Nitrogen

Review

Nitrogen Cycling and Mass Balance in the World's Mangrove Forests

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Abstract: Nitrogen (N) cycling in mangroves is complex, with rapid turnover of low dissolved N concentrations, but slow turnover of particulate N. Most N is stored in soils. The largest sources of N are nearly equal amounts of mangrove and benthic microalgal primary production. Dissolved N fluxes between the forests and tidal waters show net uptake, indicating N conservation. N_2-fixation is underestimated as rapid rates measured on tree stems, aboveground roots and cyanobacterial mats cannot currently be accounted for at the whole-forest scale due to their extreme patchiness and the inability to extrapolate beyond a localized area. Net immobilization of NH_4^+ is the largest ecosystem flux, indicating N retention. Denitrification is the largest loss of N, equating to 35% of total N input. Burial equates to about 29% of total inputs and is the second largest loss of N. Total inputs slightly exceed total outputs, currently suggesting net N balance in mangroves. Mangrove PON export equates to ≈95% of PON export from the world's tropical rivers, but only 1.5% of the entire world's river discharge. Mangrove N_2O emissions, denitrification, and burial contribute 0.4%, 0.5–2.0% and 6%, respectively, to the global coastal ocean, which are disproportionate to their small worldwide area.

Keywords: biogeochemistry; denitrification; ecosystem; mangrove forests; mass balance; nitrogen; nitrogen cycling; nitrogen fixation; nitrogen retention

1. Introduction

Nitrogen (N) is the most important nutrient element in fostering growth, reproduction, productivity, and other energetic and physiological processes that enable ecosystems to thrive. Mangrove forests and their associated waterways are major coastal ecosystems that live along the world's subtropical and tropical coastlines, requiring nitrogen and other nutrients like all other ecosystems [1]. Mangroves are an important ecological and economic resource, offering a wide variety of ecosystem goods and services, such as being important breeding sites and nursery grounds for birds, fish, crustaceans, amphibians, shellfish, reptiles, and mammals [2]. These tidal forests are a potentially renewable resource of wood and accumulate sediment, carbon, contaminants and nutrients, such as N. Mangroves also provide a vital livelihood for coastal inhabitants and offer some protection against coastal erosion and catastrophic events, such as tsunamis [1,2]. Thus, it is important to understand how these tropical ecosystems function biogeochemically.

In mangrove ecosystems where N is often limiting, native flora and fauna and their associated food webs have evolved a variety of mechanisms to conserve N. These retention mechanisms and strategies include, but are not restricted to: (1) highly efficient solute uptake between trees, microbes and soil N pools; (2) high N-use efficiency and high rates of leaf resorption; (3) low rates of N loss, such as dissolved N export and nitrous oxide (N_2O) emissions in proportion to N inputs; (4) export of highly refractory N in the form of humic and fulvic acids (tannins); (5) rapid rates of nitrogen fixation at the soil surface and on various forest components (bark, downed wood, prop roots, pneumatophores, cyanobacterial mats); and (6) a large reservoir of dead roots belowground [1,2].

Living in a low-N environment, mangroves rely greatly on the efficiency of the microbial machinery existing in their soils and tidal waters to process and conserve N in its various forms. Numbers, diversity and productivity of soil and planktonic bacterial communities are high, resulting in rapid uptake, transformation, and release of particulate and dissolved inorganic and organic N [1,3]; dissolved N pools turn over rapidly, usually in a matter of minutes to days [4]. The experimental addition of nutrients to mangrove trees in the field and laboratory indicate rapid uptake and utilization, although complex patterns often result due to various interactive factors, such as differences in forest stands in species composition, soil type (carbonate sand, terrigenous silt/clay, quartz sand, etc.), intertidal position, soil fertility, salinity, forest age, and tree and forest development stage [5–7].

Despite our knowledge of N transformation and utilization processes and rates in mangrove ecosystems, a comprehensive picture at the ecosystem-level has yet to emerge. To this day, only one complete N budget exists for a mangrove ecosystem [4] and no attempt has been made to construct a N mass balance for the world's mangrove ecosystems. This paper details such an attempt as a model tool to identify what is and what is not known about N cycling processes in mangroves. First, we will assess the standing stocks of N in the forests and associated waterways, prior to examining functional processes, including the significance of N retention and the contribution of mangroves to N flow in the global coastal ocean.

2. Nitrogen Concentrations and Standing Stocks

2.1. Dissolved N Concentrations in Tidal Waters and Porewater

Dissolved organic and inorganic N in mangrove tidal waters are dominated by dissolved organic nitrogen (DON), followed in descending order by ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-). In nearly all cases, except for some organically polluted environments, concentrations of all four species are in the micromolar (μM) range. DON, NH_4^+, NO_2^- and NO_3^- concentrations in unpolluted waterways range from 0.1 to 60 μM, 0 to 120 μM, 0 to 5 μM and 0 to 37 μM, respectively [3,4]. The major drivers of change in concentrations are rainfall, land runoff, intrusions of offshore water, groundwater and porewater inputs, leaching from litter, temperature, anthropogenic inputs, and plankton metabolic activities, especially of phytoplankton and bacterioplankton [1].

In soil porewater, dissolved N concentrations also vary greatly, depending on soil particulate N concentrations and composition, soil texture, redox status, presence of sulfides and other reductants, microbial mineralization processes, salinity, bioturbation, rate of soil accumulation, benthic community composition, and, most significantly, uptake and release from mangrove roots [1]. The chemical composition of DON in tidal waters and in porewater is not well characterized, but some evidence indicates that most DON is composed of humic acids (range: 47–91%) and to a lesser extent, of aromatic compounds, peptides and amino acids [8].

Figure 1 illustrates the importance of tree uptake on NH_4^+ porewater concentrations, showing an inverse relationship between the vertical soil depth changes in porewater NH_4^+ concentrations and live fine root biomass in three *Kandelia candel* forests in southern China [9]. A Pearson product-moment correlation (r) of porewater ammonium versus root biomass of −0.476 is significant ($p < 0.00784$). Earlier data [10,11] have similarly indicated an effect of NH_4^+ uptake by mangrove roots on porewater concentrations and profiles. Additional evidence indicates that adjacent mudflat sediments usually have higher porewater concentrations of NH_4^+ than in mangrove soils, suggesting that the difference is due to tree uptake [11]. These data are circumstantial, but support experimental data showing a strong preference by mangroves for ammonium (and nitrate) for their growth and nutrition [12–15]. Nitrite and nitrate are often found in mangrove porewater [4,11], but concentrations show very irregular patterns with increasing soil depth.

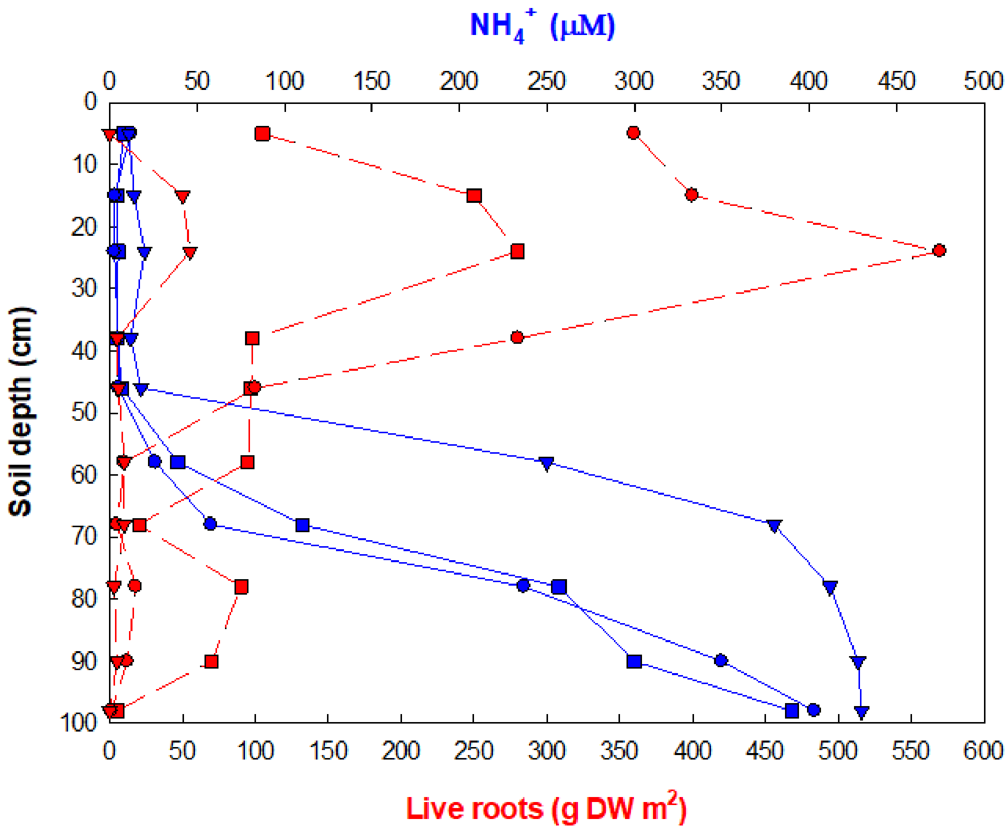

Figure 1. Vertical profiles of porewater extractable ammonium (NH_4^+, µM) compared with live root biomass (g dry weight m^2) in three *Kandelia candel* forests in the Jiulongjiang estuary, China [9].

2.2. Total N Concentrations and C/N Ratios in Forest Components and Soil

Concentrations of total nitrogen (TN) in leaves, stems, branches, roots, litter, and soil vary among forests due to many factors, including species composition, forest age, allochthonous N inputs, extent of organic pollution (if any), climate, temperature, salinity, physiological condition, nutritional status, soil composition, porewater nutrient concentrations, micronutrient availability, rate of soil organic matter accumulation, intertidal position, tidal regime, redox status, presence of sulfides and other reductants, microbial mineralization processes, bioturbation, and benthic community composition [1,4]. On average, TN concentrations in mangrove forests are very similar to those in tropical terrestrial forests for leaves and wood, and lower (Table 1) than terrestrial forest soil N (mean = 0.45% DW) and roots (mean = 0.86% DW), but higher (Table 1) than the C/N ratio (*g*/*g*) of below-ground biomass (mean = 33.2) (terrestrial forest references [16–38]).

Table 1. Mean (±1 standard error, SE) and median total nitrogen (TN) concentrations (as percentage of dry weight, DW) of various above- and belowground mangrove components, including soils to a depth of 1 m. The mean C/N ratios (*g/g*) are as follows: soil C/N = 11.3; live wood C/N = 130.4; belowground root C/N = 80.9; litter C/N = 79.4. The C/N values for biomass were calculated based on relative percentage of biomass DW in the respective components (i.e., stems + branches for wood estimate) and dead and live root and rhizome DW for belowground estimates using the carbon data and references in [39]. N data from [4,9–11,39–112] and earlier references within.

Component	Number of Observations	Mean ± 1 SE	Median	Range
Green leaves (%N)	109	1.61 ± 0.05	1.54	2.55
Stems (%N)	58	0.37 ± 0.03	0.35	1.22
Branches (%N)	55	0.31 ± 0.02	0.29	0.65
Roots (%N)	63	0.49 ± 0.03	0.45	1.69
Litter (%N)	153	0.69 ± 0.03	0.64	2.04

2.3. Global Mean N Stocks

Mean TN stock of global mangrove forests (Figure 2) totals 52.03 Mg N ha^{-1}, with 96% of total TN stock contained in soils to a depth of 1 m (mean = 50.0 Mg N ha^{-1}). In comparison, mean TN stocks in tropical terrestrial forests (rain forests, other moist forests, and peat swamps) total 22.33 Mg N ha^{-1} (Figure 2). Like mangroves, 91% of N stocks are vested in soil (mean = 20.3 Mg N ha^{-1}), suggesting similar investment of N by both mangroves and terrestrial forests in various forest components and belowground storage.

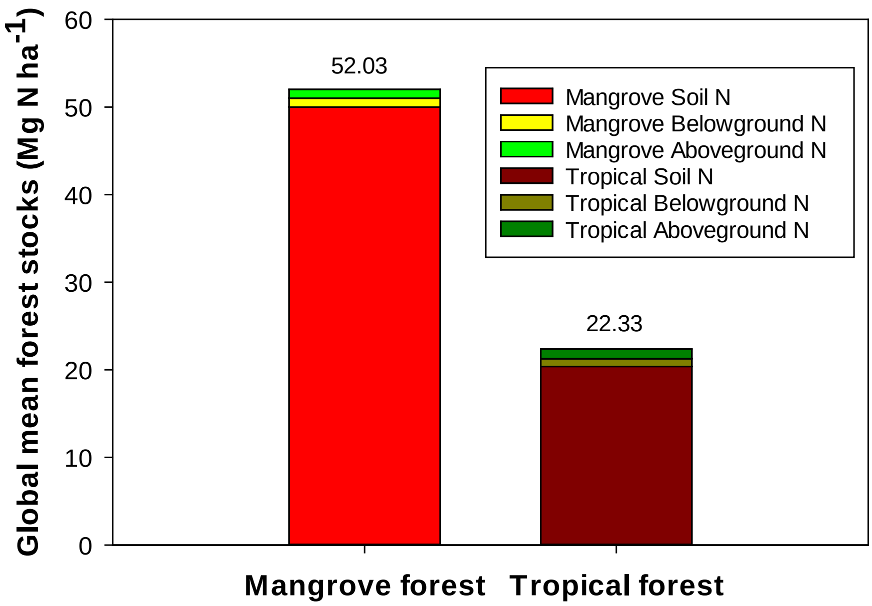

Figure 2. Mean TN stocks in mangrove above- and belowground biomass and soils to a depth of 1 m. Biomass and soil dry weight data extrapolated to N using N content or C/N ratios (*g/g*) in Table 1. Tropical terrestrial forest data are presented for comparison and includes data from moist forests, peat swamp forests, and rain forests with N, C and C/N (*g/g*) data [16–38,113–120] and earlier references within.

3. The Nitrogen Cycle in Soils

The soil nitrogen cycle (Figure 3) is composed of a series of complex transformation processes, nearly all conducted by specialized bacterial and archaeal groups, such as ammonium-oxidizers, cyanobacteria, nitrate-reducers, and nitrite-oxidizers.

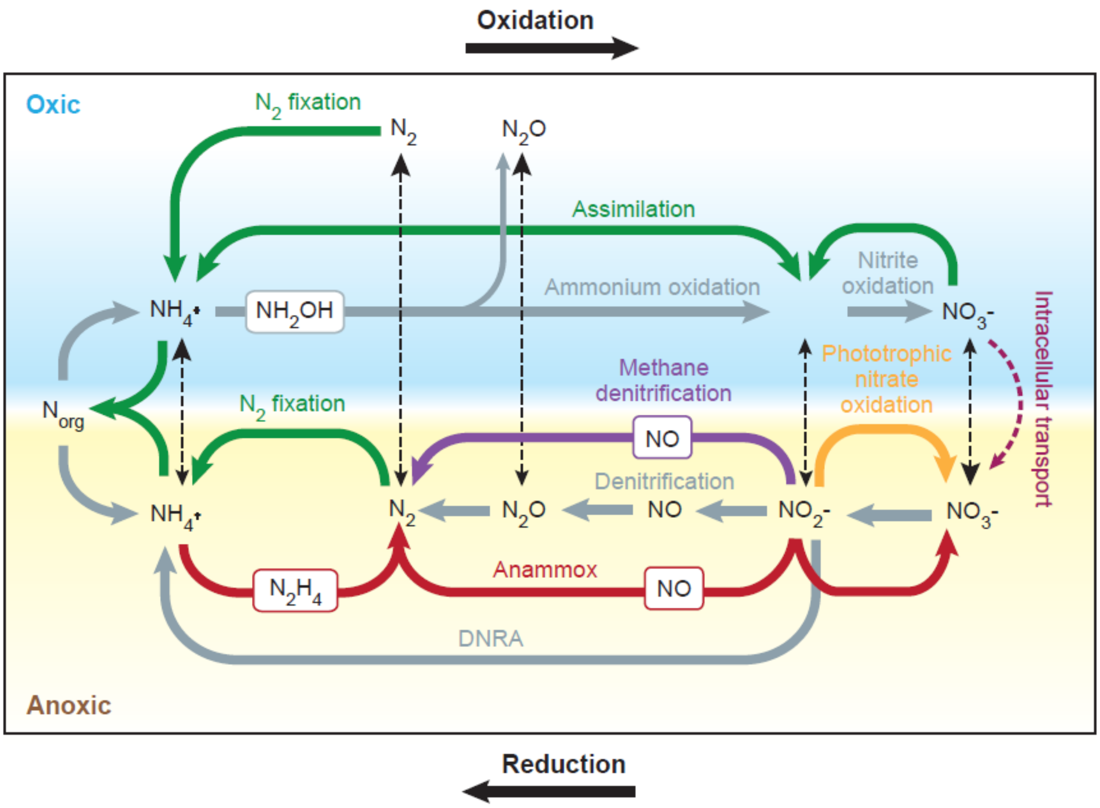

Figure 3. The nitrogen cycle showing all oxidizing and reducing transformation pathways that occur in oxidized and anoxic environments, particularly in marine sediments and waterlogged saline soils. Ammonification (shown in gray on left side) is the microbial breakdown of organic nitrogen (N_{ORG}) into ammonium (NH_4^+); the reverse process is NH_4^+ immobilization (green arrows on left). Nitrification (gray arrows in top side) is the biological oxidation of NH_4^+ to NO_2^- followed by the oxidation of the NO_2^- to NO_3^-. Black dotted arrows depict transport processes between oxic and anoxic environments. Abbreviations: DNRA = dissimilatory nitrate reduction to ammonium; Anammox = anaerobic ammonium oxidation; N_2 fixation = nitrogen fixation; NO = nitric oxide; N_2O = nitrous oxide; N_2 = nitrogen gas; NH_2OH = hydroxylamine, an intermediate in biological nitrification; N_2H_4 = hydrazine, the intermediate in the anaerobic oxidation of ammonium (anammox) process. Reproduced with permission from [121].

Fungi are also involved in organic matter decomposition and in carbon and nitrogen cycling processes, especially on litter and in roots and rhizomes [122–124]. In mangrove soils, a vast menagerie of highly diverse bacterial, archaeal, fungal and protistan communities exist, comprised mostly of members of the phyla Proteobacteria and Bacteroidetes, Bathyarchaeota and Euryarchaeota, Ascomycota, and Sarcondina, Mastigophora, Ciliophora and Myxomycota. Interkingdom biotic factors shape both community structure and function of all four kingdoms. Aside from fully oxic and anoxic conditions, mangrove soils provide microaerophilic environments, such as in and near biogenic structures and in rhizospheres where microaerophiles carry out nitrogen reactions such as ammonium oxidation [125]. All of these microbial types and communities vary greatly in composition and function in relation to such factors as temperature, mangrove species composition, tides, pH, salinity, and soil fertility, redox status, and soil type [126,127].

Several microbial groups and transformation processes have only recently been discovered (DNRA, anammox, methane denitrification), but are often quantitatively important in N cycling. For example, a nitrite-dependent anaerobic methane-oxidizing bacterium was recently discovered in mangrove soils of the Zhangjiang estuary in China [128]. This "*Candidatus* Methylomirabilis oxyfera-like" bacterium is unique in linking the carbon and nitrogen cycles. It is conceivable that new microbe species and new N transformation pathways await discovery in mangrove environments.

At the ecosystem-scale, other N processes are important in mangroves, such as the exchange of dissolved and particulate nitrogen (DN, PN) between the forests and tidal waterways and with the adjacent coastal ocean, dry and wet deposition of N, groundwater inputs, sedimentation and burial, and assimilation and retention of N by flora and fauna.

3.1. Forest Soil N Transformations

3.1.1. Nitrogen Fixation

N_2-fixation rates are highest on algal/bacterial crusts growing on tree stems (Table 2), although the few measurements preclude meaningful statistical analyses. One-way analysis of variance on ranks ($H = 46.082$; $p < 0.001$) followed by Dunn's method (Q) indicate significant differences between rates measured on the soil surface and the other forest vegetation. Rates of N_2-fixation on pneumatophores and prop roots are significantly greater than on the soil surface and vegetation components (Q values = 3.757–4.743; $p < 0.001$), except for belowground roots and rhizomes. Although few measurements have been made on vegetation and cyanobacterial mats, N_2-fixing microbial communities associated with roots, stem surfaces, and cyanobacterial mats may provide significant input of N to mangrove forests.

Table 2. Rates of nitrogen fixation (mg N m^{-2} d^{-1}) at the mangrove soil surface, cyanobacteria mats, aboveground roots (pneumatophores and prop roots), belowground roots and rhizomes, litter and senescent leaves lying on the forest floor, and microbial crusts on the bark of tree stems [1,4,9,55–58,129–161] and earlier references within. Rates presented on a g^{-1} DW/WW basis were converted to m^{-2} assuming 1 g matter = 1 cm^{-3}. Ethylene rates were converted to N using the theoretical factor of 3 C_2H_2 molecules = 1 N molecule [162].

Component	Number of Observations	Mean ± 1 SE	Median	Range
Soil surface	57	8.22 ± 1.69	3.22	0–58.92
Cyanobacteria mats	28	9.69 ± 2.62	3.43	0–60.42
Aboveground roots	18	31.78 ± 5.63	26.25	2.77–73.4
Belowground roots + rhizomes	15	6.21 ± 1.65	4.50	1.04–26.20
Litter	9	1.16 ± 0.40	0.45	0.21–3.30
Senescent leaves	7	0.75 ± 0.13	0.83	0.39–1.20
Stem bark	5	100.95 ± 36.42	100.95	17.40–201.20

3.1.2. Within-Soil Transformations

Denitrification has been measured often in mangrove soils, mostly within the upper 5–20 cm (only complete (to N_2 production) denitrification rates were considered, Table 3). Gross rates of soil ammonification are significantly greater than net ammonification rates (one-way ANOVA on ranks, $H = 33.483$; Dunn's $Q = 5.786$; $p < 0.001$). There are no significant differences between gross and net rates of soil nitrification, although mean rates of gross nitrification are nearly three times greater than net rates (Table 3), indicating significant N immobilization. Although some studies found that anammox is a minor transformation process in mangrove soils compared to complete denitrification (references in Table 3), the available data (Table 3) show no significant differences between rates of both processes (one-way ANOVA on ranks, $H = 0.788$; $p = 0.375$). Rates of microbial N metabolism depend on many drivers, including temperature, soil fertility, microbial community structure, plant metabolism and root activities, bioturbation, intertidal position, and salinity. There is evidence that other N-transforming bacterial and archaeal groups (see Section 3) are present in mangrove soils, but no rate data are available for processes, such as methane denitrification, nitrite oxidation and phototrophic nitrate oxidation.

Table 3. Rates of N transformation processes (mg N m^{-2} d^{-1}) in mangrove soils. All rates are to soil depths of 5–20 cm. Rates presented on a g^{-1} DW/WW basis were converted to m^{-2} assuming 1 g soil = 1 cm^{-3}. Abbreviations: DNRA= dissimilatory nitrate reduction to ammonium; anammox = anaerobic ammonium oxidation. Source: [9,15,55–58,129,133–192].

Transformation Process	Number of Observations	Mean ± 1 SE	Median	Range
Denitrification (complete)	165	26.25 ± 3.34	3.90	0–443.52
Gross ammonification	17	301.63 ± 50.90	267.40	77.40–898.80
Net Ammonification	52	31.40 ± 6.19	15.40	0.17–200.00
Gross nitrification	25	15.08 ± 5.81	4.74	0–141.00
Net nitrification	37	5.80 ± 1.20	1.93	0–30.80
Anammox	35	22.11 ± 5.49	4.35	0–99.4
DNRA	21	18.19 ± 6.77	4.54	0.01–108.64

3.1.3. NO, N_2O and DN Fluxes from Surface Soils

Only two measurements at one site have been made of NO fluxes across the soil–air interface (Table 4); both indicate negligible release. Rates of N_2O flux show a net mean flux to the atmosphere, although some measurements indicate net uptake by mangrove soils (Table 4).

Rates of DON, NO_2^- + NO_3^-, and NH_4^+ (Table 4) flux vary widely among forests, due mostly to differences between fluxes measured in light (clear) versus dark (opaque) chambers. Most measurements from light bottles show net uptake of solutes indicating utilization of dissolved nutrients in overlying tidal waters by microalgae, cyanobacteria, and other autotrophs on the mangrove soil surface. This fact is reflected in the mean rates of exchange being negative for all three dissolved N forms. Due to high variation, all three solutes appear to be utilized equally by benthic autotrophs.

Table 4. Estimates of net NO and N_2O gas and dissolved nitrogen fluxes across the mangrove soil surface. Units = mg N m^{-2} d^{-1}. Negative values indicate fluxes into the soil and positive values indicate fluxes from the soil to the overlying tidal water/ atmosphere. Source: [9,164,165,167,169,176,184,193–210].

Gas and Solute Soil Fluxes	Number of Observations	Mean ± 1 SE	Median	Range
N_2O soil–air flux	69	0.60 ± 0.17	0.22	−2.03–9.01
NO soil–air flux	2	0.05 ± 0.009	0.05	0.04–0.06
DON soil–water flux	41	−18.29 ± 18.14	0.00	−743–19.6
NO_2^- + NO_3^- soil–water flux	66	−4.46 ± 1.05	−0.24	−29.04–3.36
NH_4^+ soil–water flux	78	−1.48 ± 2.20	−0.16	−88.7–55.19

4. Tidal Water N Processes

4.1. N_2O Fluxes

Fluxes of N_2O in mangrove tidal waters have been measured in more than 30 mangrove-fringed estuaries, tidal creeks, and waterways for a total of 62 measurements [211–226]. Net flux is to the atmosphere, averaging (±1 SE) 0.11 ± 0.03 mg N m^{-2} d^{-1} with a median of 0.02 mg N m^{-2} d^{-1} and ranging from net uptake (−0.06 mg N m^{-2} d^{-1}) to net release (1.32 mg N m^{-2} d^{-1}).

4.2. Tidal Exchange

Rates of exchange between mangrove forests and adjacent tidal waterways vary greatly within and among sites, as reflected in the wide range of estimates for NH_4^+, NO_2^- + NO_3^- and DON flux (Table 5). Despite the variability, net exchange is into the mangroves for all DN species based on mean rates; median rates indicate little net exchange (Table 5). The behavior of DN in transport between tidal waters and mangroves depends on a wide range of factors, including tidal prism, geomorphology, climate, seasonal weather patterns, the ratio of forest to waterway area, temperature, salinity, pH, dissolved oxygen levels, and plankton metabolism [1,3,4].

Table 5. Rates of NH_4^+, DON and $NO_2^- + NO_3^-$ exchange between mangrove forests and adjacent tidal waterways, including mangrove-fringed estuaries. Source: [1,4,227–241] and references within. Import into the mangroves is shown as a negative value and export to adjacent tidal waters is a positive value. Units = mg N m^{-2} water d^{-1}.

Component	Number of Observations	Mean ± 1 SE	Median	Range
NH_4^+ import	26	−9.81 ± 4.35	−1.57	−100.76–−0.006
NH_4^+ export	23	8.00 ± 3.63	0.39	0.03–62.40
NH_4^+ net exchange	49	−1.45 ± 3.12	−0.01	−100.76–62.4
DON import	9	−4.69 ± 2.17	−2.87	−21.84–−0.91
DON export	10	1.45 ± 0.33	1.37	0.08–3.27
DON net exchange	19	−1.46 ± 1.24	0.08	−21.84–3.27
$NO_2^- + NO_3^-$ import	24	−3.62 ± 1.52	−0.73	−28.80–−0.003
$NO_2^- + NO_3^-$ export	27	1.84 ± 0.55	0.29	0.05–11.90
$NO_2^- + NO_3^-$ net exchange	51	−0.73 ± 0.85	0.08	−28.8–11.90

5. An Ecosystem-Level View of Mangrove Forests: A N Budget

Using the data in the preceding tables, a preliminary N budget for the world's mangrove forests was constructed (Figure 4). The mean values used in the budget are not absolute, but the budget is an instructive research tool to pinpoint the major and minor pathways and transformations of N flow in mangrove ecosystems, and will help to identify where further research is needed.

The budget was constructed based on several assumptions: (1) the current (2014) global mangrove area is 86,495 km^2 [242]; (2) although mangrove tidal creeks and waterways are only a small fraction of total mangrove area, the total global mangrove area was used to calculate all tidal exchanges because the data includes many measurements taken from mangrove-fringed estuaries that are likely in toto to be of equivalent area; (3) litter export (PON) was estimated by converting litter C export [243] to N assuming a litter C/N of 79.4 (Table 1); (4) wood, litter, root and benthic microalgal NPP were estimated by converting the C values in [243] using the C/N ratios (*g*/*g*) in the Table 1 legend and using a microalgal C/N ratio (*g*/*g*) of 12 [244]; (5) standing stocks of soil and belowground roots and aboveground forest were derived from Figure 2; (6) the input of the total belowground root + soil pool (441,150 Gg N) to N burial (1127 Gg a^{-1}) was estimated by the difference between the mean N burial value (1239 Gg a^{-1}) minus the inputs from root production (62 Gg a^{-1}) and litter production (50 Gg a^{-1}); (7) wet N deposition was estimated from the only two studies available [4,245]; and (8) the differences between gross and net ammonification and nitrification represent N immobilization.

Not included in the budget are: (1) direct inputs from groundwater and upstream; (2) marine and terrigenous particle flux and deposition at the soil surface; (3) pelagic and benthic production; (4) dry deposition; (5) consumption and assimilation by fauna and flora; (6) N_2-fixation on tree stems, cyanobacterial mats, aboveground roots, senescent leaves and litter; the latter are not included because of the inability to extrapolate these rates to more than a small area given the lack of knowledge of their areal coverage in a "typical" mangrove forest, and (7) rates of soil N transformations such as ammonification and denitrification likely account for only a part of total N flux in soils as most studies measured these rates only to soil depths of 5–20 cm. C mineralization is active to a soil depth of 1 m [243], so it is likely that significant N mineralization occurs in deeper soils.

Further, mangroves differ in their location and climate, and N-cycle pathways are significantly affected by physicochemical and biological factors, such as temperature, grazing, presence of biogenic structures, tides, pH, soil nutrients, soil type and rate of N input. Such variations have not, of course, been included in the mass balance, but must be kept in mind when considering the N cycle in mangroves. Thus, individual mangrove forests and ecosystems vary significantly from the global averages used here. For example, N cycling in a tropical mangrove ecosystem that is mature and luxuriant in terms of biomass and productivity is almost certainly to be more rapid and complex that N transformations in a subtropical fringing forest that is younger, less productive and smaller in terms of biomass.

Despite these significant shortcomings, the budget does suggest rapid rates of N cycling and transformations in mangrove forests, especially in the soil. Burial equates to about 29% of total N inputs. Net tidal exchange of dissolved N is into the forest or near zero, indicating N conservation. Anammox is as important a transformation process as denitrification. Denitrification equates to 35% of total N input, within the range found in other coastal ecosystems [246]. Net immobilization (8825 Gg N a^{-1}) is the single largest transformation process, underscoring its significance in conserving N in mangrove soils. In terms of N, benthic microalgae appear to be the most important primary producers, although the cyanobacterial mats are not represented. Net uptake of dissolved N by soils from overlying tidal waters is a significant N conservation mechanism, likely reflecting uptake by algae, cyanobacteria and other autotrophs on the soil surface. Alongi [11] measured high rates of dissolved N uptake by stems, logs, prop roots, and twigs, supporting the idea that microbial communities on these surfaces also function as an N conservation mechanism.

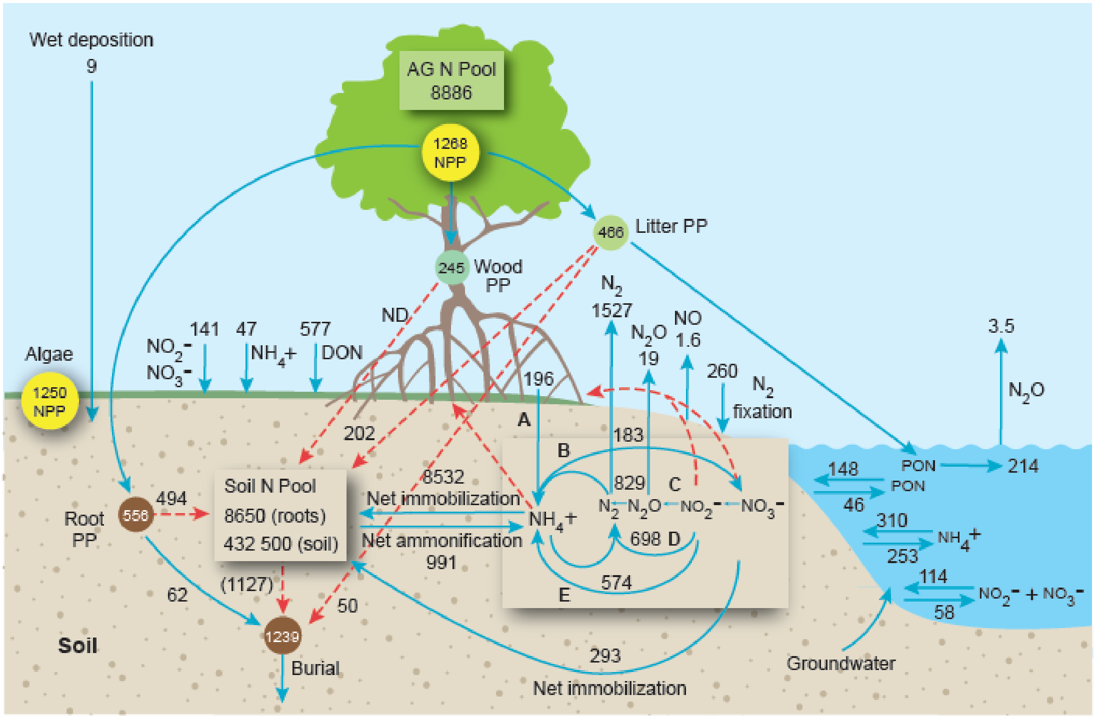

Figure 4. Nitrogen cycling in the world's mangrove ecosystems. Mean fluxes = Gg N a^{-1}; mean standing stocks = Gg N. The model assumes a global mangrove area of 86,495 km^2 [242]. Soil N transformations are lettered as: (**A**) root + rhizome N_2-fixation; (**B**) net nitrification; (**C**) denitrification; (**D**) anammox; (**E**) dissimilatory nitrate reduction to ammonium. Dashed red arrows represent mean values estimated indirectly (by difference); solid blue arrows represent mean values based on empirical measurements (see text for explanation and references). The N pool (both roots and soil) in soils to a depth of 1 m is presented as a box on left in the forest floor. N transformation in soils to depths of 5–20 cm is presented as a box on the right in the forest floor. Unquantified inputs and outputs of dissolved nitrogen from land-derived groundwater and organic matter inputs from adjacent marine waters and catchments are not represented. Abbreviations: ND = no data; AG N Pool = aboveground forest N biomass pool; PP = primary production; NPP = net primary production; NO_2^- + NO_3^- = nitrite plus nitrate; NH_4^+ = ammonium; N_2 = gaseous nitrogen; N_2O = nitrous oxide; NO = nitric oxide; PON = particulate organic nitrogen.

The budget indicates a burial efficiency (burial/total input × 100) of 29% and a mineralization efficiency (gross ammonification-net ammonification/total input × 100) of 141%, which will be more realistically lower when other inputs (e.g., N_2-fixation from stems, etc.) are eventually included. In any case, it appears that soil N is very efficiently mineralized, as found in individual forests in

Asia [9,57,58,136]. For instance, in Chinese mangroves (*Kandelia candel*), burial efficiencies ranged from 8 to 31% and mineralization efficiencies from 69 to 92% [9]. In Thai mangroves, N burial efficiencies ranged from 4 to 12% and N mineralization efficiencies from 68 to 88% [57] and in Malaysian forests [136] burial and mineralization efficiencies ranged from 10 to 29% and 67 to 81%, respectively.

A mass balance of all inputs and outputs (Table 6) indicates a net positive gain of 957.9 Gg N a^{-1} which equals 12% of all inputs and outputs, well within the sum of systematic errors of the many measurements made of N cycling. Considering that several important processes are not included, it is possible that N flow in mangrove ecosystems may be in approximate balance. However, considering the high rates of N_2-fixation on tree stems, cyanobacterial mats, aboveground roots, senescent leaves and litter, it is likely that ecosystem N inputs would need to be revised upwards when further studies with a proper sampling design incorporating the great spatial variability of this process (coupled to an appropriate computer algorithm) would warrant their inclusion in the N budget. The budget would be unbalanced with a larger net positive gain, but consumption and assimilation of these unquantified N_2-fixers by mangrove-associated fauna would perhaps redress the imbalance. Many organisms such as gastropods and other benthic invertebrates commonly dwell on tree stems, cyanobacterial mats, prop roots, pneumatophores, leaves and litter and readily consume organic particles, micro- and macroalgae, bacteria, and detritus on these surfaces [1,2]. Further, as pointed out by Reis et al. [247], N cycling in mangroves is unbalanced when forests are subjected to additional nutrients from anthropogenic sources, such as effluents from aquaculture ponds and human and animal sewage, so only relatively pristine mangroves would be expected to exhibit balanced N flow.

Table 6. A nitrogen mass balance of the world's mangrove ecosystems. Units = Gg N a^{-1}. Values are from Figure 4.

Inputs		Outputs	
Component	**Gg N a^{-1}**	**Component**	**Gg N a^{-1}**
Net primary production	1250	Burial	1239
Wood	245	Soil NO release	1.6
Litter	466	Soil N_2O release	19
Roots	556	Denitrification/Anammox	1527
Microalgae	1250	Water-air exchange	
N_2-fixation		N_2O	3.5
Roots	196	Tidal exchange	
Soil	260	DON	58
Precipitation	9	$NO_2^- + NO_3^-$	46
Tidal exchange		NH_4^+	253
DON	148	PON	214
$NO_2^- + NO_3^-$	114		
NH_4^+	310		
Soil-Water exchange			
DON	577		
$NO_2^- + NO_3^-$	141		
NH_4^+	47		
Total	4319	TOTAL	3361.1
Inputs − Outputs = 957.9 (Net Gain)			

At the global scale, mangroves contribute variable percentages of N to the coastal ocean. Mangrove PON export (2474 kg N km^{-2} a^{-1}) equates to 95% of PON export (2612 kg N km^{-2} a^{1}) from the world's major tropical rivers. However, most rivers in low latitudes have not been measured for PON export [248] so the true contribution is probably considerably smaller. Mangrove PON export accounts for only 1.5% of the entire world's river discharge [249]. The contributions of mangrove N_2O emissions, denitrification, and burial to the global coastal ocean [250] are modest (0.4%, 0.5–2.0% and 6%, respectively), but are disproportionate relative to their small area (0.31%) [251].

6. Conclusions

N cycling in mangrove forests and associated tidal waterways is complex, with rapid turnover of low concentrations of dissolved N but slow turnover of particulate N; 96% of the latter is stored in soils with a total N stock of global mangrove forests of 52.03 Mg N ha^{-1} which is considerably greater than their tropical terrestrial counterparts (22.33 Mg N ha^{-1}). The largest sources of N are nearly equal amounts of mangrove net primary production and production of benthic microalgae, the latter being a major source of nutrition for most mangrove-associated fauna. These benthic autotrophs are likely responsible for the net uptake of dissolved N species, mostly in the form of DON. Tides exchange dissolved and particulate N, with net uptake of dissolved N by mangroves and net release of particulate N as litter. N_2-fixation is an underestimated source of N; very high rates of N_2-fixation have been measured on tree stems, aboveground roots, and cyanobacterial mats but due to their very high patchiness and the lack of data to extrapolate beyond a small area, their contribution is unquantifiable at the whole-forest scale. Net immobilization, estimated as the difference between gross and net ammonification and nitrification, is the single largest (8825 Gg N a^{-1}) flux, reflecting its significance in conserving N. Denitrification is the largest loss pathway, equating to 35% of total N input, which is within the range measured in other coastal ecosystems. Burial in soil equates to about 29% of total N inputs and is the second largest loss of N. Overall, total inputs (4319 Gg N a^{-1}) slightly exceed total outputs (3361 Gg N a^{-1}) at present, suggesting net balance of N flow in mangrove ecosystems. Globally, mangrove PON export (2474 kg N km^{-2} a^{-1}) equates to 95% of PON export (2612 kg N km^{-2} a^{-1}) by the world's major tropical rivers; mangrove PON export accounts for only 1.5% of the entire world's river discharge. The contributions of mangrove N_2O emissions, denitrification, and burial to the global coastal ocean are modest (0.4%, 0.5–2.0% and 6%, respectively), but are disproportionate relative to their small area.

Despite these findings, many aspects of nitrogen flow in mangroves need to be properly quantified. These include: (1) the need to develop formulae to extrapolate N_2-fixation rates on stems, aboveground roots and cyanobacterial mats to the whole-forest scale; (2) measurement of N transformation processes in soils deeper than 20 cm; (3) direct groundwater inputs and inputs from upstream and marine sources, including deposition at the soil surface; (4) the contribution of fauna in N cycling, especially benthic crabs, epiphytes and plankton; and (5) wet and dry deposition.

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