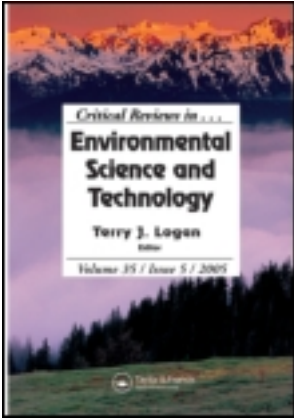


This article was downloaded by: [McGill University Library]

On: 10 January 2012, At: 06:06

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Critical Reviews in Environmental Science and Technology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/best20>

Biogeochemistry of Nitrogen Across the Everglades Landscape

P. W. Inglett^a, V. H. Rivera-Monroy^b & J. R. Wozniak^c

^a Soil and Water Science Department, University of Florida, Gainesville, FL, USA

^b Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, LA, USA

^c Texas Research Institute for Environmental Studies, Sam Houston State University, Huntsville, TX, USA

Available online: 19 Feb 2011

To cite this article: P. W. Inglett, V. H. Rivera-Monroy & J. R. Wozniak (2011): Biogeochemistry of Nitrogen Across the Everglades Landscape, *Critical Reviews in Environmental Science and Technology*, 41:S1, 187-216

To link to this article: <http://dx.doi.org/10.1080/10643389.2010.530933>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Biogeochemistry of Nitrogen Across the Everglades Landscape

P. W. INGLETT,¹ V. H. RIVERA-MONROY,² and J. R. WOZNIAK³

¹Soil and Water Science Department, University of Florida, Gainesville, FL, USA

²Department of Oceanography and Coastal Sciences, Louisiana State University,
Baton Rouge, LA, USA

³Texas Research Institute for Environmental Studies, Sam Houston State University,
Huntsville, TX, USA

Compared to phosphorus (P), nitrogen (N) has received little attention across the Everglades landscape. Despite this lack of attention, N plays important roles in many Everglades systems, including being a significant pollutant in Florida Bay and the Gulf of Mexico, the limiting nutrient in highly P-impacted areas, and an important substrate for microbial metabolism. Storage and transport of N throughout the Everglades is dominated by organic forms, including peat soils and dissolved organic N in the water column. In general, N sources are highest in the northern areas; however, atmospheric deposition and active N₂ fixation by the periphyton components are a significant N source throughout most systems. Many of the processes involved in the wetland N cycle remain unmeasured for most of the Everglades systems. In particular, the lack of in situ rates for N₂ fixation and denitrification prevent the construction of system-level budgets, especially for the Southern mangrove systems where N export into Florida Bay is critical. There is also the potential for several novel N processes (e.g., Anammox) with an as yet undetermined importance for nitrogen cycling and function of the Everglades ecosystem. Phosphorus loading alters the N cycle by stimulating organic N mineralization with resulting flux of ammonium and DON, and at elevated P concentrations, by increasing rates of N₂ fixation and N assimilation. Restoration of hydrology has a potential for significantly impacting N cycling in the Everglades both in terms of affecting N transport, but also by

Address correspondence to P. W. Inglett, Soil and Water Science Department, University of Florida, 106 Newell Hall, Gainesville, FL 32611, USA. E-mail: pinglett@ufl.edu.

altering aerobic-anaerobic transitions at the soil-water interface or in areas with seasonal drawdowns (e.g., marl prairies). Based on the authors' understanding of N processes, much more research is necessary to adequately predict potential impacts from hydrologic restoration, as well as the function of Everglades systems as sinks, sources, and transformers of N in the South Florida landscape.

KEYWORDS: wetlands, nitrogen fixation, denitrification, 15N, mineralization, nitrification

1. INTRODUCTION

Without question phosphorus (P) is the element regulating productivity in the vast majority of the natural Everglades ecosystem. Consequently, P has received most of the attention in studies and in the literature. Despite this fact, other macroelements such carbon (C), nitrogen (N), and sulfur (S) also play key roles in processes of the Everglades system. Most coastal marine systems are N-limited, and therefore N is significant as a limiting element in the marine portion of the Everglades (i.e., mangrove systems and Florida Bay; e.g., Glibert et al., 2004). Likewise, in the P-enriched portions of the Everglades, N can become a limit to productivity (McCormick and O'Dell, 1996). For these reasons, an understanding of N dynamics is crucial to understanding not only the impacts to Florida Bay, but perhaps the spread of P impacts in the Northern Everglades systems as well.

The N cycle is complex with a variety of potential inputs/sources (natural and anthropogenic), a variety of forms, associated transformations, and losses. This review is designed to introduce these biogeochemical processes affecting N cycling, and discuss their importance to the various hydrologic units of the Everglades. Hydrologic connections in the Everglades can be considered within the river continuum concept, where upstream ecosystem processes effect downstream systems. For this reason, this review is also organized according to the flow paths of the major Everglades systems, namely (a) the upstream systems including Lake Okeechobee and the Everglades Agricultural Area (EAA); (b) the Northern Marshes including Water Conservation Areas (WCAs) 1, 2, and 3; (c) the Southern Marshes of Everglades National Park (ENP) consisting of Shark River and Taylor Sloughs; and (d) the downstream Mangrove systems at the interface with the Gulf of Mexico and Florida Bay (Figure 1).

2 NITROGEN CONTENTS AND PATTERNS

The diversity of habitats and the large extent of the Everglades system results in a wide range of N forms and concentrations (Figure 2). Water column concentrations are generally in the range of 2–3 mg L⁻¹ of total N (TN). However,

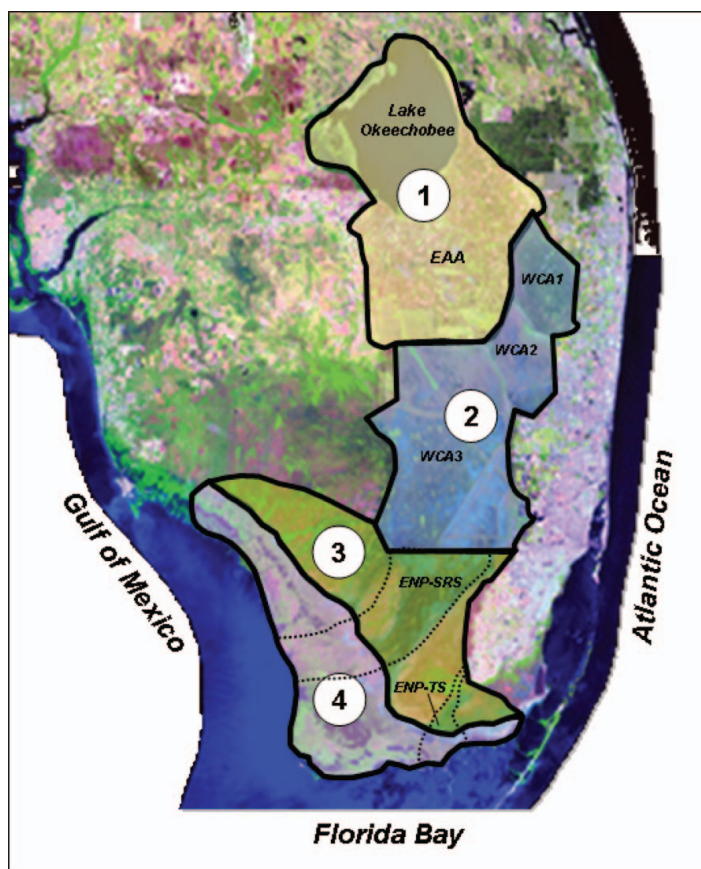


FIGURE 1. Overview of systems used to describe nitrogen processes in this review. (a) Lake Okeechobee and the Everglades Agricultural Area; (b) Water Conservation Areas (WCAs) 1, 2, and 3, and Northern Marshes; (c) Southern Marshes of Everglades National Park (ENP) including Shark River Slough (SRS) and Taylor Slough (TS); (d) Mangrove Ecotone wetlands of Everglades National Park. (This figure is available in color online).

farming practices in the EAA can influence the forms and concentrations of N, with values of water TN ranging from 1.8 to 77 mg N L⁻¹ being reported for canals draining various fields (Capone et al., 1995). Throughout the majority of the rest of the Everglades system, there is little NH₄⁺ or NO₃⁻ in the water column with most dissolved N existing as organic N forms (Rudnick et al., 1999). Particulates have been shown to contribute less than 10% of the TN content of surface water (Noe et al., 2007). Pore water concentrations are, on average, approximately two-fold higher than surface water both for NH₄⁺, as well as dissolved organic N (DON; Qualls and Richardson, 2003).

Like most wetlands, soil TN concentrations are dominated by organic N forms. Concentrations range from <1% in marl soils and mangroves at the mouth of Shark River Slough (SRS; Chen and Twilley, 1999) to >4% being

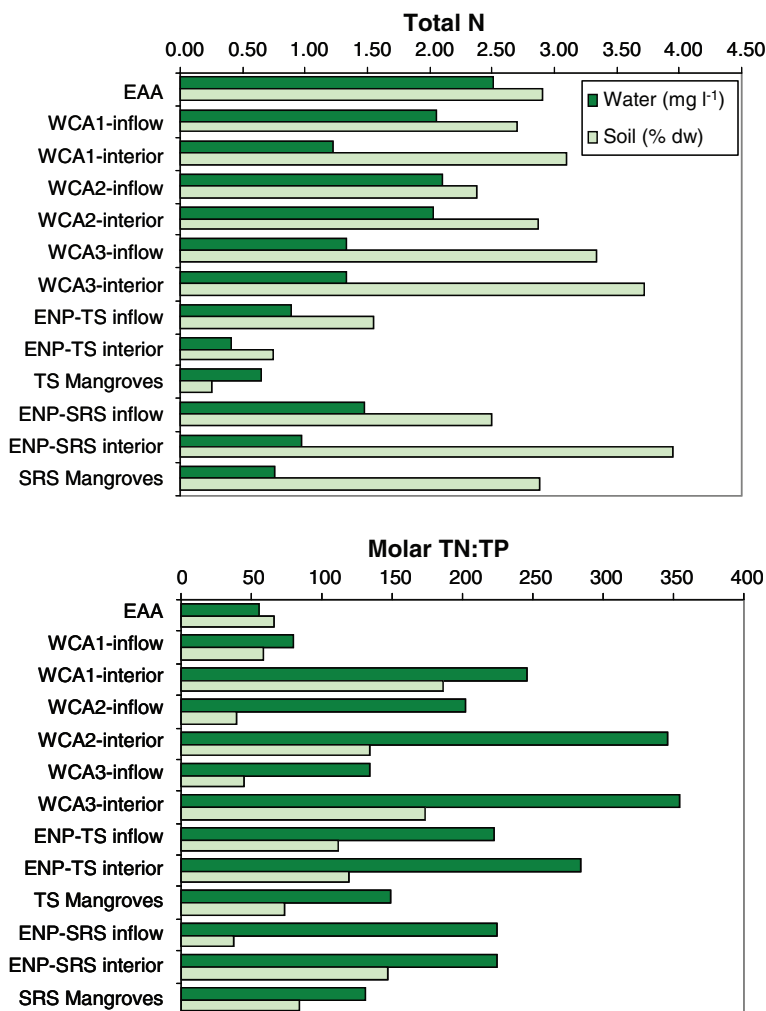


FIGURE 2. Concentrations of total N and molar TN:TP ratios of water and soils in various Everglades systems. ENP = Everglades National Park; TS = Taylor Slough; SRS = Shark River Slough. Based data obtained from Amador and Jones (1993), DeBusk et al. (1994), Diaz et al. (1994), Newman et al. (1997), Penton and Newman (2007), Reddy and DeLaune (2008), Rubio and Childers (2006), Rudnick et al. (1999), South Florida Ecosystems Report (2009), Wright et al. (2009), and Ye et al. (2009). (This figure is available in color online).

reported in peats of WCA-3A (Craft and Richardson, 1993). Extractable N levels are much higher in eutrophic marshes of the north (73 mg N kg⁻¹ soil; Newman et al., 1997) as compared to levels in southern marl soils (29 mg N kg⁻¹ soil; Li and Norland, 2001). Extractable N is mostly NH₄⁺ in the flooded soils, while in drained or seasonally dry areas, NO₃⁻ can be highly significant (Hanlon et al., 1997).

Following surficial leaching, most plant litter of the Everglades have extremely high C:N ratios resulting in slow initial decomposition and high rates of N immobilization during the first year (S. E. Davis et al., 2003; DeBusk and Reddy, 2005; Newman et al., 2001). Typical C:N ratios of the peat range from (11–14 for WCA-2A and WCA-3A; Craft and Richardson, 1993; ~25 molar for SRS mangroves; Chen and Twilley, 1999). The DOC:DON ratio is reasonably consistent throughout systems (Qualls and Richardson, 2003), but there is a significant decrease progressing from north (22) to south (16). Phosphorus limitation means that N:P ratios are also very high throughout most of the systems except where P loading has occurred (26–80 for WCA-2A and WCA-3A; Craft and Richardson, 1993) or for mangrove soils as they approach the salinity interface with Florida Bay (<20; Chen and Twilley, 1999). Perhaps the most striking range of N:P ratios are found in the tree islands, where relatively low N content (~2% DW) combine with very high levels of TP (>2% DW), resulting in N-limited conditions in the tree island hammock (molar TN:TP < 1; Ross et al., 2006).

3 NITROGEN CYCLE PROCESSES

The N cycle is quite complex especially when compared to that of P. The presence of numerous N forms, ranging from particulate and dissolved organic (PON and DON), to dissolved inorganic (NO_3^- , NH_4^+) and gaseous (N_2 , N_2O , NH_3) species combined with the diversity of processes regulating transformations, makes the N cycle one of the most difficult to determine and quantify in wetlands (Figure 3). Here, we will briefly review these processes beginning with the N inputs.

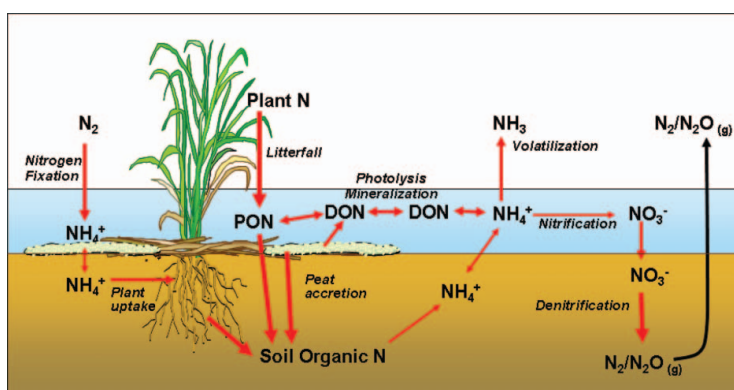


FIGURE 3. Schematic diagram of nitrogen cycle processes in wetland systems. From Reddy and DeLaune (2008). PON = particulate organic N; DON = dissolved organic N. (This figure is available in color online).

3.1 Atmospheric Deposition

Nitrogen can enter wetlands through a variety of pathways including atmospheric deposition, biological N₂ fixation, or through surface or ground water inputs. Atmospheric deposition is highly variable and can contribute anywhere from ≈ 0.005 g N m⁻² yr⁻¹ in remote areas to >2 g N m⁻² yr⁻¹ in areas near urbanized centers (Galloway et al., 2004). Deposition rates monitored at the National Atmospheric Deposition Program (NADP) station in Everglades National Park (ENP) have recorded an average inorganic N deposition of 0.25 g N m⁻² yr⁻¹ since 1981 and an average of 0.33 g N m⁻² yr⁻¹ for the last decade. This deposition consists of slightly more NO₃⁻ (60%) than NH₄⁺ (40%), and exhibits a very slight increasing trend (0.005 g N m⁻² yr⁻¹) over the period (NADP). Sutula et al. (2001) used a factor of 1.45, reported by Hendry et al. (1981), to estimate bulk TN deposition including organic forms. Using this factor yields a present estimate of 0.48 and 0.15 g N m⁻² yr⁻¹ of total- and organic-N deposition, respectively. This input can be highly significant, particularly in the dry season where in the Southern marshes and mangroves it can be twice the surface water input of N (Sutula et al., 2001).

3.2 Biological N₂ Fixation

The process of biological N₂ fixation converts atmospheric N₂ gas into biologically available NH₄-N, and thus is a source of N to ecosystems. This process is carried out solely by prokaryotes having the nitrogenase enzyme including bacteria, cyanobacteria, and Archaea. These include phototrophic and chemotrophic as well as autotrophic and heterotrophic organisms. System components that may contribute to N₂ fixation within the Everglades system include extensive amounts of standing and surface detritus, soils, and the abundant algal forms in the surface soils and in the water column. In particular, Everglades cyanobacterial mats exhibited a strong seasonality in nitrogenase activity and were estimated to add up to >100 mg N m⁻² d⁻¹ to low P areas of WCA-2A (Figure 4; Inglett et al., 2004). Comparatively much lower rates were observed in soils where presumably NH₄⁺ levels are sufficiently high to suppress nitrogenase activity. High rates of nitrogenase have also been found with surface litter of macrophytes (Inglett et al., 2004; Pelegri et al., 1997) while lower, but significant rates were observed in water (Inglett et al., 2004).

These high rates are similar to other systems, where cyanobacterial mats have been shown to exhibit rates of N₂ fixation as high as >200 mg N m⁻² d⁻¹ (Howarth et al., 1988). Such high rates of fixation help contribute to the high productivity of these mats and other conspicuous periphytic forms. N₂-fixing organisms usually dominate in systems limited by N; therefore, it is somewhat puzzling why cyanobacteria in the form of periphyton mats

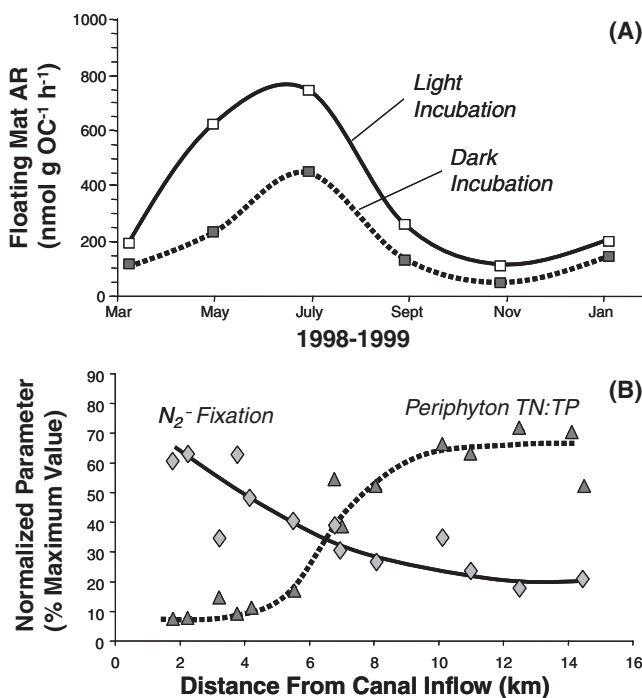


FIGURE 4. Seasonal (A) and spatial (B) Patterns of nitrogenase activity as acetylene reduction (AR) for floating periphyton mats in Water Conservation Area 2A of the Everglades. OC = organic carbon. From the study of Inglett et al. (2004, 2009).

would be prevalent in an ecosystem so dramatically limited by P. In many other aquatic systems, P is shown to be a primary determinant of observed N₂ fixation rates, and in impacted areas of the Everglades, high levels of P and low TN:TP ratios easily explain high rates of N₂ fixation (Figure 4; Inglett et al., 2004, 2009).

Perhaps one explanation of high N₂ fixation rates in the natural oligotrophic areas of the Everglades could be associated with the high carbon flux in the systems including plant detritus, peat soils, and exudates by the periphyton communities. In litter decomposition, P appears to have little effect on N₂ fixation and rather seems to depend more on stage of litter decomposition rather than N:P ratio or species of mangrove litter (Pelegri et al., 1997; Pelegri and Twilley, 1998). These results indicate that changes in microbial colonization or C:N during decomposition stages are perhaps a more important determining factor, however, in their study of P loading to mesocosms, Newman et al. (2001) also found that N accumulation in decomposing litter was enhanced at P loads greater than 1.6 g m⁻² y⁻¹. Both of these studies indicate that N availability is integral to the decomposition process in the Everglades.

3.3 Mineralization

The dominance of macrophytes and peat soils throughout the Everglades system indicates that mineralization of organic N will be a significant source of N. Products of mineralization include soluble organic N compounds and NH_4^+ , and the production of these begins immediately upon senescence through the action of aerial decay and leaching (S. E. Davis et al., 2003). These leaching products are highly dependent on plant species both in terms of the quantity of N leached as well as its composition. For example, the TN content of Everglades plant species was shown to range from 0.7 to 19% dry weight and corresponding ranges in mass ratios of C:N and N:P of 23–60 and 10–26, respectively (Osborne et al., 2007). Similarly, leachates from these different plant materials vary in their concentration of total N (0.9–6.6 g per kg), mass C:N (10–52), and N:P (2–15; Osborne et al., 2007).

Consistent with other wetland systems, higher levels of N mineralization are found in recently deposited litter and detrital floc material than in the highly decomposed underlying peat (White and Reddy, 2000). Draining of peat soils results in higher levels of N mineralization, particularly for the decomposed peat (Martin et al., 1997). This observation is similar to that of other organic-based systems where high amounts of labile N forms are protected under anaerobic conditions. P additions stimulating microbial communities also result in N release from Everglades soils (Inglett et al., 2007; Newman et al., 2001; White and Reddy, 2000). This N is released as both NH_4^+ (Inglett et al., 2007; Newman et al., 2001) and DON (Inglett et al., 2007). Concentrations of 1.0 mg P L^{-1} were sufficient to enhance potentially mineralizable N rates in bottle studies (White and Reddy, 2003), while experiments using P additions to mesocosms demonstrated a net flux of NH_4^+ after only one month from soils receiving P that loading rates as low as 0.4 g P $\text{m}^{-2} \text{y}^{-1}$. Elevated levels of P combined with increased macrophyte productivity result in threefold higher levels of potentially mineralizable N in areas affected by canal inflows (White and Reddy, 2003). Yet, at extreme levels of P loading, higher rates of N immobilization and assimilation can result in lower levels of N release (Inglett et al., 2007). A graphical summary of the impact of P loading on N mineralization and N limitation is presented in Figure 5.

3.4 Photolysis

Dissolved ON is a major component of transportable N throughout the Everglades (Jones et al., 2005; Qualls and Richardson, 2003) approaching 95% of the total water column N. The composition of this DON is derived mostly from leaching of soluble components (proteins) for macrophytes, periphyton, and soils, with a small component derived from bacterial biomass (Jones et al., 2005, 2006; Maie et al., 2006). Despite being considered chemically

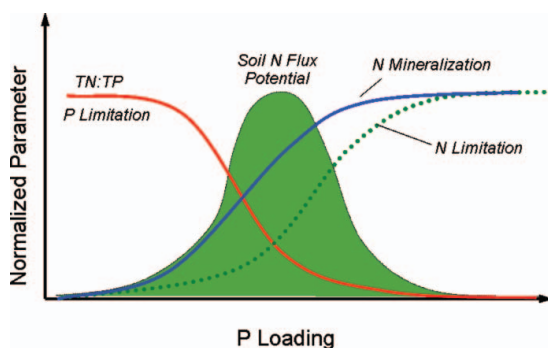


FIGURE 5. Idealized diagram depicting response of nitrogen flux processes to phosphorus (P) loading in Everglades systems. (This figure is available in color online).

fresh, much of this DON is considered recalcitrant with only a small portion of this DON considered bioavailable (Jaffé et al., 2005; Maie et al., 2006). In addition to enzymatic processes, another mechanism that can hydrolyze organic N molecules is photolysis by exposure to sunlight (UV and PAR; Qualls and Richardson, 2003). There is a differential in mineralization of C relative to N photolysis, which is higher for C (20.5% in 21 days' exposure, 1% d⁻¹) than N (7% in 21 days' exposure, 0.3% d⁻¹). Exposure to UV light during surface water transport from the northern Everglades systems to the south is a potentially a dominant mechanism to reduce levels of DON (Figure 2).

3.5 Ammonia Volatilization

The product of mineralization is NH_4^+ , which is a biologically available form of N. In high-pH conditions (e.g., >8.5), chemical speciation increasingly favors the gaseous ammonia form, which can volatilize from the water column. High-pH regions can occur in several parts of the Everglades system including shallow water areas with extensive algal photosynthesis or in areas dominated by SAV beds. In areas of high periphyton productivity, pH can be highly variable and during the day often exceed 10. Such extremes may be a reason why floodwater NH_4^+ levels are generally low.

3.6 Ammonium Oxidation

The process of nitrification converts NH_4^+ into NO_3^- . In the Everglades, this process is very poorly understood, but likely follows theory similar to other wetland systems. Accordingly, areas where NH_4^+ encounters oxidized zones are the locations for nitrifying microorganisms, including locations within the water column and surfaces (plant stems, epiphyton), the soil water interface, and plant oxidized rhizospheres. It is also likely that there is a tight coupling between this process supplying NO_3^- and denitrification converting the NO_3^-

into N_2 gas. To date, only one study has explored rates of nitrification in Everglades soils (White and Reddy, 2003). In this study, potential rates of nitrification were measured for WCA-2A soils in 2-day incubations using stirred reactors. Rates were highest in the detritus (average of $28.5 \text{ mg N kg}^{-1} \text{ d}^{-1}$) and surface soils ($12.8 \text{ mg N kg}^{-1} \text{ d}^{-1}$) and were significantly correlated with levels of extractable NH_4^+ .

More recently, organisms have been identified in Everglades soils which are capable of anaerobically oxidizing NH_4^+ using nitrite (the Anammox process; Penton et al., 2006). The product of the Anammox reaction is N_2 gas making this process similar in biogeochemical function to denitrification and raising the question of the importance of this process to N budgets. Anammox bacteria appear to be autotrophic, and the presence of organic matter slows the overall process. Another important requirement for the Anammox process is the presence of NO_2^- , a seldom-measured transient compound of the nitrification, denitrification, and dissimilatory reduction of nitrate to ammonium (DNRA) pathways. Nitrite accumulation is possible, however, and several conditions may be adequate for NO_2^- accumulation leading to Anammox activity including (a) a lack of suitable organic substrates or high concentrations of NO_3^- relative to organic C leading to incomplete denitrification; (b) low pH and low oxygen relative to NH_4^+ can result in partial ammonium; and (c) at high pH, free ammonia (NH_3) can inhibit *Nitrobacter* spp., which are responsible for the oxidation of NO_2^- (Anthonisieu et al., 1976; Smith et al., 1997).

These scenarios have been reported in the aquatic environment (Herbert, 1982; Smith et al., 1997) with higher than expected NO_2^- levels ($100\text{--}200 \text{ mg N l}^{-1}$) being found in some European watersheds receiving nitrogenous pollution (Kelso et al., 1997; Smith et al., 1995). In one study, NO_2^- accumulation in six Irish rivers was found to coincide with NO_3^- declines via DNRA activity in areas with high organic matter contents (Kelso et al., 1999). All of these studies suggest NO_2^- may be much more abundant than previously thought, and all of these conditions may be found in Everglades systems, either as intrinsic or transient conditions. Therefore, it is likely that NO_2^- levels may be sufficient to support Anammox in more aquatic ecosystems than previously thought.

3.7 Denitrification and Dissimilatory NO_3^- Reduction

This aspect of the Everglades N cycle is perhaps the most poorly studied given its significance to the overall N cycle and budgets of N within the Everglades system. The dominance of peat soils with ample carbon and anaerobic conditions suggests a high capacity for denitrification in the Everglades as a whole. Therefore, as in most anaerobic systems, NO_3^- availability is generally the limiting factor. In eutrophic areas, macrophyte shading and net heterotrophic conditions in the water column limit the production of

NO_3^- (White and Reddy, 2003), therefore significant rates are likely only observed in areas receiving the small amounts of NO_3^- through direct canal inputs. It is likely a much more complex situation in the natural Everglades systems where oxygen levels in the water column can be high leading to higher rates of nitrification, with subsequent denitrification of NO_3^- by diffusing into anaerobic soil or at night when low oxygen levels can extend into the water column. Furthermore, denitrification has been observed to be an active component of cyanobacterial mats with shifting periods of oxygen production and consumption (Joye and Paerl, 1993, 1994), so it is also likely that simultaneous nitrification and denitrification processes would be occurring in areas of thick periphyton accumulation.

Recent advances in our understanding of the N cycle have identified a renewed importance of a number of processes affecting the fate of NO_3^- (Burgin and Hamilton, 2007). In highly reducing conditions with excess carbon relative to N, NO_3^- may be converted to NH_4^+ through the process of dissimilatory NO_3^- reduction to NH_4^+ (DNRA). This process has been little studied in Everglades environments, but because there are many highly reducing peat environments, it is plausible that this DNRA could be a significant fate of NO_3^- . Alternatively, it may also be true that with few mechanisms contributing to NO_3^- production in continuously anaerobic areas, DNRA may be of limited importance in the fate of NO_3^- in the Everglades.

There are also other pathways that may result in the reduction of NO_3^- in areas closer to the zones of nitrification. For example, the presence of methane as well as significant inputs of sulfur does not exclude the possibility of alternate pathways of denitrification using electron donors other than organic matter. In particular, the presence of methane in peat soils could be leading to the conversion of NO_3^- to N_2 coupled with the oxidation of methane as it diffuses through the aerobic/anaerobic interface at the soil surface or through periphytic growths and floating mats. It is also possible that eutrophic areas generate significant quantities of sulfide, which may diffuse into areas where NO_3^- is present and serve as the electron donor for the reduction process. Once again, these pathways have been largely unexplored in the Everglades systems.

4 HYDROLOGIC UNITS

4.1 Okeechobee/Everglades Agricultural Area

The primary systems serving as the headwaters for the Everglades watershed are Lake Okeechobee and its basin and the EAA. Inputs and outputs of nutrients to the systems can have a direct effect on downstream systems via their export of nutrients. Similar to that observed for P, the Okeechobee basin is a significant source of N to downstream systems. The primary form of this N is that of organic N derived from leaching of rangelands, connected

wetland systems in the flow path, and Lake Okeechobee itself. The concentration of N leaving Lake Okeechobee is approximately 0.9 mg L^{-1} , with the predominant N form being DON. In Lake Okeechobee, elevated levels of P can also lead to blooms of N_2 fixing cyanobacteria which result in increased N levels for export (Philips et al., 1997). However, the proportion of N in Lake Okeechobee produced by this mechanism remains limited based on the measured outflow loads of N (Zhang et al., 2009).

The EAA can also be a significant source of N from oxidation of peat/histosols (Capone et al., 1995; Hanlon et al., 1997). In particular, drained soils produced soluble N ranging from 217 to $509 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ while flooded soils release approximately one third less. Flooded conditions result in less N loss due to a reduction of the NO_3^- component in these drainage waters (less than 3% of the TN; Martin et al., 1993). The lack of nitrification under flooded conditions and the denitrification of any available NO_3^- explain this observation. Overall, different management approaches (e.g., for vegetables, sugarcane, rice, flooded fallow) and the variety of the EAA soils leads to a wide range of concentrations in TN ($1.83\text{--}77.04 \text{ mg L}^{-1}$), NH_4^+ ($<0.02\text{--}6.02 \text{ mg L}^{-1}$), and NO_3^- ($<0.04\text{--}32.01 \text{ mg L}^{-1}$) in canal drainage waters (Capone et al., 1995). Average values of TN, NH_4^+ , and NO_3^- in canal drainage waters are 5.0, 0.41, and 1.0, respectively (Capone et al., 1995). Based on these concentrations, it is apparent that the dominant form of N in these drainage waters is organic, with levels of 5.0 mg L^{-1} DON in shallow EAA pore water, 1.8 mg L^{-1} DON in ditches, $\sim 1.5 \text{ mg L}^{-1}$ DON in canals leaving the EAA having been observed (Qualls and Richardson, 2003).

4.2 Stormwater Treatment Areas

The primary function of the STAs is to remove P and therefore N cycling is of secondary importance. Like other systems receiving P loading, the STA systems become progressively more N-limited as they accumulate P. In this way, the uptake of P and accumulation in the soil is regulated by N availability, which should cause the stoichiometric limit to plant growth and soil P accretion. This theory is supported by N:P ratios of the plants in these areas (indicating N limitation; White et al., 2004) and in other P-impacted Everglades systems, where N and P accumulation rates are closely correlated (Craft and Richardson, 2008; Reddy et al., 1998). Biological N_2 fixation, especially that associated with macrophyte litter, has not been measured but should be enhanced based on findings by Inglett et al. (2008) for high-P areas of WCA-2A.

Nitrogen loading from canals is primarily in the form of DON with only small amounts of NH_4^+ and NO_3^- . The small amount of NO_3^- present in the canal waters is essentially completely removed by denitrification in the highly eutrophic areas near the canal discharges. In these areas denitrification is limited by the availability of NO_3^- , which is only produced in aerobic

areas such as the water column or oxidized rhizospheres of wetland macrophytes (White and Reddy, 1999, 2003). The high productivity of these areas combined with the shading of dense macrophytes results in poor oxygenation of the water column, and therefore NO_3^- production is highly limited in the STA areas. High levels of P in these areas fuel the rapid turnover of macrophyte detritus resulting in production of NH_4^+ and DON compounds (White and Reddy, 2000).

In periphyton- or SAV-dominated STAs, water-column oxygen production is enhanced leading to greater potential formation of NO_3^- . In areas with intense productivity by periphyton or SAV, pH values may frequently rise above 8.5 and in many cases approach 9 (*pers. obs.*). Under these high-pH conditions NH_4^+ is quickly converted to ammonia gas, which can be lost from the system through volatilization. To date, there has been no study demonstrating the importance of this process, which would likely be limited by the availability of NH_4^+ in the water column. Lowering of water column N levels by ammonia volatilization could have an impact on the ability of periphytic or SAV-based treatments to remove P as N is required for production of the biomass to sequester P in organic forms.

4.3 Water Conservation Areas/Northern Marshes

The WCAs have had a history similar to that of the STAs, where canal water was discharged for the purpose of nutrient removal and water storage prior to water being discharged into Everglades National Park. The nutrient and vegetation changes in these areas are well documented (see other articles in this volume), with an overall accumulation of P near the discharge areas and a shift from the native sawgrass and sloughs to monotypic stands of cattail. In the areas with high P loading it has been observed that a shift from P to N limitation occurs. This is evident in the low N:P ratios of water column nutrients. Algal growth assays also indicate that N limitation is prevalent in areas near the discharges (McCormick and O'Dell, 1996).

Increased N limitation reduces primary production. This is evidenced by low N:P ratios of plants (see review by Noe et al., 2001) and most recently through the use of natural abundance ^{15}N as an indicator of plant N demand (Inglett et al., 2009). Thus, following addition of P, N availability is a significant regulator of cattail expansion. Rates of N_2 fixation by cyanobacteria in the water column as well as microbes in the soil are increased in these areas (Inglett et al., 2004). This elevated N_2 fixation combined with accelerated decomposition through microbial activity results in a high gradient of NH_4^+ and dissolved organic N concentrations between shallow pore water (6 mg L^{-1}) and floodwater (3.5 mg L^{-1}) in these areas (Qualls and Richardson, 2003). For this reason, there is a significant flux of excess N from P-impacted areas.

As already mentioned, in nonimpacted areas of the WCAs, high rates of N_2 fixation can be observed (Inglett et al., 2004). Thus, there are two

potential sources of N to the low-P areas, namely N_2 fixation and surface water inputs of N primarily in the form of DON. Very little is understood about the dynamics and interaction of the periphyton community and surface water N. The high rates of N_2 fixation imply a high demand for N in these communities while the large quantities of DON suggest a low bioavailability of this N source. Both NO_3^- and NH_4^+ are considered available forms of N in the water column. Studies using the stable isotope ^{15}N are able to trace the fate of N within systems, however to date, only one study attempting to trace N through system components has been conducted in the WCAs. In this study by Inglett et al. (Inglett et al., manuscript in prep) added $^{15}NH_4^+$ was used to track N uptake, conversion, and fate in a low-P slough system of WCA-2A. Among the key findings of this study were a very rapid uptake of NH_4^+ from the water column ($0.47 \text{ mg N m}^{-2} \text{ h}^{-1}$) and very high biomass specific uptake rates by the floating periphyton mats ($0.99 \text{ mg N g}^{-1} \text{ dw h}^{-1}$). There was also a very high rate of conversion of NH_4^+ into the water column DON with up to 27% of the added N being transformed after three hours. Two pathways may be responsible for the appearance of ^{15}N in the DON pool including bacterial immobilization onto DOM or active uptake and excretion of organic compounds (e.g., amino acids) by algal communities (Myklestad, 1995).

After one month of the dosing study, Inglett et al. recovered approximately 40% of the added N indicating both a significant accumulation rate for N in these systems and a potentially low rate of N loss through denitrification. Qualls and Richardson (2003) concluded that surface water inputs of N to WCA-2A were balanced by the outputs requiring that much of the N being fixed into this system should be accumulated and not balanced by denitrification. Using isotopic markers (^{137}Cs , ^{210}Pb), Craft and Richardson (2008) indicated a range of N accumulation rates within the Everglades system from <2 to $>14 \text{ g N m}^{-2} \text{ y}^{-1}$. The lowest rates recorded were in the Loxahatchee National Wildlife Refuge (WCA-1) while the highest rates were observed in the P enriched areas of WCA-2A. These findings suggest that soil N accumulation in the WCA-2A has increased in response to the long-term nutrient loading from the agricultural drainage as a result of higher peat accretion rates and incorporation of nutrients into the peat. In the summary by Craft and Richardson (2008), higher rates of N accumulation were also observed in the southern, deeper water areas of WCA-3A indicating that the effect of hydroperiod may have a significant effect on N accumulation rates, but this could also be occurring through the accumulation of organic matter or with processes surrounding the flow-dependent transport of flocculent material (floc).

4.4 Southern Marshes/Everglades National Park

Located between the WCAs to the north and the mangrove ecotone to the south, are the freshwater sloughs and marshes of the southern Everglades.

This region includes the ridge and slough ecosystem of Shark River Slough (SRS), which is located within the boundaries of the Everglades National Park (ENP), as well as the marl-based wet prairies of Taylor Slough (TS) and the C-111 Basin/ENP Panhandle. Much like in the freshwater marshes to the north, P remains the limiting nutrient in the southern Everglades (Noe et al., 2001). However, there is a gradual transition to more N-limited systems occurring further downstream towards Florida Bay where P derived from the Gulf of Mexico is much more abundant (Childers et al., 2006). Despite the fact that P is limiting in the southern Everglades, N remains in constant flux, cycling throughout the various ecosystem components (Wozniak et al., 2008).

Like the marshes of the northern systems, the flow of water across the southern Everglades landscape is dictated by the dominant hydrological inputs to the region. These points of freshwater inflow also represent potential sources of N to southern Everglades sloughs and marshes primarily through the addition of DON compounds (Rudnick et al., 1996). In addition to being a source of N, hydrology also plays a vital role in shaping ecosystem structure and function, and is essential in defining the rate of N processing and the eventual export. Periphyton is a key component of the N cycle in the southern systems as well. Although no values of N₂ fixation have been reported, the dominance of cyanobacterial communities again suggests that high rates may be possible in southern marshes. Unlike the peat-dominated SRS, TS and the C-111 Basin are dominated by calcium carbonate rich marl soils. This difference is primarily driven by the fact that TS and C-111 have lower water levels than the long-hydroperiod, deeper sloughs of SRS. These marl systems undergo a seasonally pulsed dry-down period that is directly associated with decreased rainfall during the dry season (Ewe et al., 2007). Drawdowns and dryouts in these marshes would lead to a periodic cycle of reduced periphyton productivity and result in aerobic events (increasing rates of mineralization and nitrification), and thus, are key to effecting the fate of N in these systems. Despite this potential, however, little is known about importance of these processes.

Calcareous periphyton mats are capable of withstanding these periods of dry-down, showing resilience upon rehydration (Gottlieb et al., 2005; Thomas et al., 2006). In addition to the dominant macrophyte (sawgrass) cyanobacterial mats are of critical importance to both primary production (Iwaniec et al., 2006) and the N cycle. Mean TN for periphyton mats in the C-111 are 7.71 mg N g⁻¹ dry wt and periphyton molar N:P is 78; in Taylor Slough periphyton TN equals 9.05 mg N g⁻¹ dry wt (Iwaniec et al., 2006). The high productivity of these mats (similar to the periphyton of the northern systems) makes it is clear that periphyton mats are a vital ecosystem component with an important role in the initial uptake of canal-borne inorganic N (Wozniak et al., 2008). For example, Rudnick et al. (1999) observed that no change in TN occurs over a transect from canal discharge into Taylor Slough, but a decrease in the DIN fraction from 26% to less than 5%.

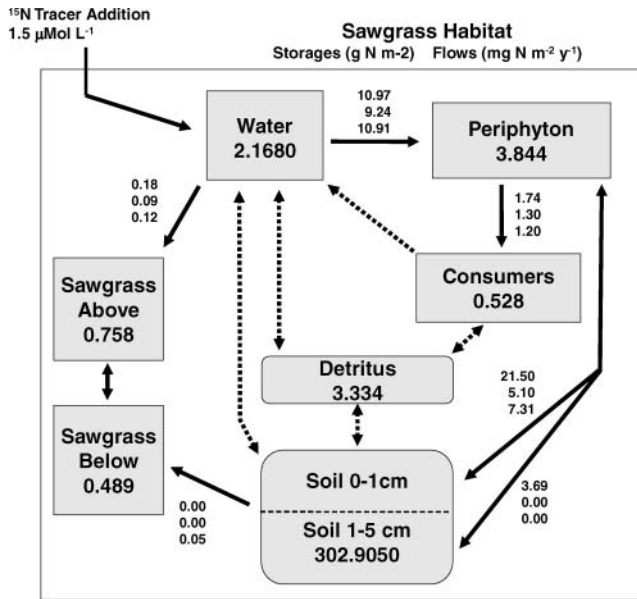


FIGURE 6. Box-model depictions of isotope dosing experiment of Wozniak (2006) in the sawgrass dominated zones of C-111 marsh (see text for discussion). Values in boxes represent storages of N (g N m⁻²) while values above each arrow refer to calculated rates (mg N m⁻² y⁻¹) for recovery of added label after 21 days. Individual rate values refer to rates in response to addition of 0 (top value), 6.66 (middle value), and 66.6 mg P m⁻² (bottom value).

Also, Wozniak et al. (2008) conducted a similar isotope dosing study to that of Inglett et al. In this study, Wozniak et al. (Manuscript in prep 2008), added ¹⁵NO₃⁻ and traced it into ecosystem components (Figure 6). The major conclusion of this isotope tracing study was similar to that of Inglett et al. (Inglett et al., Manuscript in prep) where periphyton exhibited a high potential for DIN uptake (ranging from 11.0 to 20.9 mg N m⁻² y⁻¹ at sites along both the canal-marsh and mangrove interfaces; Wozniak, 2006). Uptake rates were highest for periphyton at the mangrove ecotone while the effect of added P (up to 66.6 mg P m⁻²) was inconsistent, having no clear effect on uptake rate at the canal-marsh site and reducing uptake at the mangrove interface. Another interesting finding of the study by Wozniak (2006) was a very high incorporation of added N into consumers grazing on periphyton biomass. The long term effect of P additions were mixed, however, with no clear effect on periphyton N uptake and a lower overall recovery of added N in the consumers, soil, and macrophyte components after 21 days (Figure 6). The reduction of N recovery may reflect the increase in N availability resulting from increase microbial turnover of N following initial P addition.

Recent mass balance studies show that hydrologic import to Taylor Slough was within the range of estimated sediment P burial, while N sediment burial exceeded estimated hydrologic N import (Sutula et al., 2001).

These N flux discrepancies were attributed to N₂ fixation and denitrification. However, the rates of these important processes were assumed, and other N transformations that may also be important have not been quantified. The N budget of these systems is particularly important in light of potential shifts in vegetation communities associated with increased freshwater delivery, and thus altering upstream N and P fluxes. It is clear that these freshwater sloughs and marshes can no longer be considered as passive conduits for N, providing the uninterrupted passage for N to downstream coastal systems. Rather, the freshwater ecosystems of the southern Everglades must be viewed as vital components of the greater Everglades landscape, which have a significant influence in determining the degree of processing, transformation and ultimate fate of N to downstream ecosystems.

4.5 Mangrove Fringe

Mangrove forests border the Florida Coastal Everglades and influence the net exchange of organic and inorganic material between these systems. Although mangrove wetlands cover a large expanse of the Southern Everglades there is limited information about the role of these wetlands as sinks, sources or transformers of N (Chen and Twilley, 1999; Koch and Snedaker, 1997; Pelegri et al., 1998). Despite the potential of mangrove sediments for the removal of N from surface waters (Rivera-Monroy et al., 1995; Rivera-Monroy and Twilley, 1996), there is no complete data set for constructing N budgets (Figure 7) or to assess the effect of P enrichment on N cycling in mangroves of the Florida Everglades ecosystem.

Organic N concentrations in water flowing from the higher wetlands decreases in the mangrove zone where some of the reductions are indeed higher than expected due to conservative mixing indicating net removal of TN (Rudnick et al., 1999). Concentrations of N inputs to Shark River Slough are about two times higher than Taylor Slough (Rudnick et al., 1999). A distinct seasonality (wet vs. dry seasons) in nutrient concentrations indicates that the main source of N into the mangrove forest is advecting water masses from the Gulf of Mexico (Rivera-Monroy et al., 2007). Nitrate and NH₄⁺ concentrations typically range from 0.0 to 0.05 and from 0 to 0.07 mg L⁻¹, respectively, while mean TN concentrations are approximately 0.53 mg L⁻¹ (Rivera-Monroy et al., 2007). DIN concentrations in water flowing down the Taylor Slough from the upper wetlands increase in the mangrove tidal creeks and Florida Bay to about 0.10 mg L⁻¹ (Rudnick et al., 1999).

Nutrient fluxes within the mangrove ecotone have been quantified on a smaller scale (<20 m²) where S. E. Davis et al. (2001b) showed that in a dwarf mangrove wetland in Taylor Slough there was consistent uptake of NH₄⁺ (0.09–0.44 mg m⁻² h⁻¹) and of TN (1.37–7.03 mg m⁻² h⁻¹), whereas NO₃⁻ (0.1–1.95 mg m⁻² h⁻¹) was released off to the water column. Fluxes were studied in the same area using the flume technique along Taylor River.

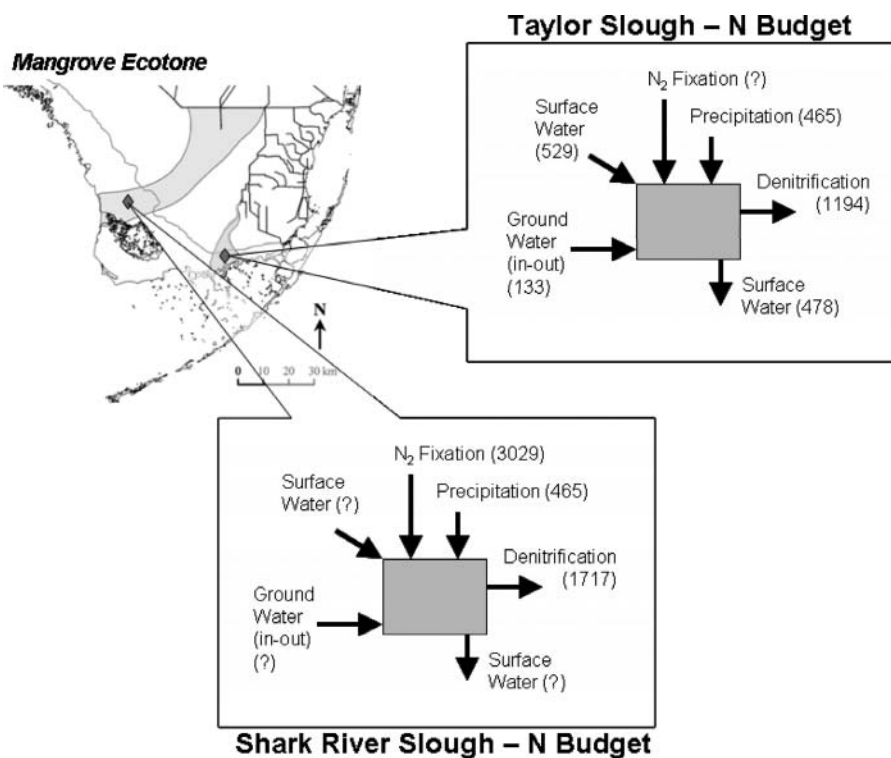


FIGURE 7. Summarized budget depiction of nitrogen inputs and outputs ($\text{mg N m}^{-2} \text{y}^{-1}$) using available data for the mangroves of Taylor and Shark Rivers. Based on the work of Pelegri et al. (1997), Rudnick et al. (1999), Sutula et al. (2001, 2003), and Rivera-Monroy et al. (2007).

No net annual import or export was found and direction and magnitude of nutrient fluxes between the mangrove wetland and the water column was correlated with wind, precipitation, and upland runoff (S. E. Davis et al., 2001a; S. M. Davis, 2004). Fluxes of TN from the Taylor creek mangrove ecotone into Florida Bay are significant ($26.8 \times 10^6 \text{ g yr}^{-1}$), but the similarity between this N input and that derived from atmospheric deposition has led to the hypothesis that hydrological restoration of the Everglades is unlikely to affect the Florida Bay via increased N loading from the Everglades (Rudnick et al., 1999).

Nitrogen fixation represents the new source of N to the system. It has been recognized that N₂ fixation accounts for 15–64% of N immobilization during decomposition of mangrove leaf litter on the forest floor (van der Valk and Attiwill 1984; Woitchik et al., 1997). In spite of this, there are few studies that have assessed the contribution of this N source to the Everglades mangrove forests (Pelegri et al., 1997; Pelegri and Twilley, 1998; Table 2). Pelegri et al. (1997) estimated rates of N₂ fixation on leaf litter, sediments,

and pneumatophores in two mangrove sites located along a fertility gradient in the Shark River Slough. Overall rates of ethylene production ranged from 0 to 539 nmol C₂H₄ g dry wt⁻¹ h⁻¹, with higher rates (7.3–539 nmol C₂H₄ g dry wt⁻¹ h⁻¹) observed in aged litter. Based on these rates, Pelegri et al. (1997) estimated that N₂ fixation could account for 45 to 100% of the total N immobilized in leaf litter (1–8 mg N dry wt⁻¹ N enrichment). However, N₂ fixation only could supply at about 7% (8.3 mg N m⁻² d⁻¹) of the N required (53 mg N m⁻² d⁻¹) for mangrove growth into this forest.

There is presently no published information on *in situ* denitrification rates in the mangrove ecotone region. However, recent studies along Taylor and Shark River using the isotope pairing technique (Nielsen 1992; Steingruber et al., 2001) and ¹⁵N flux method (Mulvaney and Boast, 1986; Mulvaney and Kurtz, 1982) indicate that denitrification rates were similar between riverine and scrub mangrove regions (Rivera-Monroy et al., 2007). Rates ranged from 0.01–0.35 mg N m⁻² h⁻¹ (in May 2007). The highest denitrification rate (0.20 mg N m⁻² h⁻¹) in SRS was registered after enriching cores with added NO₃⁻. This particular study also included estimates from a tree island ecosystem where the lowest denitrification rates were recorded (<0.07 mg N m⁻² y⁻¹), apparently due to the high demand for inorganic N in highly organic sediments. When inorganic enrichment was increased in cores collected in May 2008 in one site in Taylor river, denitrification rates doubled, reaching up to 1.05 mg N m⁻² d⁻¹. These results show a high potential for N₂ production, but overall denitrification rates are very low in the mangrove ecotone due to low NO₃⁻ availability in pore waters and water column throughout the year.

Sediment N and P accumulation rates for freshwater and estuarine mangrove wetlands have been reported for Taylor Slough in southern Everglades (Sutula et al., 2001). Estimates were calculated based on a 1.5-year study of seasonal and annual water and nutrient budgets of the Taylor Slough/C-111 basin wetlands. N burial rates for freshwater wetlands (1.32–2.97 g m⁻² yr⁻¹) were consistently lower when compared to mangrove forests (3.60–7.20 g m⁻² yr⁻¹). Unpublished results show greater nutrient accumulation rates along the Shark River and Taylor Slough mangroves (5.1–25.0 g m⁻² yr⁻¹) than those reported by Sutula et al. (2001) in the same area. These higher rates are within the range of values reported for wetlands in the northern Everglades (2.01–14.1 g m⁻² yr⁻¹; Craft and Richardson, 1993; Reddy et al., 1993).

5 RESEARCH NEEDS

5.1 N Cycle Processes

The presence of extreme P limitation generally leads to the supposition that apart from organic matter accumulation, the only significant fate of N throughout the Everglades system is to pass through or be transformed rather

than accumulate (Qualls and Richardson, 2003). However, high uptake potential for N (Inglett et al., Manuscript in prep) Wozniak et al., 2008) with rapid production of DON (Inglett et al., Manuscript in prep) in both the northern and the southern marshes indicate that N cycling is highly significant to the functioning of the periphyton as well as the Ridge-Slough system. In this regard, N movement is not just a function of in/out balance, but rather is a function of N processes related to biotic uptake, excretion, and decomposition. Much of the N cycling through the Everglades occurs in the form of DON, but processes of mineralization, nitrification, and denitrification affect N fate as well. The studies of isotope dosing and tracing have indicated that available N forms are rapidly taken up with a subsequent rapid conversion to DON. The exact pathways and processes responsible for this conversion are unidentified, and moreover the ecological role of this is unexplained.

Most of the DON is not available for biotic uptake (Jaffé et al., 2004), and exposure to UV light has been shown to mineralize more N from this pool than enzymatic processes (Qualls and Richardson, 2003). Recalcitrance/lability of this DON is undoubtedly tied to its source. Therefore differences between algal and macrophyte as well as between individual types of macrophytes (e.g., *Typha* vs. *Cladium*) could be a significant determinant of N fate. For this reason, shifts in macrophyte species composition and abundance may have important implications for N fate, especially for downstream systems. Ultimately, the processing of N within the mangrove systems directly determine the export of N to Florida Bay, and it has been shown that organic N forms may pose an elevated threat for cyanobacterial bloom formation in these areas. Presently it is unknown how the cycling of N in the northern marshes may indirectly affect this process.

The Everglades is a highly diverse and unique ecosystem, and our understanding of its processes are still limited. The functioning of many of the intricate components and biotic communities gives rise to the higher-order functions of the Everglades ecosystem. The presence of cyanobacterial N fixing communities and the role of N in decomposition indicate that N processes are integral to the functioning of the ecosystem. Very little has been studied in this regard, and combined with our recently discovered importance of alternate N-cycle processes, there is a great potential for increasing our understanding in this area. Pathways utilizing alternate electron donors for denitrification is a potentially promising example. In particular, the abundance of methane in the systems indicates there may be a high potential for its use in denitrification. Also, identification of the presence of anaerobic NH_4^+ oxidizing bacteria in soils of WCA-2A also indicates a potential for the Anammox pathway in the Everglades.

5.2 Role of Hydrology in the Everglades N Cycle

The abundance of peat and organic N forms in the Everglades soils highlights the concern for hydrologic management to prevent exposure of these soils

and subsequent enhanced decomposition and microbial oxidation releasing stored N to downstream Everglades systems. This has been well studied in the EAA to the north, but also has significant implications for N cycling in southern systems such as marl prairies and tree Islands, where hydrologic connection was shown to be a major factor contributing to nutrient sequestration (in particular N) and controlling litter decomposition (Troxler and Childers, 2009). Hydrology also has implications for the functioning of cyanobacterial mat communities throughout the Everglades system (Gottlieb et al., 2005). For example, it is unclear how water depth affects balance of net phototrophy or heterotrophy in periphyton (floc or benthic mats), and thus it is also unclear what effect water depth has on its potential for N uptake or the functions of N_2 fixation, nitrification, and denitrification. The effect of other environmental variables (e.g., temperature, light, fire) on the function of these periphyton and surficial floc communities as an N sink or source is presently undetermined.

Floc (i.e., flocculent material) is found in the deeper water sloughs and long-hydroperiod marshes and is low-density detrital organic material found directly above the soil and comprises sloughed periphyton material, detritus from vegetation, and microorganisms (Neto et al., 2006). Due to decreased hydrological flow and compartmentalization over past decades, deeper water habitats of the ridge and slough landscape have begun to fill in with soil, resulting in a system that is more uniform both topographically with similar vegetation assemblages (Leonard et al., 2006). Of particular interest is the importance of floc in the processing and transport of N. However, to date little work has been done at the ecosystem scale to gauge N processing (Wozniak et al., 2008), the role that floc plays in site-specific N cycling, or the landscape scale potential for downstream transport of floc-N

5.3 N Cycling in the Mangrove Ecotone at the Landscape Level

Although there is limited information on N cycling in the mangrove ecotone, it is possible to identify some general trends in the Shark and Taylor River regions (Figure 7). Sutula et al. (2001, 2003) estimated a net annual net import of $649 \pm 263 \text{ mg N m}^{-2} \text{ yr}^{-1}$; they hypothesized that this residual should be equal to the sum of denitrification and burial minus N_2 fixation (assuming no change in plant and faunal biomass). This annual import needs to be revised as more information is obtained from in situ experiments, particularly since the budget of Sutula et al. (2001) was constructed using denitrification and fixation rates from other areas. In contrast to the TS region, there is not enough information on fluxes to estimate an N budget for SRS region. Lack of information on groundwater, surface water intertidal exchange, and water flow fluxes at the mangrove ecotone boundary upstream limit the construction of N budgets for this region. As hydrologic restoration activities are implemented at the Northeast Shark Slough over the next three years, it is critical to perform field studies to assess potential eutrophication risk in

the Shark River estuary and adjacent coastal systems (e.g., Ponce de Leon Bay).

6 IMPLICATIONS FOR RESTORATION

6.1 Hydrologic Restoration

Presently, of particular interest in the southern Everglades is the significant amount of hydrological restoration underway. The two major hydrological restoration efforts include the deconstruction of the L-29 levee with the raising of Tamiami Road (Tamiami Bridge Project) and the construction of the C-111 Spreader Canal. The Comprehensive Everglades Restoration Program (CERP) will result in a considerably increase the total flow of freshwater through the southern Everglades and increase the degree of hydrological connectivity across the marsh landscape.

This increase in freshwater inflows has the potential to impact the N cycle via changes in N delivery (N-loading) and the physical processing of N (flow-mediated processing). The Tamiami Bridge project and the construction of the C-111 Spreader Canal will have pronounced influences on the movement of water from WCA 3A to SRS; however, the potential of nutrient enrichment and increase N loading to SRS is possible. How this hydrological restoration will impact the N cycling of SRS and more downstream coastal ecosystems (i.e., the mangrove ecotone) is unknown. Work done in the C-111 basin after the removal of the southern levee indicates that restoration of hydrology will have significant impacts on N cycling. These include near-canal effects on nutrient concentrations (i.e., elevated N concentration; Parker, 2000; Wozniak *et al.*, 2008), tree island structure, and nutrient dynamics (Troxler *et al.*, 2005). While increasing hydrological connectivity and water flow is often considered to be a positive restoration step, the effects of elevated water levels have the potential to decrease macrophyte growth, specifically in sawgrass (Childers *et al.*, 2006). The C-111 spreader canal also has the potential to disrupt the wet/dry seasonality of the system unless regulated.

6.2 Habitat Restoration

Restoration of impacted areas is a key component of managing the Everglades ecosystem. The N cycle plays a key role in this process both as a limiting nutrient with an impact from P (contributing to the expansion of cattails), and as a limiting nutrient during reestablishment of vegetation following soil removal to eradicate Brazilian pepper (Inglett and Reddy, 2006). Other ecological drivers such as hydrology and fire undoubtedly play an integral role in affecting N. Hydrology and fire are already major consideration of the Everglades restoration scheme, but in addition, determining the forms,

availability, and sources of N should also be a major focal point of our study in the Everglades system.

One technique presently being explored in the highly eutrophic areas is to remove the cattails allowing light to penetrate into the water column (Cattail Habitat Improvement Project; http://www.sfwmd.gov/portal/page/portal/xrepository/sfwmd_repository_pdf/cattailhabitatimprovementproject.pdf). The goal of this opening of the canopy is primarily to stimulate autotrophic processes and allow a more complete food web to develop. This approach also has implications for N cycling in these highly impacted areas. The addition of light will increase greatly the production of oxygen in the water column leading to enhanced rates of nitrification with the subsequent likelihood of denitrifying this NO_3^- once it is produced. Increased autotrophic growth of cyanobacteria should lead to enhanced rates of N_2 fixation. Also, the exposure to UV light should result in an enhanced photodegradation of DON compounds. Because the process of N_2 fixation and denitrification could potentially cancel one another, it is uncertain what the net effect of cattail habitat improvement approach will have on the N budget of these impacted areas.

6.3 Nutrients

It is well known that P has had a major impact on the N cycle in the Everglades. As discussed in this review, in low-nutrient areas, elevated P enhances decomposition and release of N forms from the peat soil. In contrast, in areas where excess P has been accumulated, N availability and potentially increasing P accumulation. For this reason, N availability and cycling in STAs should be explored to better understand P retention in these newly accreted soils. Between these two extremes of P availability, there is a zone of stimulated N mineralization but in the absence of elevated N demand. This situation leads to a zone of impact where enhanced N mineralization results in a leading front of increased N flux (as NH_4^+ and DON) from the soils into the water column. The fate of this N is unknown, however throughout most of the Everglades this likely has little negative effect. Only in the regions immediately upstream from the mangrove systems does this pose a significant concern.

7 SUMMARY

It is clear that there is a distinct need for additional research on N-cycle dynamics in the Everglades. Many aspects of the cycle including system components, processes and pathways, and rates for use in constructing N budgets are poorly understood. Little is known about the specific role periphyton mats play in the process of N fixation in marl wet prairies, how

near-canal marshes may act to buffer downstream ecosystems from potential N-loading events, or the specifics of how these marshes internally process N to determine subsequent N fate. The need to further our understanding of N dynamics is further highlighted by the potential for large-scale impacts by restoration (primarily hydrological modifications) across the Everglades landscape.

It is vital to collect baseline data on N processes prior to restoration efforts so that the effects of increased freshwater flows can be identified. System managers will also need to consider relationships of the ecological role of N-cycle processes to function and health of the natural Everglades system. Natural and managed events such as hurricanes, droughts, and fires will have to be considered in light of effects on the biotic and abiotic system components and their consequences for the input, transformation, and export of N. This will require a keen awareness of water quality in more northern Everglades' marshes, as well as the role that N plays in the restoration of highly impacted areas. Furthermore, our understanding of N dynamics is also of critical value in determining how the marshes, sloughs, and tree islands of northern areas operate collectively to determine the natural function of the Everglades to process N prior to its export to the mangroves and Florida Bay to the south.

ACKNOWLEDGEMENT

VHRM and JW were supported by the National Science Foundation under Grant No. DBI-0620409 and Grant No. DEB-9910514 (Florida Coastal Everglades, Long-Term Ecological Research).

REFERENCES

- Amador, J. A., and Jones, R. D. (1993). Nutrient limitations on microbial respiration in peat soils with different total phosphorus-content. *Soil Biology & Biochemistry*, 25, 793–801.
- Anthonsieu, A. C., Loehr, R. C., Prakasam, T. B. S., and Srinath, E. G. (1976). Inhibition of nitrification by ammonia and nitrous acid. *J. Water Pollut. Control Fed.* 48, 835–850.
- Burgin, A. J., and Hamilton, S. K. (2007). Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways. *Frontiers in Ecology and the Environment*, 5, 89–96.
- Capone, L. T., Izuno, F. T., Botcher, A. B., Sanchez, C. A., Coale, F. J., and Jones, D. B. (1995). Nitrogen concentrations in agricultural drainage water in South Florida. *Transactions of the ASAE* 38, 1089–1098.
- Chen, R. H., and Twilley, R. R. (1999). Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River estuary, Florida. *Estuaries*, 22, 955–970.

- Childers, D. L., Boyer, J. N., Davis, S. E., Madden, C. J., Rudnick, D. T., and Sklar, F. H. (2006). Relating precipitation and water management to nutrient concentrations in the oligotrophic “upside-down” estuaries of the Florida Everglades. *Limnology and Oceanography*, 51, 602–616.
- Craft, C. B., and Richardson, C. J. (1993). Peat accretion and n, p, and organic c accumulation in nutrient-enriched and unenriched everglades peatlands. *Ecological Applications*, 3, 446–458.
- Craft, C. B., and Richardson, C. J. (2008). “Soil Characteristics of the Everglades Peatland.” Chapter 3. In C. J. Richardson (Ed.), *The Everglades Experiments: Lessons for Ecosystem Restoration* (pp. 335–379). Springer, New York.
- Davis, S. E., Childers, D. L., Day, J. W., Rudnick, D. T., and Sklar, F. H. (2001a). Nutrient dynamics in vegetated and unvegetated areas of a southern Everglades mangrove creek. *Estuarine Coastal and Shelf Science*, 52, 753–768.
- Davis, S. E., Childers, D. L., Day, J. W., Rudnick, D. T., and Sklar, F. H. (2001b). Wetland-water column exchanges of C, N, and P in a southern Everglades dwarf mangrove. *Estuaries*, 24, 610–622.
- Davis, S. E., Corronado-Molina, C., Childers, D. L., and Day, J. W. (2003). Temporally dependent C, N, and P dynamics associated with the decay of *Rhizophora* mangrove L. leaf litter in oligotrophic mangrove wetlands of the Southern Everglades. *Aquatic Botany*, 75, 199–215.
- Davis, S. M. (1994). Phosphorus inputs and vegetation sensitivity in the Everglades. In S. M. Davis and J. Ogden (Eds.), *Everglades: The ecosystem and its restoration* (pp. 357–378). St. Lucie Press, Delray Beach, FL.
- Debusk, W. F., Reddy, K. R., Koch, M. S., and Wang, Y. (1994). Spatial-distribution of Soil nutrients in a Northern Everglades marsh—Water Conservation Area 2A. *Soil Science Society of America Journal* 58, 543–552.
- DeBusk, W. F., and Reddy, K. R. (2005). Litter decomposition and nutrient dynamics in a phosphorus enriched everglades marsh. *Biogeochemistry*, 75, 217–240.
- Diaz, O. A., Reddy, K. R., and Moore, P. A. (1994). Solubility of inorganic phosphorus in stream water as influenced by pH and calcium-concentration. *Water Research*, 28, 1755–1763.
- Ewe, S. M. L., Gaiser, E. E., Childers, D. L., Iwaniec, D., Rivera-Monroy, V. H., and Twilley, R. R. (2006). Spatial and temporal patterns of aboveground net primary productivity (ANPP) along two freshwater-estuarine transects in the Florida Coastal Everglades. *Hydrobiologia*, 569, 459–474.
- Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., Asner, G. P., Cleveland, C. C., Green, P. A., Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, A. R., and Vorosmarty, C. J. (2004). Nitrogen cycles: past, present, and future. *Biogeochemistry* 70, 153–226.
- Glibert, P. M., Heil, C. A., Hollander, D., Revilla, M., Hoare, A., Alexander, J., and Murasko, S. (2004). Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay. *Marine Ecology—Progress Series*, 280, 73–83.
- Gottlieb, A., Richards, J., and Gaiser, E. (2005). Effects of desiccation duration on the community structure and nutrient retention of short and long-hydroperiod Everglades periphyton mats. *Aquatic Botany*, 82, 99–112.

- Hanlon, E. A., Anderson, D. L., and Diaz, O. A. (1997). Nitrogen mineralization in histosols of the Everglades Agricultural Area. *Communications in Soil Science and Plant Analysis* 28, 73–87.
- Hendry, C., Brezonik, P. and Edgerton, E. S. (1981). Atmospheric deposition of nitrogen and phosphorus in Florida. In: Eisenreich SJ (Ed.) *Atmospheric Pollutants in Natural Waters*. *Ann Arbor Science*.
- Herbert, R. A. (1982). Nitrate dissimilation in marine and estuarine sediments. In D. B. Nedwell and C. M. Brown (ed.), *Sediment microbiology*. Academic Press, London, United Kingdom, p. 53–71.
- Howarth, R. W., Marino, R., Lane, J., and Cole, J. J. (1988). Nitrogen-fixation in freshwater, estuarine, and marine ecosystems .1. Rates and importance. *Limnology and Oceanography*, 33, 669–687.
- Inglett, P. W., D'Angelo, E. M., Reddy, K. R., McCormick, P. V., and Hagerthey, S. E. (2009). Periphyton nitrogenase activity as an indicator of wetland eutrophication: spatial patterns and response to phosphorus dosing in a northern Everglades ecosystem. *Wetlands Ecology and Management*, 17, 131–144.
- Inglett, P. W., and Reddy, K. R. (2006). Investigating the use of macrophyte stable C and N isotopic ratios as indicators of wetland eutrophication: Patterns in the P-affected Everglades. *Limnology and Oceanography*, 51, 2380–2387.
- Inglett, P. W., Reddy, K. R., and McCormick, P. V. (2004). Periphyton chemistry and nitrogenase activity in a northern Everglades ecosystem. *Biogeochemistry*, 67, 213–233.
- Inglett, P. W., Reddy, K. R., Newman, S., and Lorenzen, B. (2007). Increased soil stable nitrogen isotopic ratio following phosphorus enrichment: historical patterns and tests of two hypotheses in a phosphorus-limited wetland. *Oecologia*, 153, 99–109.
- Iwaniec, D. M., Childers, D. L., Rondeau, D., Madden, C. J., and Saunders, C. (2006). Effects of hydrologic and water quality drivers on periphyton dynamics in the southern Everglades. *Hydrobiologia*, 569, 223–235.
- Jaffé, R., Boyer, J. N., Dailey, S. K., Maie, N., and Childers, D. (2005). *Dissolved organic nitrogen in the Taylor Slough, Taylor River and Florida Bay: Molecular biogeochemistry, bioavailability, and potential contribution to the microbial loop*. Final Report to the National Oceanic Atmospheric Administration: NA 16 OP 2549.
- Jones, V., Collins, M. J., Penkman, K. E. H., Jaffe, R., and Wolff, G. A. (2005). An assessment of the microbial contribution to aquatic dissolved organic nitrogen using amino acid enantiomeric ratios. *Organic Geochemistry*, 36, 1099–1107.
- Jones, V., Parish, K., Thomson, A., Wolff, G. A., Maie, N., and Jaffe, R. (2006). Molecular characterization of proteinaceous material in the Florida coastal Everglades. *Hydrobiologia*, 569, 129–133.
- Joye, S. B., and Paerl, H. W. (1993). Contemporaneous nitrogen-fixation and denitrification in intertidal microbial mats—Rapid response to runoff events. *Marine Ecology-Progress Series*, 94, 267–274.
- Joye, S. B., and Paerl, H. W. (1994). Nitrogen cycling in microbial mats—rates and patterns of denitrification and nitrogen-fixation. *Marine Biology*, 119, 285–295.

- Kelso, B. H. L., Smith, R. V., Laughlin, R. J., and Lennox, S. D. (1997). Dissimilatory nitrate reduction in anaerobic sediments leading to river nitrite accumulation. *Applied and Environmental Microbiology* 63, 4679–4685.
- Kelso, B. H. L., Smith, R. V., and Laughlin, R. J. (1999). Effects of carbon substrates on nitrite accumulation in freshwater sediments. *Applied and Environmental Microbiology* 65, 61–66.
- Koch, M. S., and Snedaker, S. C. (1997). Factors influencing *Rhizophora mangle* L. seedlings development into the sapling stage across resource and stress gradients in subtropical Florida. *Biotropica*, 29, 427–439.
- Leonard, L., Croft, A., Childers, D., Mitchell-Bruker, S., Solo-Gabriele, H., and Ross, M. (2006). Characteristics of surface-water flows in the ridge and slough landscape of Everglades National Park: implications for particulate transport. *Hydrobiologia* 569, 5–22.
- Li, Y., and Norland, M. (2001). The role of soil fertility in invasion of Brazilian pepper (*Schinus terebinthifolius*) in Everglades National Park, Florida. *Soil Science*, 166, 400–405.
- Maie, N., Parish, K. J., Watanabe, A., Knicker, H., Benner, R., Abe, T., Kaiser, K., and Jaffe, R. (2006). Chemical characteristics of dissolved organic nitrogen in an oligotrophic subtropical coastal ecosystem. *Geochimica Et Cosmochimica Acta*, 70, 4491–4506.
- Martin, H. W., Ivanoff, D. B., Graetz, D. A., and Reddy, K. R. (1996). Water table effects on Histosol drainage water carbon, nitrogen, and phosphorus. *Journal of Environmental Quality*, 26, 1062–1071.
- McCormick, P. V., and O'Dell, M. B. (1996). Quantifying periphyton responses to phosphorus in the Florida Everglades: A synoptic-experimental approach. *Journal of the North American Benthological Society*, 15, 450–468.
- Mulvaney, R. L., and Boast, C. W. (1986). Equations for determination of nitrogen-15 labeled dinitrogen and nitrous oxide by mass spectrometry. *Soil Sci. Soc. Am. J.*, 50, 360–363.
- Mulvaney, R. L., and Kurtz, L. T. (1982). A new method for determination of ¹⁵N-labeled nitrous oxide. *Soil Sci. Soc. Am. J.*, 46, 1178–1184.
- Myklestad, S. M. (1995). Release of extracellular products by phytoplankton with special emphasis on polysaccharides. *Science of the Total Environment*, 165, 155–164.
- Newman, S., Kumpf, H., Laing, J. A., and Kennedy, W. C. (2001). Decomposition responses to phosphorus enrichment in an Everglades (USA) slough. *Biogeochemistry*, 54, 229–250.
- Newman, S., Reddy, K. R., DeBusk, W. F., Wang, Y., Shih, G., and Fisher, M. M. (1997). Spatial distribution of soil nutrients in a northern Everglades marsh: Water conservation area 1. *Soil Science Society of America Journal*, 61, 1275–1283.
- Nielsen, L. P. (1992). Denitrification in sediment determined from nitrogen isotope pairing. *FEMS Microbial Ecology*, 86, 357–362.
- Noe, G. B., Childers, D. L., and Jones, R. D. (2001). Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the everglades so unique? *Ecosystems*, 4, 603–624.

- Noe, G. B., Harvey, J. W., and Saiers, J. E. (2007). Characterization of suspended particles in Everglades wetlands. *Limnology and Oceanography*, 52, 1166–1178.
- Neto, R. R., Mead, R. N., Louda, J. W., and Jaffe, R. (2006). Organic biogeochemistry of detrital flocculent material (floc) in a subtropical, coastal wetland. *Biogeochemistry* 77, 283–304.
- Osborne, T. Z., Inglett, P. W., and Reddy, K. R. (2007). The use of senescent plant biomass to investigate relationships between potential particulate and dissolved organic matter in a wetland ecosystem. *Aquatic Botany*, 86, 53–61.
- Parker, F. *Quantifying Spatial and Temporal Variability in Marsh—Water Column Interactions in a Southern Everglades Marsh*. MS Thesis, Florida International University, 2000.
- Pelegri, S. P., Rivera-Monroy, V. H., and Twilley, R. R. (1997). A comparison of nitrogen fixation (acetylene reduction) among three species of mangrove litter, sediments, and pneumatophores in south Florida, USA. *Hydrobiologia*, 356, 73–79.
- Pelegri, S. P., Rivera-Monroy, V. H., and Twilley, R. R. (1998). A comparison of nitrogen fixation (acetylene reduction) among three species of mangrove litter, sediments, and pneumatophores in south Florida, USA. *Hydrobiologia*, 361, 239–240.
- Pelegri, S. P., and Twilley, R. R. (1998). Heterotrophic nitrogen fixation (acetylene reduction) during leaf-litter decomposition of two mangrove species from South Florida, USA. *Marine Biology*, 131, 53–61.
- Penton, C. R., Devol, A. H., and Tiedje, J. M. (2006). Molecular evidence for the broad distribution of anaerobic ammonium-oxidizing bacteria in freshwater and marine sediments. *Applied and Environmental Microbiology*, 72, 6829–6832.
- Philips, E. J., Cichra, M., Havens, K., Hanlon, C., Badylak, S., Rueter, B., Randall, M., and Hansen, P. (1997). Relationships between phytoplankton dynamics and the availability of light and nutrients in a shallow subtropical lake. *Journal of Plankton Research*, 19, 319–342.
- Qualls, R. G., and Richardson, C. J. (2003). Factors controlling concentration, export, and decomposition of dissolved organic nutrients in the Everglades of Florida. *Biogeochemistry*, 62, 197–229.
- Reddy, K. R., and Delaune, R. D. (2008). *Biogeochemistry of wetlands: Science and applications*. CRC Press, Boca Raton, FL.
- Reddy, K. R., Delaune, R. D., Debusk, W. F., and Koch, M. S. (1993). Long-term nutrient accumulation rates in the everglades. *Soil Science Society of America Journal*, 57, 1147–1155.
- Rivera-Monroy, V. H., Day, J. W., Twilley, R. R., Vera-Herrera, F., and Coronado-Molina, C. (1995). Flux of nitrogen and sediment in a fringe mangrove forest in Terminos Lagoon, Mexico. *Estuarine Coastal and Shelf Science* 40, 139–160.
- Rivera-Monroy, V. H. and Twilley, R. R. (1996). The relative role of denitrification and immobilization in the fate of inorganic nitrogen in mangrove sediments (Terminos Lagoon, Mexico). *Limnology and Oceanography* 41, 284–296.
- Rivera-Monroy, V. H., de Mutsert, K., Twilley, R. R., Castaneda-Moya, E., Romigh, M. M., and Davis, S. E. (2007). Patterns of nutrient exchange in a riverine mangrove forest in the Shark River Estuary, Florida, USA. *Hydrobiologica*, 17, 169–178.

- Ross, M. S., Mitchell-Bruker, S., Sah, J. P., Stothoff, S., Ruiz, P. L., Reed, D. L., Jayachandran, K., and Coultas, C. L. (2006). Interaction of hydrology and nutrient limitation in the Ridge and Slough landscape of the southern Everglades. *Hydrobiologia*, 569, 37–59.
- Rubio, G., and Childers, D. L. (2006). Controls on herbaceous litter decomposition in the estuarine ecotones of the Florida everglades. *Estuaries and Coasts*, 29, 257–268.
- Rudnick, D. T., Chen, Z., Childers, D. L., Boyer, J. N., and Fontaine, T. D. (1999). Phosphorus and nitrogen inputs to Florida Bay: The importance of the everglades watershed. *Estuaries*, 22, 398–416.
- Smith, R. V., Foy, R. H., Lennox, S. D., Burns, C. Jordan, L. C., Cooper, J. E. and Stevens, R. J. (1995). Occurrence of Nitrite in the Lough Neagh River System Published in *Journal of Environmental Quality* 24, 952–959.
- Smith, R. V., Burns, L. C., Doyle, R. M., Lennox, S. D., Kelso, B. H. L., Foy, R. H., and Stevens, R. J. (1997). Free ammonia inhibition of nitrification in river sediments leading to nitrite accumulation. *J. Environ. Qual.* 26, 1049–1055.
- Steingruber, S. M., Friedrich, J., Gachter, R., and Wehrli, B. (2001). Measurement of denitrification in sediments with the ^{15}N isotope pairing technique. *Applied and Environmental Microbiology*, 67, 3771–3778.
- Sutula, M., Day, J. W., Cable, J., and Rudnick, D. (2001). Hydrological and nutrient budgets of freshwater and estuarine wetlands of Taylor Slough in Southern Everglades, Florida (USA). *Biogeochemistry*, 56, 287–310.
- Sutula, M. A., Perez, B. C., Reyes, E., Childers, D. L., Davis, S., Day, J. W., Rudnick, D., and Sklar, F. (2003). Factors affecting spatial and temporal variability in material exchange between the Southern Everglades wetlands and Florida Bay (USA). *Estuarine Coastal and Shelf Science*, 57, 757–781.
- Thomas, S., Gaiser, E. E., Scinto, M. Gantar, and L. J. (2006). Quantifying the responses of calcareous periphyton crusts to rehydration: A microcosm study (Florida Everglades). *Aquatic Botany* 84, 317–323.
- Troxler, T. G., and Childers, D. L. (2009). Litter decomposition promotes differential feedbacks in an oligotrophic southern Everglades wetland. *Plant Ecology*, 200, 69–82.
- Troxler, T. G., Childers, D. L., and Rondeau, D. N. (2005). Ecosystem structure, nutrient dynamics, and hydrologic relationships in tree islands of the southern Everglades, Florida, USA. *Forest Ecology and Management*, 214, 11–27.
- Van der Valk, A. G., and Attiwill, P. M. (1984). Decomposition of leaf and root litter of *Avicennia marina* at Westernport Bay, Victoria, Australia. *Aquat. Bot.* 18, 205–221.
- White, J. R., and Reddy, K. R. (1999). Influence of nitrate and phosphorus loading on denitrifying enzyme activity in Everglades wetland soils. *Soil Science Society of America Journal*, 63, 1945–1954.
- White, J. R., and Reddy, K. R. (2000). Influence of phosphorus loading on organic nitrogen mineralization of everglades soils. *Soil Science Society of America Journal*, 64, 1525–1534.
- White, J. R., and Reddy, K. R. (2003). Nitrification and denitrification rates of everglades wetland soils along a phosphorus-impacted gradient. *Journal of Environmental Quality*, 32, 2436–2443.

- White, J. R., Reddy, K. R., and Moustafa, M. Z. (2004). Influence of hydrologic regime and vegetation on phosphorus retention in Everglades stormwater treatment area wetlands. *Hydrological Processes*, 18, 343–355.
- Woitchik, A. F., Ohowa, B., Kazungu, J. M., Rao, R. G., Goeyens, L., and Dehairs, F. (1997). Nitrogen enrichment during decomposition of mangrove leaf litter in an east African coastal lagoon (Kenya): relative importance of biological nitrogen fixation. *Biogeochemistry* 39, 15–35.
- Wozniak, J. R. (2006). *Quantifying nitrogen cycling rates in freshwater marshes of the southern Everglades using ¹⁵N tracer techniques*. Doctoral dissertation, Florida International University, Miami, FL.
- Wozniak, J. R., Childers, D. L., Anderson, W. T., Rudnick, D. T., and Madden, C. J. (2008). An in situ mesocosm method for quantifying nitrogen cycling rates in oligotrophic wetlands using N-15 tracer techniques. *Wetlands*, 28, 502–512.
- Wright, A. L., Reddy, K. R., and Newman, S. (2009). Microbial Indicators of eutrophication in Everglades wetlands. *Soil Science Society of America Journal*, 73, 1597–1603.
- Ye, R. Z., Wright, A. L., Inglett, K., Wang, Y., Ogram, A. V., and Reddy, K. R. (2009). Land-use effects on soil nutrient cycling and microbial community dynamics in the Everglades Agricultural Area, Florida. *Communications in Soil Science and Plant Analysis*, 40, 2725–2742.
- Zhang, J., James, R. T., and McCormick, P. (2009). Chapter 10: Lake Okeechobee Protection Program—State of the Lake and Watershed Protection Area. In: *2009 South Florida Environmental Report—Volume I*, South Florida Water Management District, West Palm Beach, FL.