33,155,156]. There is limited potential for Nr accumulation due to the dynamic nature of coastal ecosystems. In addition, although the potential for Nr transfer to continental shelf regions is large, there is limited transport to the shelf because of the high rates of denitrification (mostly as N_2), and the Nr that is transferred is mostly converted to N_2 before its transport to the open ocean. With coastal systems acting as Nr sinks, atmospheric deposition becomes a potentially important source of Nr for the open ocean, especially in oligotrophic mid-ocean gyres (Figure 6).

Although Nr has a short residence time in coastal ecosystems compared with terrestrial ecosystems, its residence time there can have a profound impact on the coastal ecosystem. Primary production in most coastal rivers, bays and seas of the temperate zone is limited by Nr supplies[14,98,155]. As a consequence, greater Nr inputs lead to increased growth of algae. In the tropics, P rather than N often limits relatively pristine coastal ecosystems. However, increased nutrient loading can shift these systems toward Nr limitation[157,158] and, as in temperate-zone systems, Nr is a major contributor to coastal eutrophication in tropical coastal systems[76,155,159].

Table 6. Characteristics of different ecosystems relevant for the nitrogen cascade[153]

System	Accumulation potential	Transfer potential	N_2 production potential	Links to systems down the cascade	Effects potential
Atmosphere	Low	Very high	None	All, but groundwater	Human and ecosystem health; climate change
Agroecosystems	Low–moderate	Very high	Low–moderate	All	Human and ecosystem health; climate change
Forests	High	Moderate–high in places	Low	All	Biodiversity, NPP, mortality, groundwater
Grasslands	High	Moderate–high in places	Low	All	Biodiversity, NPP, groundwater
Groundwater	Moderate	Moderate	Moderate	Surface water; atmosphere	Human and ecosystem health; climate change
Wetlands, streams, lakes, rivers	Low	Very High	Moderate–high	Atmosphere, marine coastal ecosystems	Biodiversity, ecological structure, fish
Marine coastal regions	Low–moderate	Moderate	High	Atmosphere	Biodiversity, ecological structure, fish, HABs

NPP, Net primary productivity; HABs, Harmful algal blooms.

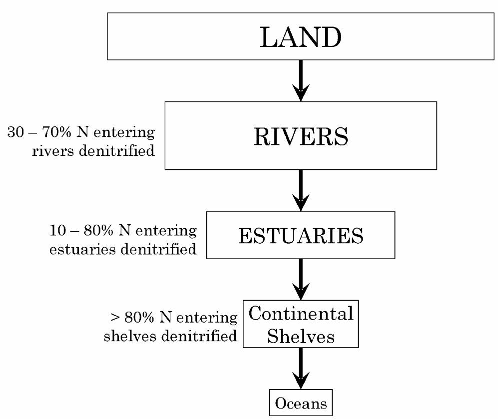

Figure 6. Transport of reactive nitrogen (Nr) from terrestrial to oceanic systems decreases at each step along the river-estuarine–continental shelf system (adapted from Galloway[153]).

Other major effects of increasing Nr in coastal regions include loss of seagrass beds, macroalgal beds and changes in coral reefs[155,160–162]. Reactive N additions can increase the incidence and duration of harmful algal blooms[155]. Thus, Nr inputs to coastal ecosystems have increased significantly over the last few decades. Although most Nr is eventually denitrified to N_2 within the coastal ecosystems and associated shelf, Nr pollution has significant and widespread impacts on various ecosystem components and on human health (Table 6).

Denitrification potential in the wetland–stream–river–estuary–shelf continuum

Along the entire aquatic continuum, from wetlands to headwater streams to the continental shelf and eventually to the open ocean, not only is Nr rapidly cycled among the various forms (e.g., NH_4^+, NO_3^-, and particulate and dissolved organic N), there is great potential for loss of Nr from the biosphere through the conversion of NO_3^- to N_2 (denitrification). The most active sites for denitrification in aquatic systems are benthic sediments, which are often anoxic below the first few millimetres, even though the overlying water is well oxygenated. Even when nitrate concentrations are low in sediments, denitrification rates could be high if other conditions are favourable, because of the close spatial and temporal coupling of nitrification and denitrification.

Nr inputs increase, increase in the NO_3^- concentration in the water column and thus increase the diffusive supply of nitrate to the sediments was also observed[153]. Increased inputs of Nr can also enhance primary production, particularly in Nr-limited estuarine and continental shelf waters, thus increasing organic matter deposition to the sediments and subsequent sediment nitrification and denitrification. However, if Nr inputs result in the water column becoming anoxic, sediment nitrification and consequently denitrification can markedly decrease. Reactive N not removed within the wetland–river network is transported to estuaries or discharged by large rivers directly onto the continental shelf. In estuaries, water residence time again is an important factor controlling the proportion of Nr inputs that are removed by denitrification. In estuaries with a water residence time ranging from 0.1 month to over a year, the total Nr inputs removed by denitrification[98] ranged from less than 10 to approximately 75%. Nr that has not been removed by denitrification in rivers or estuaries is subject to removal on the continental shelf[163,164]. In fact, Nr removed by denitrification in shelf sediments probably exceeds Nr exported to coastal areas by rivers. Additional measurements of denitrification and Nr inputs for other continental shelf regions throughout the world's oceans are needed to better understand the Nr balance and final fate of land-based Nr inputs[153].

Nearly all of the Nr that is injected into surface waters is denitrified along the stream–river–estuary–shelf continuum (Figure 6). While most of this Nr is converted to N_2, a fraction is converted to N_2O and NO. Model estimates of global N_2O emissions suggest that rivers, estuaries and continental shelves account for approximately 30% of the total global anthropogenic N_2O emissions[165]. As inputs of Nr to rivers increase[33], so will the rates of creation of NO and N_2O. Transfer of Nr from the atmosphere, agro-ecosystems, forests and grasslands into the wetland–stream–river–estuary hydrosphere continuum is increasing and has resulted in numerous effects, including acidification, eutrophication and human health problems. However, throughout the continuum there is a large potential for conversion of Nr to N_2, especially in wetlands, large rivers, estuaries and the continental shelf. Thus, while the N cascade begins at the point of Nr creation, and while Nr will accumulate in and cycle among most terrestrial systems, the cascade reaches an end at the continental margins, where its primary continuation is N_2O production during nitrification.

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