Plant Soil (2017) 410:1–19
DOI 10.1007/s11104-016-3123-7

MARSCHNER REVIEW

Global overview on nitrogen dynamics in mangroves and consequences of increasing nitrogen availability for these systems

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Received: 6 June 2016 / Accepted: 20 November 2016 / Published online: 14 December 2016

Abstract

Background and scope Mangroves provide several ecosystem goods and services to society. However, mangroves are frequently subjected to land conversion, overharvesting, and pollution including increased nitrogen (N) availability. Aiming to provide useful information to predict effects of N enrichment on mangroves, we evaluated literature data on N transformation rates in sediment, dissolved N (DN) fluxes across the sediment-water interface, and natural abundance of N stable isotopes ($\delta^{15}N$) in the sediment-plant system in conserved mangroves and those subjected to anthropogenic N enrichment.

Conclusions Mangroves and terrestrial tropical forests exhibit a great overlap in rates of biological N fixation (BNF) and denitrification and nitrous oxide flux rates. Mangroves can be highly efficient users of DN forms from tidal waters, related to rapid plant uptake and an efficient conservation of DN in sediment by microbial activity. The main factors limiting N transformation rates in mangrove sediment are inorganic DN availability and microbial immobilization. The $\delta^{15}N$ data indicated that fringe forests exhibit higher N transformation rates in sediment and higher N losses to atmosphere, compared to other mangrove types. Except for BNF, all other N transformation and flux rates seem to be intensified by increasing N availability.

Keywords Biological nitrogen fixation · Nitrogen mineralization · Sediment-water interface fluxes · Denitrification · Nitrous oxide · Nitrogen stable isotopes

Abbreviations

ARA	Acetylene reduction activity
BNF	Biological nitrogen fixation
C	Carbon
DIN	Dissolved inorganic nitrogen
DN	Dissolved nitrogen
DOC	Dissolved organic carbon
DON	Dissolved organic nitrogen
HC	Heterocystous cyanobacteria
H_2S	Sulfide
N	Nitrogen
NH_3^+	Ammonia
NH_4^+	Ammonium
NO_2^-	Nitrite
NO_3^-	Nitrate
NO_x^-	Nitrite plus nitrate
N_2	Atmospheric nitrogen
N_2O	Nitrous oxide
$\delta^{15}N$	Nitrogen stable isotope ratio
O_2	Oxygen
P	Phosphorus
PN	Particulate nitrogen

Responsible Editor: Philippe Hinsinger.

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Introduction

Mangroves are intertidal coastal wetlands colonized by a group of 62 plant species in the Indo-West Pacific and only 12 species in the Atlantic and Eastern Pacific, including trees, shrubs, a palm, and a ground fern (also termed mangroves) sharing adaptations to periodic flooding, highly variable salinities, and oxygen depleted sediments (Spalding et al. 2010; Schaeffer-Novelli et al. 2000). There are about 152,000 km^2 of mangroves distributed in 123 countries and territories of tropical, subtropical and warm temperate regions. Despite their broad distribution, only 12 countries have about 68% of the world's mangroves, with the top three being Indonesia (31,894 km^2), Brazil (13,000 km^2), and Australia (9,910 km^2) (Spalding et al. 2010). Mangroves originally occupied more than 200,000 km^2 of coastlines (Spalding et al. 2010). However, about 25 to 35% of mangrove forest area has already been lost due to land conversion to aquaculture, agriculture, urbanization, tourism, overharvesting, and pollution (Valiela et al. 2001; Alongi 2002; van Lavieren et al. 2012). Beyond these regional pressures affecting mangrove forests around the world, these ecosystems are also threatened by human-induced global environmental changes such as climate change and the associated sea-level rise (e.g., Alongi 2008; Gilman et al. 2008; Lovelock et al. 2015), and the increased reactive nitrogen creation related to the large-scale use of nitrogen (N) fertilizers, legume cultivation, and N emissions to the atmosphere during fossil-fuel combustion (Bleeker et al. 2011; see also Erisman et al. 2008),

Nitrogen availability strongly regulates the structure and functioning of both terrestrial and aquatic ecosystems (Elser et al. 2007; Lebauer and Treseder 2008; Chapin et al. 2011). Nitrogen enrichment is therefore recognized as one of the major threats to conservation of natural ecosystems and maintenance of human activities (Rockström et al. 2009; Erisman et al. 2013). In terrestrial ecosystems, the excess of N favors biological invasions and modifies the competitive ability among species, resulting in changes of dominance patterns, and loss of plant and soil biota biodiversity (e.g., Bobbink et al. 2010; Bradley et al. 2010; Eisenhauer et al. 2012). Nitrogen enrichment in terrestrial ecosystems also has the potential to increase soil N mineralization rates, nitrous oxide (N_2O) emissions to atmosphere, and nitrate (NO_3^-) losses to aquatic systems, modifying productivity patterns and increasing mortality (e.g., Fenn et al. 1998; Matson et al. 1999). Biodiversity loss associated with alterations in ecosystems functioning may adversely affect the provision of important ecosystem services to society (Díaz et al. 2006; Chapin et al. 2000; Comptom et al. 2011).

Mangroves potentially play an important role in the global context of N enrichment. They provide many ecosystem goods and services to society, which can be impaired by increasing N availability, including the following: (1) support of coastal fisheries by providing food, shelter, and/or nursery grounds for commercially important species that spend at least part of their life cycle in mangroves (e.g., Mumby et al. 2004; Crona and Rönnbäck 2005; Aburto-Oropeza et al. 2008); (2) access to food sources (e.g., fish, molluscs, crustaceans, fruits, sugar, and honey), wood products (firewood, charcoal, and timber for construction), and non-wood products (e.g., thatch, fodder, tannins, wax, dyes, and herbal remedies) associated with the livelihood of human communities living in or near mangroves (e.g., Bandaranayake 1998; Glaser 2003; Walters et al. 2008; Hussain and Badola 2010; Warren-Rhodes et al. 2011; Baba et al. 2013); (3) trapping and storage of sediment, organic matter, nutrients, and heavy metals from surrounding waters originating from anthropogenic sources (e.g., Tam and Wong 1995, 1996; Alongi and Mckinnon 2005; Jordan et al. 2011); and (4) efficient carbon (C) sequestration because of high primary productivity and C allocation in belowground biomass, low sediment respiration rates, substantial long-term organic C burial in sediments, and considerable exportation of refractory dissolved organic C to the ocean, contributing to the C burial in marine sediments (e.g., Komiyama et al. 2008; Kristensen et al. 2008; Donato et al. 2011; Duarte et al. 2013). In addition, mangrove forests are the only forest formations occurring in the confluence of terrestrial, marine, and freshwater systems (Alongi 2002). Therefore, alterations in mangroves functioning as a consequence of N enrichment may affect not only the important ecosystem goods and services they provide to society but also affect surrounding ecosystems.

There are still many knowledge gaps in the functioning of mangroves that need to be addressed to allow us to infer the consequences of global environmental changes to mangroves and the ecosystem goods and services they provide. Among these gaps are included N dynamics and alterations following N enrichment in the different types of mangroves. In the Americas, at the local scale, two main types of mangrove forests (fringe and basin) are currently recognized by physiographic aspects determined by water flow and the type of landform occupied, but some authors have also recognized other subtypes of mangroves (riverine, overwash, dwarf, and scrub) (Schaeffer-Novelli et al. 2000). Fringe forests develop on inclined slopes bordering estuaries, deltaic channels, coastal lagoons, and rivers (termed as riverine), under great influence of tidal flushing or river discharge. Overwash designates small self-enveloping fringe islands entirely covered by water during high tide. Basin forests develop in shallow depressions of more inland areas flooded by spring tides, seasonal sea level elevations, or freshwater pulses. At basin stands, water moves slowly as sheet flows maintaining waterlogged conditions for long periods of time. Dwarf is a subtype of basin forest that develops in carbonate or deep peat sediments and exhibit low stature (usually up to 1.5 m) stunted by nutrient limitations. The term "scrub" is employed as a descriptor of both fringe and basin forests of reduced structural development imposed by other stressors than nutrient limitations (Schaeffer-Novelli et al. 2000, 2005; Spalding et al. 2010). Currently, there are no data on the extension area occupied by each mangrove physiographic type in the Americas, but fringe forests are usually more conspicuous formations, while basin forests occupy smaller inland areas in coastal systems. However, there are places where dwarf mangroves are found occupying extensive areas such as in southern Florida (Davis et al. 2003), Panama (Lovelock et al. 2005), and Belize (Feller 1995). These mangrove types differ in water movement, hydroperiod, edaphic conditions, and inputs of freshwater and nutrients, which result in differences of structural development (Schaeffer-Novelli et al. 1990, 2000; see Cunha-Lignon et al. 2011) and of nutrient dynamics and ecosystem functioning (e.g., Twilley et al. 1986a; Twilley 1988; Rivera-Monroy et al. 1995a; Rivera-Monroy and Twilley 1996). These mangrove types may, therefore, exhibit different responses to N enrichment, which can also modulate different responses to climatic changes.

In order to provide useful information for the discussion about the major consequences of N enrichment on mangroves, here we provide an updated overview on the general patterns of N dynamics in mangrove forests from previous synthesis and advance: 1. At regional scale on the understanding of N dynamics in mangroves by evaluating differences in N dynamics between mangrove physiographic types in the Americas and 2. At global scale on major alterations of N dynamics following N enrichment, identified with an extensive review of the literature and evaluation from a global database.

Material and methods

The search for publications was performed in the databases of Springer (http://www.springer.com), JSTOR (http://www.jstor.org), and Web of Science (http://thomsonreuters.com/web-of-science) using the word "mangrove" in keyword, title, and abstract searches. From the resulting lists, publications containing information on N dynamics in conserved and subjected to anthropogenic N enrichment mangroves were selected and data of N transformation rates in sediment (biological nitrogen fixation, mineralization, ammonification, nitrification, denitrification, and volatilization), N fluxes across the sediment-water interface, and natural abundance of N stable isotopes ($\delta^{15}N$) in the sediment-plant system were collected and tabulated. Data published as figures were extracted using the software Plot Digitizer 2.6.3 (Huwaldt and Steinhorst 2013). To expand the search, each publication had its reference list assessed as well as the new publications obtained until no additional item was found. Data of sediment within mudflats, tidal creeks or coastal lagoons were not included. The biological N fixation data published as acetylene reduction activity (ARA) rates were converted to N fixation rates using the conversion factor of 4 (C_2H_4:N_2 ratio of 4:1) (Postgate 1982), which is a reasonable assumption for mangroves, since studies using $^{15}N_2$ calibration have shown ratios ranging from 1.9 to 6.3 (Potts 1984; Hicks and Silvester 1985). In all, data were obtained from 62 studies, but also data from previous reviews by Howarth et al. (1988), Alongi et al. (1992), and Purvaja et al. (2008), totaling 123 mangrove sites comprising areas in the Atlantic Ocean, Caribbean Sea, Gulf of Mexico, and Indo-Pacific coasts (Fig. 1). The countries with a greater number of study sites include Australia (22), India (21), the United States of America (18), Belize (12), Puerto Rico (10), China (7), and Papua New Guinea (7). Other countries had four or fewer study sites each. Data from N-enriched mangrove stands included sites affected by sewage pollution (Corredor and Morell 1994; Corredor et al. 1999; Kreuzwieser et al. 2003; Allen et al. 2007; Purvaja et al. 2008; Chen et al. 2010, 2012), fertilizers from agriculture (Kreuzwieser et al. 2003; Chauhan et al. 2008; Chen et al. 2012), aquaculture pond effluent (Alongi et al. 2005; Chauhan et al. 2008; Chen

Fig. 1 Location of the 123 study sites considered in this review from studies that quantified nitrogen cycling and flux rates and the natural abundance of nitrogen stable isotopes in mangroves. Because of the map scale, nearby study sites were overlaid

et al. 2012), and ferromanganese mine discharge effluent (Fernandes et al. 2010; Fernandes and LokaBharathi 2011; Fernandes et al. 2012a, 2012b), and also mangrove stands that were sites of a failed shrimp farm (Alongi et al. 2002). Data of tropical terrestrial forests are presented for comparative purposes since they are well recognized as being the most productive forested ecosystems on Earth (see Chapin et al. 2011) with the highest rates of N cycling (Vitousek and Sandors 1986; Martinelli et al. 1999; Vitousek et al. 2002). For data analysis, normality was evaluated using the Shapiro-Wilk *W*-test. Comparisons between two data groups were performed using the non-parametric Mann-Whitney *U*-test. Comparisons between more than two groups were assessed by the nonparametric test of Kruskal-Wallis *H*-test followed by post hoc pairwise comparisons as described by Siegel and Castellan (1988). Statistical analysis was performed using the software R (R Core Team 2014). Differences at the 0.05-level were considered significant.

Results and discussion

Biological N fixation

One of the main pathways by which N enters mangrove ecosystems is biological N fixation (Alongi 2002, 2009), the process whereby atmospheric N (N_2) is reduced to ammonia (NH_3^+) carried out by microorganisms that possess the nitrogenase enzyme complex (termed as diazotrophs). Biological N fixation (BNF) has been detected in mangrove stands associated with plant roots (associative BNF) and free in sediments, microbial mats (i.e., centimeter-thick multilayered structures of microorganisms as defined by Reitner 2011), leaf litter (and senescent leaves incubated on sediment), pneumatophores, and cyanobacterial crusts growing on trunks (free-living BNF) (Fig. 2), at rates that overlap those reported for tropical terrestrial forests. Mean estimates of free-living BNF in tropical terrestrial forests (including rainforests, deciduous forests, and forested floodplains) fall within 0.9 and 2.1 $mgN.m^{-2}.d^{-1}$ with rates ranging from 0.03 to 16 $mgN.m^{-2}.d^{-1}$ (Reed et al. 2011). There is a wide range of rates of BNF in symbiotic associations with plant roots reported for tropical terrestrial forests, from 0.07 to 66.5 $mgN.m^{-2}.d^{-1}$, but global estimates fall within 1.5 to 16.6 $mgN.m^{-2}.d^{-1}$ (Sylvester-Bradley et al. 1980; Cleveland et al. 1999; Reed et al. 2011; Sullivan et al. 2014). Comparisons to associative BNF rates in mangroves, from which plants can also directly benefit, are difficult due to the reduced number of estimates reported on an areal basis for mangroves. Nevertheless, these estimates range from 2 to 10 $mgN.m^{-2}.d^{-1}$, falling within the global estimates range of symbiotic BNF in tropical terrestrial forests. There was no evidence of regional differences in BNF rates from our database. However, negligible and highly variable rates were often reported (e.g., Nedwell et al. 1994; Alongi et al. 2004a; Romero et al. 2012), so that not all mangroves may sustain high BNF rates, such as the Australian mangroves studied by Alongi (2013).

Several factors that can regulate aboveground BNF rates in mangroves have been reported. Potts (1979) pointed out reduced light intensity, water content, and phosphorus (P) availability, as well as photorespiration and to a lesser extent endogenous oxygen (O_2) production and reduced dissolved organic C (DOC) availability constrained N fixation rates in heterocystous cyanobacterial (HC) communities on pneumatophores of *Avicennia marina* (Forssk.) Vierh. in mangrove stands in Sinai, Egypt. Sheridan (1991, 1992) demonstrated that high salinity and low percent moisture restricted N fixation rates in HC communities growing on trunks of *Avicennia germinans* (L.) L. in mangrove stands in Guadeloupe, Lesser Antilles. Joye and Lee (2004) and Lee and Joye (2006) found that light intensity, endogenous O_2 production, water content, sulfide (H_2S) concentration, DOC availability, and the dominance by HC or non HC species regulated N fixation rates in mangrove microbial mats in Twin Cays, Belize. BNF rates were enhanced after DOC amendments, which was attributed to stimulation of O_2 respiration and, consequently, of H_2S oxidation and alleviation of H_2S-inhibition, as well as stimulation of heterotrophic N fixation. Gotto and Taylor (1976) and Pelegrí and Twilley (1998) reported an O_2 suppression and a C stimulation, respectively, of BNF rates in leaf litter from mangrove sites in Florida, US, while Zuberer and Silver (1978) and Hicks and Silvester (1985) found no effect of these factors on BNF rates in mangrove leaf litter from Florida and Auckland, New Zealand, respectively. These conflicting results on factors regulating N fixation in mangrove leaf litter may rely on the community type of N fixers, which seems to be more variable for leaf litter than other mangrove compartments (see Gotto and Taylor 1976; Hicks and Silvester 1985; Pelegrí et al. 1997; Pelegrí and Twilley 1998).

On the other hand, only few studies investigated factors regulating N fixation rates in mangrove belowground compartments. Zuberer and Silver (1978) and Pelegrí and Twilley (1998) reported marked increases in BNF rates in sediment after C sources amendments in mangrove stands in Florida. Because of the relatively long lag periods before BNF rate enhancement following C additions (12 to 24 h), Zuberer and Silver (1978) suggested that the increase in BNF rates would primarily result from diazotrophic population growth and/or nitrogenase synthesis, instead of an immediate increase in energy sources. Zuberer and Silver (1978) also added C sources to washed excised roots of *A. germinans, Rhizophora mangle* L., and *Laguncularia racemosa* (L.) C.F. Gaertn. seedlings but found no response, suggesting that the diazotrophic bacteria attached to mangrove roots may have had ample access to C and energy sources. Sengputa and Chaudhuri (1991) isolated and identified diazotrophic bacteria associated with root samples of several mangrove species including *Acanthus ilicifolius* L., *Avicennia spp.*, *Bruguiera spp.*, *Ceriops decandra* (Griff.) W. Theob., *Rhizophora mucronata* Lam., *Sonneratia apetala* Buch-Ham, *Aegialitis rotundifolia* Roxb., and *Excoecaria agallocha* L. from mangrove stands in Sundarban, India. There was no specificity of any of the bacterial isolates to any of the plant species. Regardless of plant identity, root samples from tidally inundated mangrove sites sustained higher BNF rates compared to root samples from occasionally inundated or drier highland sites. This was attributed to the presence of a larger number of more efficient N_2-fixing bacterial strains belonging to a greater number of O_2 response groups in the tidally inundated mangrove sites.

Comparing BNF rates on a dry-weight basis between mangrove compartments (Fig. 2), leaf litter sustained the highest "intrinsic capacity" of fixing N followed by roots and cyanobacterial crusts on trunks, while incubated senescent leaves, sediment, and pneumatophores exhibited the lowest dry-weight based rates ($H = 23.64$, $df = 5{,}54$, $p = 0.0002$). Pelegrí et al. (1997) and Pelegrí and Twilley (1998) also found higher BNF rates on a dry-weight basis for leaf litter (up to 0.09 $\text{mgN.g}^{-1}.\text{d}^{-1}$) compared to incubated senescent leaves (up to 0.01 $\text{mgN.g}^{-1}.\text{d}^{-1}$), sediments (up to 0.005 $\text{mgN.g}^{-1}.\text{d}^{-1}$), and pneumatophores (up to 0.0008 $\text{mgN.g}^{-1}.\text{d}^{-1}$) in mangrove stands at the Everglades National Park, with the latter two not significantly differing from each other. These differences in "intrinsic capacity" of fixing N can be related to differences in the community type of N fixers and in C availability between compartments. N fixation in mangrove sediment and roots are dominated by heterotrophic bacteria, and pneumatophores is dominated by cyanobacteria, while mangrove leaf litter seems to have a variable contribution of both groups. Mangrove leaf litter and roots were reported to provide

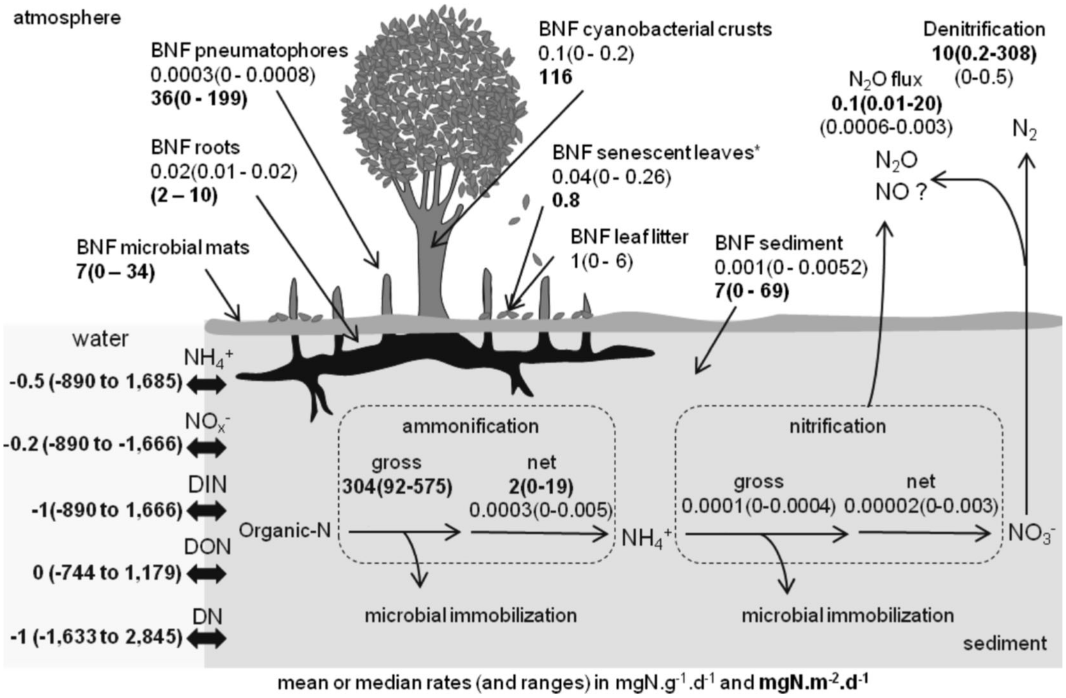

Fig. 2 Nitrogen cycling rates in mangroves. Median rates (and ranges) in mgN.g^{-1}.d^{-1} (unbold values) and mgN.m^{-2}.d^{-1} (bold values) are presented, including biological nitrogen fixation (BNF), nitrous oxide (N_2O) flux, and fluxes of ammonium (NH_4^+), nitrite plus nitrate (NO_x^-), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), and total dissolved nitrogen (DN) between mangrove sediment and overlying water. Negative values indicate net flux into the sediment. For BNF, mean rates are presented. * incubated on the forest floor. Source: Hesse (1961); Kimball and Teas (1975) *apud* Alongi et al. (1992); Gotto and Taylor (1976); Viner (1979) *apud* Howarth et al. (1988); van der Valk and Attiwill (1984); Hicks and Silvester (1985); Iizumi et al. (1986) *apud* Alongi et al. (1992); Myint et al. (1986) *apud* Alongi et al. (1992); Shaiful et al. (1986) apud Alongi et al. (1992); Kristensen et al. (1988); Mann and Steinke (1989) *apud* Alongi et al. (1992); Boto and Robertson (1990); Sengputa and Chaudhuri (1991); Sheridan (1991, 1992); Kristensen et al. (1992); Alongi et al. (1993); Nedwell et al. (1994); Rivera-Monroy et al. (1995a); Alongi (1996); Pelegrí et al. (1997); Woitchik et al. (1997); Kristensen et al. (1998); Pelegrí and Twilley (1998); Chen and Twilley (1999); Corredor et al. (1999); Alongi et al. (1999, 2000); Kristensen et al. (2000); Davis et al. (2001a, b); Bauza et al. (2002); Lugomela and Bergman (2002); Mohammed and Johnstone (2002); Muñoz-Hincapié et al. (2002); Kyaruzi et al. (2003); Kreuzwieser et al. (2003); Alongi et al. (2004a); Joye and Lee (2004); Lee and Joye (2006); Chauhan et al. (2008); Purvaja et al. (2008); Krishnan and LokaBharathi (2009); Chen et al. (2010); Fernandes et al. (2010, 2012a, 2012b); Romero et al. (2012); and Reis et al. (2016)

ample C sources for N fixation (in intermediate stages of leaf litter decay) while N fixation in sediment and pneumatophores were demonstrated to be C-limited (Zuberer and Silver 1978; Potts 1979; Pelegrí and Twilley 1998). Despite the differences in N fixing "intrinsic capacity", mangrove roots, pneumatophores, sediment, and microbial mats exhibited similar BNF rates on an areal basis, suggesting that these compartments make similar contributions to the total N input in mangroves ($H = 2.84$, $df = 3{,}51$, $p = 0.4167$). No BNF rates on an areal basis for mangrove leaf litter were found in the literature. Despite their high "intrinsic capacity" of fixing N, many mangroves exhibit low-standing leaf litter, ranging from about 0.02 to 5 Mg.ha^{-1} (Twilley et al. 1986b; Twilley et al. 1997), suggesting that the total contribution of leaf litter to N input in many mangroves can be low compared to other compartments.

N fluxes across the sediment-water interface

Another important pathway by which N enters (and leaves) mangrove ecosystems is tidal exchange (Alongi 2002, 2009). Several studies have attempted to determine whether mangroves act as an N sink or source for coastal waters, but results are often highly variable and controversial, especially regarding dissolved N forms (Adame and Lovelock 2011). Studies investigating dissolved N (DN) fluxes between mangrove sediment and overlying water based on direct measurements have shown that mangroves can be highly efficient users of DN forms from tidal waters (Fig. 2). Even when concentration gradients between porewater and overlying water suggested dissolved N release into overlying water, DN net fluxes were often negligible or into the sediment (e.g., Kristensen et al. 1988; Alongi et al. 1993; Kristensen et al. 1998). This ability has been attributed to a rapid uptake of DN by plants and benthic microalgae and an efficient conservation of DN in sediment by microbial activity (e.g., Kristensen et al. 1988; Alongi et al. 1993; Kristensen et al. 1998; Alongi 2013). Findings concluding that DN fluxes at the sediment-overlaying water interface are largely driven by sediment microbial activity include Stanley et al. (1987), who found measurable amino acid efflux from sediment only after poisoning microbial populations, and Alongi et al. (1993) and Mohammed and Johnstone (2002), who reported high DN fluxes into sediment associated with high microbial productivity and biomass, respectively. However, the range of DN flux rates were high, indicating that while some mangroves tend to act as net “sinks” for DN from tides, others may primarily export DN for adjacent water bodies. Studies that quantified DN fluxes between tidal creek or estuarine waters in mangrove areas and coastal or ocean waters indicated that mangroves can also act as a DN source for adjacent water bodies (Adame and Lovelock 2011).

N mineralization

Together with BNF and tidal exchange, N also becomes available to plants through N mineralization. It is the microbial mediated process by which organic N is converted to inorganic forms, including the steps of ammonium (NH_4^+) production termed ammonification, and NH_4^+ oxidation to nitrite (NO_2^-) and NO_3^- termed nitrification. Mangroves and tropical terrestrial forests differ in the most common DIN form in sediment and soil, respectively, NH_4^+ for mangroves (Alongi et al. 1992) and NO_3^- for tropical terrestrial forests (e.g., Reiners et al. 1994; Silver et al. 2000). However, net ammonification and nitrification rates on a weight basis reported for mangrove sediments (Fig. 2) overlap net N mineralization (−0.02 to 0.008 $mgN.g^{-1}.d^{-1}$) and nitrification rates (−0.002 to 0.005 $mgN.g^{-1}.d^{-1}$) reported for terrestrial tropical forests (Vitousek and Matson 1987; Luizão et al. 2004; Silver et al. 2005). The differences in magnitude between gross and net ammonification rates (i.e., gross production minus microbial immobilization) in mangrove sediments (Fig. 2) indicate that an efficient microbial immobilization of NH_4^+ may constrain net ammonification rates in mangrove sediment. Only Chen and Twilley (1999) investigated factors regulating net ammonification rates under natural conditions in mangroves. They found a very strong positive correlation of net ammonification rates with P availability in mangrove stands in Florida, suggesting a P-limitation of microbial activities. Factors limiting nitrification in mangroves have received little attention. Rivera-Monroy and Twilley (1996) conducted sediment incubation experiments with $^{15}NH_4^+$ and found that nitrification (coupled with denitrification) was constrained by NH_4^+ availability and microbial immobilization in sediment. Kristensen et al. (1998) reported higher potential nitrification rates with depth in vegetated-mangrove compared to non-vegetated tidal flat sediments from Phuket Island, Thailand. This was attributed to more oxic conditions provided by root activity in vegetated compared to non-vegetated sediments. Krishnan and LokaBharathi (2009), however, found that nitrification rates were regulated by Mn availability, suggesting the occurrence of anoxic nitrification at the expense of this element in mangrove sediments from Goa, India. Other factors reported to regulate nitrification rates by Krishnan and LokaBharathi (2009) were NH_4^+ and organic C availability, the latter as a C source for heterotrophic nitrifiers.

N losses to atmosphere

Besides N losses through tidal exchange, some microbial mediated N transformations in sediment also result in gaseous N losses from mangroves. Denitrification is the reduction process of NO_3^- and NO_2^- to N_2O and N_2 mainly. There are two types of denitrification: direct denitrification, which is supported by NO_3^- that diffuses from overlying water into sediment, and coupled denitrification, which is supplied with NO_3^- from nitrification. The differences in magnitude between denitrification and net ammonification and nitrification rates reported for mangrove sediments (Fig. 2) suggest that direct denitrification is an important pathway contributing to gaseous N losses in mangroves. Few studies investigated direct and coupled denitrification rates in mangrove sediment. Using ^{15}N enrichment techniques, Rivera-Monroy and Twilley (1996) found higher potential direct denitrification rates, up to 74 $mgN.m^{-2}.d^{-1}$, compared to potential coupled denitrification rates, up to about 10 $mgN.m^{-2}.d^{-1}$, in mangrove sediments from Isla del Carmen, Mexico. These authors also reported that in sediments subjected to $^{15}NH_4^+$ enrichment, none of the added ^{15}N was denitrified but was recovered in the non-extractable sediment N pool, suggesting that coupled denitrification rates were constrained by microbial immobilization of NH_4^+ and NO_3^- in sediment. Earlier, Rivera-Monroy et al. (1995b) reported that less than 10% of the $^{15}NO_3^-$ added to mangrove sediments was denitrified, while the remaining was recovered as particulate N (PN) in sediment, suggesting that direct denitrification rates were also constrained by NO_3^- availability and microbial immobilization in sediment. The denitrification and N_2O fluxes rates on areal basis reported for mangroves also greatly overlap denitrification (0.5 to 8.2 $mgN.m^{-2}.d^{-1}$) and N_2O fluxes rates (0.02 to 13.7 $mgN.m^{-2}.d^{-1}$) reported for tropical terrestrial forests (Silver et al. 2000; Kiese et al. 2003; Fang et al. 2015). The higher maximum denitrification rates reported for mangroves may in part reflect the importance of direct denitrification in mangroves, supplied with NO_3^- from flood tides (e.g., Rivera-Monroy and Twilley 1996). However, the range of denitrification and N_2O fluxes rates in mangrove sediments were large, indicating that not all mangroves may exhibit high rates of N losses to atmosphere, such as some Australian mangroves (Alongi 2013).

N stocks

Few studies provided direct measurements on N stocks in mangroves. Alongi et al. (2003) and Bulmer et al. (2016) reported total N stocks of up to 12.2 and 15.4 ± 1.0 $MgN.ha^{-1}$ for mangrove forests in Australia and New Zealand, respectively. Khan et al. (2007) estimated a total N stock of 3.5 $MgN.ha^{-1}$ for a pioneer mangrove forest in Japan, while Fujimoto et al. (1999) estimated N stocks in sediment of up to 56 $MgN.ha^{-1}$ for mangrove forests in Micronesia (Fujimoto et al. 1999). We estimated a total N stock for mangroves of about 20 $MgN.ha^{-1}$, from indirect calculation considering the global averages of C stocks in sediment (about 718 $MgC.ha^{-1}$) and in above and below ground compartments in mangroves (99 and 138 $MgC.ha^{-1}$, respectively) (Alongi 2014), and the C:N ratios reported for sediment (40) (Rivera-Monroy et al. 1995b; Rivera-Monroy and Twilley 1996), for litter (100) (Kristensen et al. 1995), and for roots (79) in these ecosystems (Alongi et al. 2003, 2004b). This estimate is similar to the N stocks for non-flooded lowland evergreen tropical forest in Brazilian Amazon, which is up to 22 $MgN.ha^{-1}$, including soil and above and below ground biomass compartments (PBMC 2014).

Differences in N dynamics between mangrove physiographic types

Few studies investigated possible differences in BNF between mangrove physiographic types. Sheridan (1991) reported mean ARA rates of 1943 and 3046 $nmolC_2H_4.mgChlorophyll a^{-1}.h^{-1}$ for cyanobacterial crusts on trunks in dwarf mangrove stands, while no activity was found in a seaward fringe forest in Guadeloupe, Lesser Antilles. Laboratory and field experiments revealed that ARA rates were constrained by increasing salinity and desiccation. As ARA rates in the fringe remained below the detection limit after 2 days of heavy rainfall, it can be supposed that a higher windborne salt delivery in fringe compared to inland dwarf stands may have constrained BNF. Lee and Joye (2006) reported a greater importance of BNF in cyanobacterial dominated microbial mats in dwarf stands compared to fringe forests in Twin Cays, Belize (Table 1). According to their findings, this could be attributed to the presence of O_2 and desiccation-tolerant HC species in dwarf microbial mats, while fringe microbial mats were dominated by non-HC species, and also to a higher benthic surface light availability in dwarf stands compared to fringe forests. Studies that evaluated BNF rates in mangrove sediment also suggested that dwarf mangroves can sustain higher BNF rates compared to other mangrove types (Table 1). Despite some evidence that mangrove physiographic types may differ in BNF rates, none of the other studies surveyed for this review evaluated possible differences in BNF between mangrove physiographic types. More studies are needed to evaluate the importance of BNF in different compartments and of total N input via BNF in the different physiographic types of mangroves.

Concerning N fluxes between mangrove sediment and overlying water, Rivera-Monroy et al. (1995a) investigated net PN and DN fluxes between a fringe forest and an adjacent tidal creek, and an inland basin forest in Isla del Carmen, Mexico. The fringe forest imported NH_4^+ and NO_x^- from both tidal creek and basin forest, while exported DON and PN to both basin forest and tidal creek. These results suggest that fringe forests might primarily act as sink for DIN and a source of

Table 1. Nitrogen cycling rates in sediment and microbial mats from mangrove physiographic types. Median rates (and ranges) are presented, including biological nitrogen fixation (BNF), net nitrous oxide (N_2O) flux, ammonia (NH_3^+) volatilization, and fluxes of ammonium (NH_4^+), nitrite plus nitrate (NO_x^-), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), total dissolved nitrogen (DN), and particulate nitrogen (PN) between mangrove sediment and overlying water. Negative values indicate net flux into the sediment or microbial mat. When reported by authors, *P*-values of statistical comparison tests are presented. Source: (1) Kimball and Teas (1975) *apud* Alongi et al. (1992); (2) Rivera-Monroy et al. (1995a); (3) Rivera-Monroy et al. (1995b); (4) Rivera-Monroy and Twilley (1996); (5) Davis et al. (2001a); (6) Davis et al. (2001b); (7) Bauza et al. (2002); (8) Muñoz-Hincapié et al. (2002); (9) Joye and Lee (2004); (10) Lee and Joye (2006); (11) Fogel et al. (2008); (12) Romero et al. (2012); and (13) Reis et al. (2016)

	Fringe	Basin	Dwarf	Unit	*P*-value	Location
Sediment						
BNF	0.255	0.118 and 0.189	(0.027 to 0.310)	mgN.m^{-2}.d^{-1}	-	Florida, EUA (1)
BNF	-	-	18.2 (0 to 68.5)	mgN.m^{-2}.d^{-1}	-	Twin Cays, Belize (12)
NH_4^+ flux	-1.1	0.2	-	mgN.m^{-2}.d^{-1}	-	Terminos Lagoon, Mexico (2)
NO_x^- flux	-0.05	0.003	-	mgN.m^{-2}.d^{-1}	-	Terminos Lagoon, Mexico (2)
DIN flux	-1	0.2	-	mgN.m^{-2}.d^{-1}	-	Terminos Lagoon, Mexico (2)
DON flux	0.08	-0.2	-	mgN.m^{-2}.d^{-1}	-	Terminos Lagoon, Mexico (2)
DN flux	-1	-0.05	-	mgN.m^{-2}.d^{-1}	-	Terminos Lagoon, Mexico (2)
PN flux	1.4	-0.2	-	mgN.m^{-2}.d^{-1}	-	Terminos Lagoon, Mexico (2)
NH_4^+ flux	-0.71 to 0.26	-	-7.0 (2.2 to 10.6)	mgN.m^{-2}.d^{-1}	-	Florida, EUA (5; 6)
NO_x^- flux	-1.11 to 0.12	-	12.0 (2.4 to 47.7)	mgN.m^{-2}.d^{-1}	-	Florida, EUA (5; 6)
DIN flux	-1.34 to 0.38	-	5.04	mgN.m^{-2}.d^{-1}	-	Florida, EUA (5; 6)
Net N mineralization	0.440	0.171	-	mgN.g^{-1}.d^{-1}	0.0385	Cardoso Island, Brazil (13)
Net nitrification	0.017	0.031	-	mgN.g^{-1}.d^{-1}	0.1620	Cardoso Island, Brazil (13)
Direct denitrification	(0 to 3.2)	(0 to 1.5)	-	mgN.m^{-2}.d^{-1}	-	Isla del Carmen, Mexico (3)
Coupled denitrification	0	0	-	mgN.m^{-2}.d^{-1}	-	Isla del Carmen, Mexico (4)
Potential direct denitrification	(1.2 to74.3) [a]	-	-	mgN.m^{-2}.d^{-1}	-	Isla del Carmen, Mexico (4)
Potential coupled denitrification	(0.8 to 9.7) [a]	-	-	mgN.m^{-2}.d^{-1}	-	Isla del Carmen, Mexico (4)
Potential denitrification	(2.0 to 84.0) [a]	-	-	mgN.m^{-2}.d^{-1}	-	Isla del Carmen, Mexico (4)
Net N_2O flux	0.03 to 0.4 (0.01 to 0.9)	-	-	mgN.m^{-2}.d^{-1}	-	Magueyes Island, Puerto Rico (7; 8)
NH_3^+ volatilization	0.2	-	0.38 (0 to 1.05)	mgN.m^{-2}.d^{-1}	-	Twin Cays, Belize (11)
Microbial mats						
BNF	0.03 to 3.2	-	1.6 to 7.6	mgN.m^{-2}.d^{-1}	-	Twin Cays, Belize (10)
BNF	-	-	3.4 (0 to 6.7)	mgN.m^{-2}.d^{-1}	-	Twin Cays, Belize (9)
Denitrification	0.002 to 0.7	-	0 to 0.1	mgN.m^{-2}.d^{-1}	-	Twin Cays, Belize (10)
Denitrification	-	-	0.7	mgN.m^{-2}.d^{-1}	-	Twin Cays, Belize (9)
Potential denitrification	53.6 and 91.9	-	7.5 to 31.0 (6.7 to 67)	mgN.m^{-2}.d^{-1}	-	Twin Cays, Belize (9; 10)

(1) based on the acetylene reduction technique at 10.4 cm depth

(2) fluxes between tidal creek and fringe forest and between fringe and basin forests, based on flume technique

(3) based on ^{15}N enrichment technique at 25 cm depth

(4) based on ^{15}N enrichment technique at 25 cm depth, [a] indicate data for riverine subtype

(5) data for dwarf mangrove based on island enclosure technique

(5) data for fringe forest based on flume technique

(7; 8) based on enclosed chamber technique at 25 cm depth

(9) BNF data based on the acetylene reduction technique at 6 cm depth, and denitrification data based on the acetylene inhibition method at 5 cm depth

(10) BNF data based on the acetylene reduction technique, and denitrification data based on the acetylene inhibition method at 1 cm depth

(11) based on ammonia-sensing badges

(12) based on the acetylene reduction technique at 30 cm depth

(13) based on sediment incubation essays at 10 cm depth

organic N forms, while basin forests may exhibit the opposite pattern (Table 1). Davis et al. (2001a, b) evaluated net DIN fluxes between sediment and overlying water from fringe and dwarf stands in southern Everglades, Florida. Higher fluxes were reported for the dwarf mangrove. While the fringe forest tended to import DIN, the dwarf mangrove imported NH_4^+, but exported greater amounts of NO_x^-, resulting in a net DIN export (Table 1).

Regarding N transformation rates in sediment, Reis et al. (2016) evaluated net N mineralization and nitrification rates in fringe and basin forests in Cardoso Island, Brazil. The fringe forest exhibited higher mean net N mineralization rate but similar mean net nitrification rate compared to the basin forest (Table 1). However, there were evidences that gross nitrification might have been higher in fringe compared to basin forest. Rivera-Monroy et al. (1995b) investigated direct denitrification rates in sediment of fringe and basin forests in Isla del Carmen. The fringe forest exhibited double the highest direct denitrification rate reported for the basin forest (Table 1). Rivera-Monroy and Twilley (1996) reported negligible coupled denitrification rates in sediment from fringe and basin forests in Isla del Carmen. These authors also evaluated potential direct, coupled and total denitrification rates for a riverine forest. Potential direct denitrification fluxes attained greater values than potential coupled denitrification (Table 1). Nitrous oxide fluxes were only reported for fringe mangroves (Table 1). Lee and Joye (2006) also evaluated denitrification rates in microbial mats from fringe and dwarf mangrove stands in Twin Cays. Fringe microbial mats attained higher denitrification rates at 1 cm depth compared to dwarf microbial mats, and higher potential denitrification rates following NO_3^- addition during short- and long-term experiments. However, dwarf microbial mats at 5 cm depth attained a similar maximum denitrification rate compared to fringe microbial mats at 1 cm depth (Table 1). Fogel et al. (2008) quantified NH_3^+ volatilization rates in fringe and dwarf mangroves in Twin Cays. Higher NH_3^+ emissions were found in the dwarf mangrove stand compared to the fringe forest (Table 1). These differences were attributed to a greater development of microbial mats on the ground in the dwarf mangrove compared to the fringe forest.

N dynamics of mangrove physiographic types from $\delta^{15}N$ studies

Differences in N dynamics between terrestrial ecosystems can also be evaluated through the analysis of natural abundance of N stable isotopes ($\delta^{15}N$) in the soil-plant system (Högberg 1997; Robinson 2001; Craine et al. 2015). The $\delta^{15}N$ expresses the $^{15}N/^{14}N$ ratio in a sample (e.g., leaves, leaf litter, and soil) in relation to the $^{15}N/^{14}N$ ratio of the international standard, the atmospheric N, equals to 0.0036765. The $\delta^{15}N$ integrates the N stable isotope signature of N sources and isotope fractionations against the heavier isotope ^{15}N during N transformation reactions, mainly those mediated by microorganisms in soil such as nitrification, denitrification, and NH_3^+ volatilization. The lighter isotope ^{14}N reacts faster than ^{15}N, so that products are maintained enriched in ^{14}N, while substrates are maintained enriched in ^{15}N (Högberg 1997; Robinson 2001). Terrestrial ecosystems under lower N limitations usually exhibit higher soil N transformation rates and N losses to atmosphere, which keeps the soil-plant system enriched in ^{15}N (i.e., higher $\delta^{15}N$) (e.g., Martinelli et al. 1999; Ometto et al. 2006; Nardoto et al. 2008; Craine et al. 2009), compared to terrestrial ecosystems under higher N limitations, which usually exhibit lower N transformation rates in soil and lower N losses to atmosphere, maintaining the soil-plant system enriched in ^{14}N (i.e., lower $\delta^{15}N$) (e.g., Martinelli et al. 1999; Bustamante et al. 2004; Nardoto et al. 2008; Craine et al. 2009; Mardegan et al. 2009).

Studies that evaluated $\delta^{15}N$ patterns in mangrove physiographic types are presented in Table 2. The higher $\delta^{15}N$ in the sediment-plant-leaf litter system of fringe compared to basin and dwarf mangroves suggests that fringe mangroves may exhibit higher N transformation rates in sediment and higher N losses to atmosphere, compared to dwarf and basin mangroves. These results are consistent with the higher net N mineralization and denitrification rates in sediment and microbial mats reported for fringe compared to basin and dwarf mangroves. The lower $\delta^{15}N$ in dwarf mangroves can also reflect a greater importance of BNF, as suggested by the higher BNF rates associated with cyanobacterial crusts and microbial mats in dwarf mangroves compared to fringe forests, discussed above.

Some of the studies that evaluated leaf $\delta^{15}N$ patterns in mangroves proposed other explanations for the higher leaf $\delta^{15}N$ in fringe compared to dwarf mangroves. Fry et al. (2000) proposed that the lower leaf $\delta^{15}N$ in dwarf stands would result of the isotopic fractionation during NH_4^+ uptake by plants associated with a slower plant growth and lower N demand by plants in dwarf compared to fringe mangroves. A lower N demand would increase fractionation during N uptake because

Table 2. Mean or range of natural abundance of nitrogen stable isotopes ($\delta^{15}N$) (‰) of leaves, leaf litter and sediment from fringe, basin and dwarf mangrove forests dominated by *Rhizophora mangle*. When reported by authors, *P*-values of statistical comparison tests are presented. Source: (1) Fry et al. (2000); (2) Mckee et al. (2002); (3) Wooller et al. (2003); (4) Fogel et al. (2008); (5) Medina et al. (2010); (6) Reis et al. (2016)

Sample	Fringe	Basin/Dwarf	*P*-value	Location
Leaves	2 to 7	-5 to 2	-	Florida, USA (1)
Leaves	0.1	-5.4	-	Twin Cays, Belize (2)
Leaves	0	-10	< 0.001	Twin Cays, Belize (3)
Leaves	-0.6	-6.8	< 0.001	Twin Cays, Belize (4)
Leaves	0.2	-11.1 to −5.5	-	Ceiba, Puerto Rico (5)
Leaves	3.6	0.9[a]	< 0.0001	Cardoso Island, Brazil (6)
Leaf litter	0.1	-3.3	< 0.005	Twin Cays, Belize (3)
Leaf litter	3.3	0.2[a]	< 0.0001	Cardoso Island, Brazil (6)
Sediment	0.1	-0.5	0.0159	Twin Cays, Belize (2)
Sediment	3.6	0.7[a]	< 0.0001	Cardoso Island, Brazil (6)

[a] Indicate data for basin forests. All other data are for dwarf mangroves

not all available N would be used, resulting in lower leaf $\delta^{15}N$ in dwarf compared to fringe mangroves. Mckee et al. (2002) reached the same conclusions as Fry et al. (2000), and observing an increase in leaf $\delta^{15}N$ in dwarf stands following P amendments, these authors pointed that the enhanced P availability increased N demand by dwarf plants, reducing fractionation during N uptake and increasing leaf $\delta^{15}N$. Fogel et al. (2008) also observed an increase in leaf $\delta^{15}N$ after P amendments. They suggested that higher P availability could enhance root biomass and activate NH_4^+ transport in roots, reducing fractionation during N uptake. Fogel et al. (2008) also reported extremely low leaf $\delta^{15}N$ values in dwarf mangrove stands, up to −21.6‰, which was attributed to a foliar uptake of ^{15}N depleted atmospheric NH_3^+, given the higher volatilization rates observed in the dwarf compared to the fringe stand, especially in sites with greater microbial mat development. As isotope fractionations during N transformations in sediment such as nitrification, denitrification, and volatilization are much higher than fractionations in plants (Robinson 2001), it is most probable that leaf $\delta^{15}N$ reflects both $\delta^{15}N$ of N sources and isotope fractionations during N transformations in sediment, than fractionation during N uptake by plants. The influence of P availability on leaf $\delta^{15}N$ probably reflects the influence of a limiting nutrient on overall sediment microbial activity, and consequently, on N transformation rates in sediment, instead of an increased N uptake by plants.

Effects of N enrichment on N dynamics in mangroves

The patterns of N dynamics in mangroves discussed so far might be modified by anthropogenic N enrichment. Fernandes et al. (2012a) reported that BNF in sediment was only detected at a conserved mangrove stand, with rates reaching about 0.008 $mgN.g^{-1}.d^{-1}$, while no BNF activity was found in a mangrove stand receiving ammonium nitrate from ferromanganese mines in Goa, India. Studies that investigated long-term effects of N amendment on BNF rates in mangrove sediment also found marked reductions up to about 75% (Whigham et al. 2009; Romero et al. 2012). Alongi et al. (2002, 2005) quantified BNF rates in a mangrove plantation that was originally the site of a failed shrimp farm in Thailand and in mangrove stands subjected to intermittent discharge of aquaculture pond effluents in China. There were no difference, however, between BNF rates in sediment reported for these mangrove sites, ranging from about 0 to 8 $mgN.m^{-2}.d^{-1}$, and rates reported for non-N-enriched mangrove stands in the literature ($U = 173.00$, $df = 31,11$, $p = 0.9542$) (Fig. 3). Alongi et al. (2002) also quantified DN net fluxes across the sediment-overlying water interface. There were no differences between the mean NH_4^+ flux rates reported by these authors, from −10 to 10 $mgN.m^{-2}.d^{-1}$, and rates reported for non-N-enriched mangrove stands included in the literature ($U = 287.00$, $df = 10,64$, $p = 0.6066$); but all other mean flux rates reported by these authors,

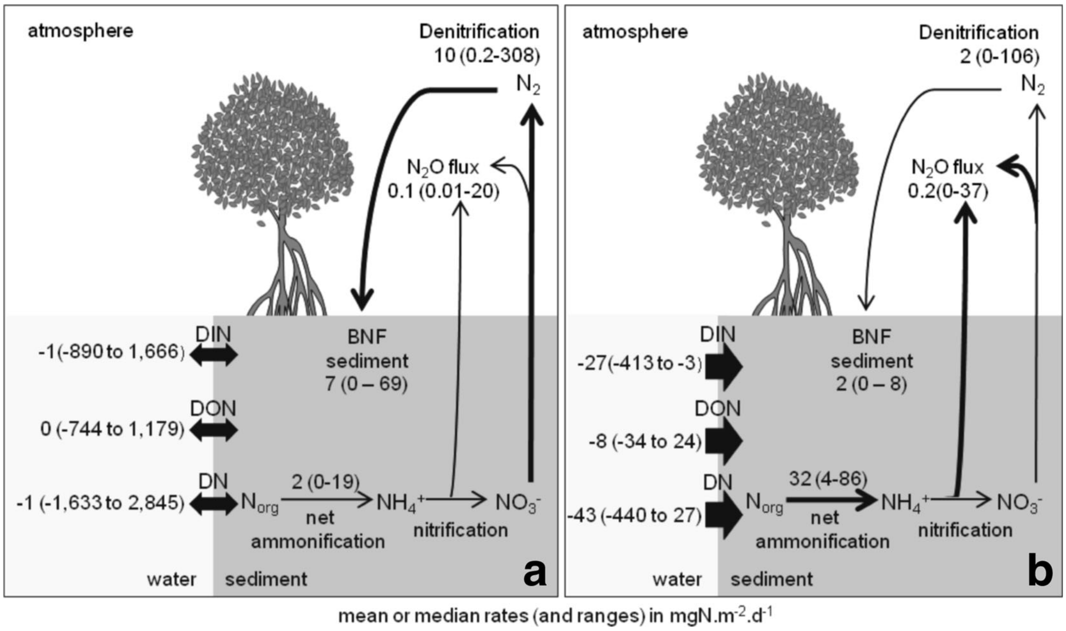

Fig. 3 Nitrogen cycling in conserved (**a**) and N-enriched mangroves (**b**). Median rates (and ranges) in mgN.m^{-2}.d^{-1} are presented, including biological nitrogen fixation (BNF), nitrous oxide (N_2O) flux, and fluxes of dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), and total dissolved nitrogen (DN) between mangrove sediment and overlying water are presented. Negative values indicate net flux into the sediment. For BNF, mean rates are presented. Data of conserved mangroves are based on studies cited in Fig. 2. Data of N-enriched mangroves are based on Corredor and Morell 1994; Corredor et al. 1999; Alongi et al. 2002; Kreuzwieser et al. 2003, Alongi et al. 2005; Purvaja et al. 2008; Chen et al. 2010; and Fernandes et al. 2010, 2012a, 2012b

including of NO_2^- plus NO_3^- (NO_x^-) (−407 to −3 mgN.m^{-2}.d^{-1}), DIN (−413 to −3 mgN.m^{-2}.d^{-1}), dissolved organic N (DON) (−37 to 37 mgN.m^{-2}.d^{-1}), and DN (−440 to 27 mgN.m^{-2}.d^{-1}) were significantly lower (i.e., higher fluxes into the sediment) (NO_x^-: $U = 45.00$, $df = 10{,}40$, $p = 0.0001$; DIN: $U = 74.00$, $df = 10{,}38$, $p = 0.0017$; DON: $U = 48.00$, $df = 10{,}21$, $p = 0.0078$; DN: $U = 48.00$, $df = 10{,}21$, $p = 0.0085$).

Concerning N mineralization, Alongi et al. (2002, 2005) also reported mean net ammonification rates from 4 to 86 mgN.m^{-2}.d^{-1}, significantly higher than net ammonification rates reported for non-N-enriched mangrove stands ($U = 51.00$, $df = 8{,}7$, $p = 0.0030$) (Fig. 3). More attention, however, has been given to possible alterations of denitrification and N_2O flux rates in response to N enrichment in mangroves. Denitrification rates reported for mangrove sediments affected by N enrichment ranged from 0 to 106 mgN.m^{-2}.d^{-1} (Corredor and Morell 1994; Corredor et al. 1999; Alongi et al. 2002, 2005; Purvaja et al. 2008; Fernandes et al. 2010; Fernandes and LokaBharathi 2011), while N_2O flux mean rates ranged from −61 to 34 mgN.m^{-2}.d^{-1} (Corredor et al. 1999; Alongi et al. 2005; Kreuzwieser et al. 2003; Allen et al. 2007; Chauhan et al. 2008; Purvaja et al. 2008; Chen et al. 2010, 2012; Fernandes et al. 2010). There were no differences between the denitrification rates reported for these N-enriched mangroves and non-N-enriched mangrove stands reported in the literature ($U = 245.50$, $df = 11{,}35$, $p = 0.1763$) (Fig.3), but N_2O flux rates were significantly higher in mangroves under N enrichment than non-N-enriched mangrove stands ($U = 947.00$, $df = 87{,}30$, $p = 0.0128$). Studies comparing denitrification (Corredor and Morell 1994; Fernandes et al. 2012a), N_2O flux rates (Kreuzwieser et al. 2003; Chen et al. 2010; Fernandes et al. 2012b), and both rates (Corredor et al. 1999; Purvaja et al. 2008; Fernandes et al. 2010) between N-enriched and non-N-enriched mangroves, however, repeatedly found that both denitrification and N_2O fluxes were higher in N-enriched mangrove stands. Studies investigating short- and long-term effects of N amendment on denitrification and N_2O flux rates in mangrove sediment also found higher rates at N-enriched sites (Muñoz-Hincapié et al. 2002; Whigham et al. 2009; Chen et al. 2011; Fernandes and LokaBharathi 2011). N availability and microbial activity are some of the main factors regulating N transformation rates in mangrove sediment.

Except for BNF, which seems to be constrained by an increased availability of a lower cost N source, all other N transformation rates in mangrove sediment seem to be intensified by increasing N availability. However, the range of these N transformation rates in both N-enriched and non-N-enriched mangroves were large, suggesting that not all N-enriched mangrove may exhibit all the reported alterations in the N cycling.

Increasing N availability and N cycling rates in mangrove sediment do not imply strictly an increase in net primary productivity (NPP) and assimilation of extra N by mangrove vegetation. Mangroves have been shown to be N- (Feller et al. 2003; Lovelock and Feller 2003; Feller et al. 2007; Lovelock et al. 2007a, 2007b; Naidoo 2009) or P-limited (Kock 1997; Kock and Snedaker 1997; Feller 1995; Feller et al. 1999, 2007), or even co-limited by N and P (Cheeseman and Lovelock 2004; Lovelock et al. 2004, 2007a), which can either switch along tidal height gradients (Feller et al. 2002; Cheeseman and Lovelock 2004; Lovelock et al. 2004, 2007a). At N-limited mangrove forests, the extra N may increase NPP, but at P-limited mangrove forests, the increased N availability might increase P-limitation, thus constraining NPP.

Conclusion

Despite large variability in N transformation and flux rates between mangrove forests, the results of the present study indicated that mangroves play a substantial role in N cycling in tropical and subtropical regions because of the high N cycling rates that mangrove forests often exhibit. Furthermore, anthropogenic N enrichment may result in extensive impact not only on the N cycling with direct effects on ecosystem functioning but also the potential indirect effects on ecosystem structure in mangrove forests. As a consequence of anthropogenic N enrichment, mangroves may increase N_2O fluxes to the atmosphere, also contributing to global warming. The results also indicated that different types of mangroves differ in N dynamics. Fringe forests have higher N transformation rates in sediment and higher N losses to atmosphere compared to other mangrove types. These differences may reveal different responses to N enrichment. While fringe forests may experience higher increases in N transformation rates in sediment on shorter timescales, basin forests may experience larger ecosystem functioning alterations given their higher nutrient limitation.

Finally, we also highlight in this review the paucity of studies that have evaluated N dynamics and alterations following anthropogenic N enrichment in mangroves, making it difficult to perform a comprehensive meta-analysis and evaluation of regional trends. More empirical and experimental data on consequences of N enrichment to N pools, fluxes, cycling rates, and stocks, as well as its relation with other nutrients availability to the resulting NPP in the different types of mangroves are needed, especially in underrepresented areas such as South America. The establishment of accessible monitoring tools to evaluate alterations following N enrichment in mangroves are also needed. There is also a critical need for the development of a single classification system of mangroves to be used worldwide, despite the richness differences between American and Indo-West Pacific mangroves. There is also a great need for developing coordinated research programs worldwide to conduct studies with standardized methodologies on higher spatial and temporal scales.

Acknowledgements The authors are thankful to Mercedes Maria da Cunha Bustamante (Universidade de Brasília - UnB), and to anonymous referees for improving the manuscript. This study was supported by the Fundação de Amparo à Pesquisa no Estado de São Paulo (FAPESP) (Processo 2011/09613), and by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) as a fellowship grant for the first author. Jim Hesson of AcademicEnglishSolutions.com revised the English.

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