GLOBALIZATION OF THE NITROGEN CYCLE

In the last century, humans have significantly altered the global nitrogen (N) cycle, resulting in a dramatic increase in the rate at which ‘fixed’ (or biologically active) N is created globally. The magnitude and scale of this increase has been remarkable: since 1970 alone, the rate at which N\textsubscript{2} has been fixed has gone up by 120% worldwide (Galloway et al. 2008). Excessive N inputs to ecological systems are linked to several environmental concerns, including
the eutrophication of inland freshwater and marine ecosystems, and the loss of species diversity e.g., Carpenter et al. 1998, Smith et al. 1999). Increasingly, elevated N inputs are also being linked to ecological changes that have negative consequence for human health (Townsend et al. 2003), including the distribution and abundance of key disease vectors, as well as the occurrence of harmful algal blooms (HABs, Cottingham et al. 2003). For these reasons, understanding controls on the cycling and fate of reactive nitrogen in regional landscape remain an important research priority.

The role of denitrification in the nitrogen cycle

Given concern over this escalation in N inputs to ecosystems, much current research focuses on understanding how bioavailable forms of N are transformed, transported, and retained within landscapes (e.g., Seitzinger et al. 2006, Mullholland et al. 2008). Indeed, large-scale budgets indicate that only 20-25% of the N added to the biosphere is exported to oceans (Howarth et al. 1996). This suggests that a significant N sink must exist within landscapes, and denitrification within riparian and aquatic habitats has been identified as the process most likely responsible for this N removal. Denitrification is a heterotrophic process in which organic matter oxidation to CO$_2$ is coupled to the reduction of dissolved nitrate (NO$_3^-$) and nitrite (NO$_2^-$). This is carried out by bacteria in anoxic, or low-oxygen environments (where O$_2$ is $< ~0.2$ mg/L), with an end product of nitrogen gas (N$_2$ or N$_2$O). Bacteria capable of denitrification are widespread in soils and sediments, and this process can occur throughout terrestrial, freshwater, and marine environments. Importantly, denitrification is thought to be the primary mechanism by which bioavailable N can be permanently removed from ecosystems.

Eutrophication in the Mobile River Basin

Widespread nutrient enrichment within the Mobile River Basin of the southeastern US has the potential to increase the delivery of nitrogen (N) and phosphorus (P) to ecosystem of the Gulf Coast. This notion is supported by research showing that variation phytoplankton abundance in several Mobile Bay estuaries is directly linked to differences in N delivery from the upstream catchment (Lehrter 2008), and is presaged by well-documented eutrophication in the northern Gulf of Mexico associated with nutrient delivery from the Mississippi River (Rabalais et al. 2002, Dodds 2006, Turner et al. 2008). The extent to which nutrient enrichment and associated anoxic conditions persist in the Mobile Bay is largely unknown; however, reducing N transport to Alabama’s coastal waterways will likely ameliorate possible loss of commercial and recreational value due to hypoxic events similar to the Dead Zones widely observed in the Gulf of Mexico. The goal of this proposed research is to evaluate the patterns and controls on sediment denitrification within the Cahaba River, a key drainage system within the Mobile basin in central Alabama.

One key observation motivating this research comes from a long-term survey of stream chemistry from multiple stations located along the Cahaba River (Fig 1; data from UA, Center for Freshwater Science).
Studies). These show sharp increases in N concentration associated with Birmingham, AL, followed by a clear decline downstream of the urban environment. **Even correcting for the effects of dilution downstream, these data indicate a strong potential for N removal in this river, and the goal of our research is to help explain this observation.** We chose to do this using two approaches, the first of which involved work at the scale of the entire river, encompassing 6 sampling sites, 2 upstream of the Fall Line in the Valley and Ridge physiographic province, 2 downstream of the Fall Line in the Coastal Plain physiographic province, and 2 along the Fall Line itself. This work was outlined in our 2009-10 proposal, and results suggested that the biological “hot spot” for N retention in the Cahaba River is associated with the shoal habitat found along the Fall Line. As a consequence, we focused a second project (proposal for 2010-11 funding) specifically on the shoal habitat, giving full attention to the temporal dynamics found at only one of the 6 original sites used in the previous year’s work. For ease of discussion we refer to the first year of funding as “Cahaba I”, and the second year of funding as “Cahaba II”.

**B. Explanation of the research methodology used**

During both the first and second year of our USGS funding our research was organized into three elements (RE I-III) that included both laboratory and field activities.

**FUNDING YEAR 2009-10:**

1) For RE I and II, we collected sediments from 6 locations in the Cahaba River as well as elsewhere in the Mobile drainage. With these, we carried out experiments designed to quantify rates of denitrification, including an assessment of the relative importance of dissolved NO$_3^-$ and labile carbon as drivers of this process. Denitrification potential assays (DNPs), involve a direct measure of anaerobic respiration in bottle experiments that are amended with varying levels of nitrate and an organic carbon source (glucose). To complete DNP assays, sediments are homogenized in the field from several subsamples at a site, brought into the laboratory, and a known mass placed into gas-tight sampling bottles. Water from each site is then amended with N and/or C and added to sampling bottles, bottles are then flushed with N$_2$ gas to create an anaerobic environment, and acetylene is added. Acetylene blocks the conversion of N$_2$O to N$_2$(g) during denitrification, so accumulation of N$_2$O over time in bottle headspace represents net denitrification. Because resource limitation and oxygen inhibition are alleviated through nutrient additions and purging bottles with N$_2$, these measurements represent rates under ideal conditions (hence the name ‘potentials’).

2) A subsample of the same sediments collected at 6 sites and used for measuring denitrification was preserved in the field for microbial community analysis. This approach for evaluating the denitrifier communities uses genetic tools to measure gene expression (mRNA) in un-manipulated sediment communities. For this analysis, samples are immediately preserved upon collection in the field to capture in situ activity. Gene expression measurements in these preserved samples targets the genes coding for a critical denitrification enzyme, nitrite reductase (gene abbreviation, *nir*). We are using the variation in different *nir* sequences found in sediments along the Cahaba River to “fingerprint” the denitrifier community. Our fingerprinting method, called terminal restriction length polymorphisms (T-RFLP), can be used to
distinguish changes in denitrifier community structure that might be indicative of shifts in N cycling along the Cahaba River. Using quantitative PCR (qPCR), we can measure the number of copies of the *nir* genes found in the samples after DNA and RNA extraction. The more copies of the genes, the more active those enzymes are in the sample. Measurements using qPCR will be completed this summer for both funding years.

3) For RE III, we completed field studies to estimate ecosystem metabolism (gross primary production; GPP and ecosystem respiration; ER) along a channel continuum in the Cahaba River using the same sites as for RE 1 and II. River metabolism was measured by monitoring changes in dissolved oxygen (DO) in the water column by recording readings every 10 minutes using a YSI sondes instrument. We will use diel measurements of dissolved oxygen to make estimates of GPP, and R (and GPP/R) following standard single-station mass balance approaches. These metrics can be used to estimate the assimilative N demand in different sections of the river (e.g., above and below the fall line), and at different seasons. Further, this effort will allow us to explore potential indirect links between river productivity and denitrification estimates made in the lab. For this effort, we collected additional environmental samples (water chemistry, turbidity, chlorophyll a, etc.) to help interpret and/or explain spatial and temporal patterns in biological activity. In addition, we conducted a pilot study to explore the potential use of via membrane inlet mass spectrometry (MIMS) to make estimates of whole-system denitrification using N\(_2\) mass-balance. To date, however, we have been unsuccessful in the application of this method in the Cahaba River.

**FUNDING YEAR 2010-11:**

1) In the first RE (REI), we evaluated the relationship between nitrate retention along the reach as it relates to in-stream flow, documenting nitrate mass balance within a study reach at varying discharge levels throughout the year. This was accomplished by taking samples of surface water at 100 m-intervals along 3 km of river from a canoe.

2) The second research element (REII) evaluated the relationship between nitrate retention along the reach and direct uptake of N by primary producers (the vascular plant *Justicia americana*), quantifying net primary production and C:N chemistry of both macrophytes and algae. This was completed by collecting 5 samples of above ground and below ground biomass of *J.americana* within one shoal, then quantifying the biomass of each compartment (below ground vs. above ground), drying the material and grinding it into a powder to be run for C:H:N analysis.

3) The third element evaluated the relationship between nitrate retention along the reach and the indirect effect of the macrophytes on rates of denitrification. This included characterization of the local heterogeneity in physical and chemical characteristics of sediments as they are related to the physical structure of the macrophyte beds, and involved measurements of denitrification potential associated with sediments collected from under the *J. americana* patches sampled in REII. In addition, in the third element we measured denitrifier community structure and activity using molecular techniques (T-RFLP and qPCR) and compared these with laboratory
measurements of denitrification potential to evaluate hotspots of denitrifier activity. These molecular analyses will be completed this summer.

Together, results from laboratory and field research shed light on the relative role of direct and indirect effects of macrophyte beds in the Cahaba Shoals on N retention in Alabama streams and rivers.

C. Principal findings and their significance

**Cahaba I Grant (2009-10)**

#1 The first objective of this study was to evaluate the controls on sediment denitrification along a stream continuum in the Cahaba River.

There were no strong differences observed in potential denitrification in river sediments collected from Valley Ridge, Fall Line, and Coastal Plain study sites (Figure 2). During the summer, there was some evidence for elevated rates of activity along the Fall Line relative to other sites, but these differences were not statistically significant, owing to high variability observed among replicates. Similarly, within sites, there was little evidence for strong seasonality in potential denitrification at Ridge and Valley and Coastal Plain sites; however, along the Fall Line there was an increase in activity between spring and summer sampling periods. Finally, results from denitrification kinetic assays were variable among sites and sampling times (Figure 3). In general, additions of nitrate and/or labile carbon to sediments had no consistent effects on denitrification potential observed during these 4 hr incubations with only two exceptions. The first exception was during the winter, when Coastal Plain sites were co-limited by N and C, possibly due to the very low primary production (and thus labile C availability) in the system during this period. Secondly, when the two locations on the Fall Line were evaluated separately, we found denitrification at the site in the center of the Fall Line with abundant macrophytes was N limited (data not shown). We hypothesize that the increase in denitrifier biomass due to increased labile organic carbon supply from the macrophyte resulted in local N limitation that was alleviated through NO$_3^-$ amendment. Furthermore, we suspect that the sequestration of water column nitrate by increased algal production prevents the delivery of nitrate to microbes living in the subsurface of these macrophyte beds, and this is a hypothesis we are currently exploring.

Overall, results suggest a persistent but low capacity for sediment denitrification in Cahaba River, regardless of regional position, or background nitrate concentration. The rates presented here represent 100-200 umol of N$_2$ consumed per m$^2$ per hour, which is within the range of published values, but on the low end of the spectrum. We calculated the loss of N via microbial conversion of N$_2$ using simple assumptions about the area of the river benthos along the Fall Line, an average denitrification rate, and an average value for discharge and nitrate concentrations in the water column. Given these assumptions, denitrification potentially consumes from 10-35% of the inorganic N load in the Cahaba River, but more work is required to refine this number. The lack of systematic effects - at all sites and seasons - of amending sediments with nitrate and labile carbon was surprising, and suggests that initial population sizes of sediment denitrifiers was too low to produce more typical kinetic responses to these experimental additions.
#2 Our second objective was to determine how spatial and temporal patterns of benthic denitrification along a river continuum relate to the structure of microbial communities.

The two functional genes we measured (nirK and nirS) do not exist in the same microbial species, and have been found to differ in their ability to respond to fluctuations in dissolved oxygen (DO). These differences in response to DO fluctuations suggest that the composition of the microbial community may determine how rates of denitrification respond to disturbances such as flooding or geomorphic variation that can control the supply of DO to subsurface sediments. In our samples, the diversity of nirK gene fragments was lower than that found for nirS, and the community structure associated with each gene differed with physiographic province (Figure 4). There were no differences in community structure when evaluating nirS gene diversity between the physiographic provinces, nor were there significant seasonal patterns (Figure 4a). However, when focusing on the nirK gene community structure, we found differences on the Coastal Plain communities, as compared to Valley and Ridge and at the Fall Line, although again no seasonal patterns (Figure 4b). These differences suggest that there is variation between these three geomorphically distinct regions in the delivery of DO to the subsurface, which likely influences the structure of nirK gene-containing denitrifier communities. Continued analysis of these samples, as well as those collected to meet our first objective, represents the central portion of the MS research of Corianne Tatariw, who plans to graduate in December 2011.

#3) Our final objective of this study was to understand the capacity for denitrification to remove NO$_3^-$ in the field, for stream and river reaches of variable size and N loading.

We monitored diel oxygen, light, and temperature from 5 locations along the Cahaba River at approximately monthly intervals for 1 year (Table 1, Figure 5). In conjunction with these measurements, we also collected samples for water chemistry (nitrate, ammonium, and soluble reactive phosphorus), turbidity, and planktonic chlorophyll a (Table 1). We are currently in the process of using both empirical and inverse modeling techniques to generate estimates of gross primary production (GPP), respiration (R), and net ecosystem production (NEP) at all sites and dates from these diel observations. This work is a central element of Elise Chapman’s dissertation at the University of Alabama. We will use these metabolic estimates in a series of multivariate statistical tests to ask how seasonal changes in water temperature, nutrient availability, discharge, and turbidity drive temporal variability in rates of ecosystem metabolism among Valley and Ridge, Fall Line, and Coastal Plain reaches. In addition, we will use measurements of ecosystem metabolism in conjunction with estimates of algal and microbial C:N:P stoichiometry, to make calculations of the potential biological demand for nutrients in different reaches of the Cahaba River over seasonal times scales. Analyses will be complete by December 2011.

Cahaba II Grant (2010-11)

#1 The goal in Objective 1 was to determine how seasonal changes in hydrology influence N retention.
To do this we use a lagrangian approach where we tracked a parcel of water downstream in a canoe and sampled the surface water at a regular distance interval to determine how chemistry changed over time as it interacted with the biota. These samples were used to determine the decline in N and P as the water moves through shoal habitat (Figure 6a), which should vary throughout the growing season if assimilation of N by the dominant macrophyte, *Justicia americana*, is an important mechanism of nitrate loss in the river reach (Figure 6b). Our initial attempt at this approach illustrated significant declines in the NO$_3^-$ along a 3 km reach of shoal habitat. We are currently repeating this technique several times over the course of seasonal macrophyte growth to assess how these primary production influence the nitrogen cycle.

*#2 The goal of Objective 2 was to estimate net primary production (NPP) of algae and the dominant macrophyte (*Justicia americana*) within the shoals, and to combine this information with tissue chemistry (%N) and areal coverage of shoals to estimate autotrophic N demand by this habitat.*

We measured above and belowground biomass of 5 randomly selected *Justicia americana* patches of a designated size approximately every 3 weeks during the growing season of 2010 (Figure 7). We found above ground height of the plants was a poor predictor of biomass, but that belowground and aboveground biomass were correlated. Plant samples were dried and homogenized to determine the C:N content of the biomass (samples currently being processed). Areal photography was taken and is being used to determine the percent area of the stream benthos covered by the macrophytes through manipulation of the georeferenced images in ArcView. Assuming an average of 250 g of *J. americana* grew per square meter in a 70 day period (Figure 8) with an average C:N of 25 and 20% coverage of the study reach, we calculated that of the nitrate loss measured in June 2010 along the 3 km reach, assimilation of N from the water column by macrophytes was 5-15% of the water column load. Using the same assumptions, belowground biomass can incorporate 4 times the amount of stream-water nitrate that above ground biomass does; therefore, macrophytes likely play an important role in direct assimilation of nitrate and removal from the water column while they are growing. This mechanism of N retention, however, likely declines from August to October, and water column algal production may become a more important mechanism of N retention later in the summer.

*#3 The goal of Objective 3 was to determine if macrophytes alter local sediment characteristics and as a result increase rates of denitrification above those found in reaches without shoals.*

Potential rates of denitrification were measured 7 times throughout the growing season under 5 patches in the shoals. Three treatments were established to test for nitrogen and carbon limitation, as well as carbon and nitrogen co-limitation (Figure 7). We found that, later in the growing season, potential denitrification rates declined and became strongly limited by nitrate. This is potentially due to the increased utilization of N by planktonic algae, periphyton, and the macrophytes themselves, which would then prevent heterotrophic bacteria from acquiring these nutrients. As stated above, we are currently testing the hypothesis that competition for nitrate by primary producers prevents delivery of those resources to denitrifiers living in the midst of macrophyte patches, creating N limitation for these microbes despite the high N concentrations usually found in the surface water. In addition, we are exploring patterns in community structure under each patch using T-RFLP, and results to date suggest that the community structure is
changing in response the growth of the macrophytes (Figure 9). We also found that the biomass of the plants in the rhizosphere is negatively correlated with the DNP rates and have generated several hypotheses as to why this might be (Figure 10). One is that the delivery of N to the interior of patches declines as algal and/or macrophyte growth throughout the growing season increases and sequesters nutrients, lowering DNP. A second is that the physical structure of the macrophyte rhizosphere limits movement of water and nutrients into the subsurface. Nutrient concentrations in the Cahaba River increase throughout the summer, so there is no concern that declining DNP is due to N supply from the basin. A third possibility is that sediment-associated denitrification rates do not adequately represent the activity of anaerobic microorganisms in the rhizosphere complex (root plus sediments), and therefore our use of only sediment without intact plant rhizomes in laboratory incubations is not representative of field rates.
Figure 2. Rates of denitrification within 3 geomorphically-distinct areas of the Cahaba River. Two locations were sampled for each area of the river. Unamended rates for each for each season (a) are compared to seasonally-determined rates in response to nitrate and carbon amendment (b-e).
Figure 3. Response of denitrification to varying levels of nitrate addition in laboratory incubations at each site in early summer and late summer. For the Fall Line site not shown carbon and nitrate additions were only made at the highest levels, so no kinetics curves are provided.
Figure 4. Graphical representation in a multidimensional scaling plot of the similarities in nirS gene sequences in samples collected simultaneously with the Cahaba River sediments used for denitrification measurements. An analysis of similarity (ANOSIM) was used to determine if there were statistically significant differences in the three major geomorphically-defined areas (VR, FL, CP). Global R and p value for each ANOSIM are shown, with the only significant pairwise comparisons being between CP and the other two areas for the nirK gene.

Table 1. Sampling periods and parameters measured for the river metabolism portion of the Cahaba I.

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*Biologically available DOC determined as the loss of DOC during a 30-day laboratory incubation of water in the dark.
Figure 5. Diel patterns in dissolved oxygen saturation throughout the year at 5 sites along the Cahaba River.
**Figure 6.** (a) Surface water chemistry along a 3 km-river reach within the Fall Line. (b) Hypothesized changes in the decline in surface water nitrate as water moves through shoal habitat at the Fall Line.

![Graph showing surface water chemistry along a 3 km-river reach within the Fall Line.](image)

**Figure 7.** (a) Changes in aboveground biomass of *Justicia americana* at 5 plots sampled throughout the growing season in shoal habitat found on the Fall Line. (b) Changes in belowground biomass of *Justicia americana* at 5 plots sampled throughout the growing season in shoal habitat found on the Fall Line. (c) Plant height within the quadrat from which aboveground biomass of *Justicia americana* was sampled (d) Relationship between above and belowground biomass of *Justicia Americana*.

![Graph showing changes in aboveground and belowground biomass of *Justicia americana*.](image)
Figure 8. Response of sediment denitrifier communities found under *Justicia americana* patches in the shoals at the Fall Line to amendments of nitrogen and carbon in laboratory measurements of denitrification.

![Denitrification Potential Rate](image)

Figure 9. Multidimensional scaling plot of the relationships between microbial community structure in sediments collected from below *Justicia americana* patches during the early growing season. 16S rDNA genes were used to generate T-RFLP data that could then been analyzed for similarities between dates. These differences were found to be statistically significant between 24 June and 14 July using ANOSIM (R=0.713, p=0.001).
Figure 10. Relationship between belowground biomass of *Justicia americana* and the denitrification potential for sediments below the rooting zone of the plant.

\[ y = -21.16 \ln(x) + 204.28 \]

\[ R^2 = 0.4029 \]

### D. Conclusions

Combined, these two research projects provide a multi-scale assessment of ecosystem function along the Cahaba River. The broad-scale assessment described in Cahaba I illustrated subtle differences in potential denitrification and denitrifiers communities among the three major physiographic regions, and suggests only a limited capacity for this process to exert influence on downstream N transport. This ‘upscale’ for potential denitrification assays should be interpreted with caution, however, and more work is required to fully understand the potential importance of this process in the Cahaba. On the other hand, the broad-scale assessment of ecosystem metabolism (still in progress) suggests the potential for rather large differences in GPP, R, and NEP over both time and space along this river system. In a general sense, these results will contribute to a recent and growing body of literature that seeks to better understand the basic ecosystem properties of mid- to large-size rivers. These results will also allow us to evaluate the potential for biological activity in mediate N transport in this system. In Cahaba II, we focus research on ‘riverine shoal reaches’ that appear to have the greatest potential for N retention in this river system. To date, our results suggest that the direct use of nutrients by dominant river macrophytes may represent a significant N sink in these ecosystems. In addition, relationships between seasonal macrophyte growth and sediment denitrification suggest important and interesting interactions between primary producers and sediment heterotrophs. Specifically, results indicate the competition for for NO\textsubscript{3} in the water column – both by macrophytes and suspended algae – may serve to reduce the delivery of this resource to sediment denitrifiers. Importantly, because assimilative uptake by plants and algae represents only transient N uptake, the degree to which these primary producers indirectly inhibit sediment denitrification has potential implications for the long term transport of N to the Mobile Bay.

### E. Publications

*In preparation*

Sponseller, RA and JW Edmonds. A conceptual model linking riverine shoal primary production to ecosystem N retention in mid-sized rivers.


Chapman, EL, JR Jarnigan, and JW Edmonds. Primary producer community structure modulates N and C cycling in shoal habitat.

F. Presentations


G. Dissertations and Theses
Tatariw, Corianne. December 2011. Exploring Community Dynamics of Nitrate-Removing Bacteria in the Cahaba River. “MS Dissertation”, Department of Biological Sciences, College of Arts and Sciences, University of Alabama, Tuscaloosa, AL

Jarnigan, Julie. December 2012. Microbial Community Dynamics in Shoal Habitats. “MS Dissertation”, Department of Biological Sciences, College of Arts and Sciences, University of Alabama, Tuscaloosa, AL

Chapman, Elise. May 2013. Relationships among geomorphology, ecosystem metabolism, and nitrogen (N) retention a mid-sized river “PhD Dissertation”, Department of Biological Sciences, College of Arts and Sciences, University of Alabama, Tuscaloosa, AL

H. Literature cited


