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COMPARING FUNCTIONAL ASSESSMENTS OF WETLANDS TO MEASUREMENTS OF SOIL CHARACTERISTICS AND NITROGEN PROCESSING

Thomas E. Jordan[1], Mary Pittek Andrews[1,2], Ryan P. Szuch[1,3], Dennis F. Whigham[1], Donald E. Weller[1] and Amy Deller Jacobs[4,5]

[1]*Smithsonian Environmental Research Center*
647 Contees Wharf Road, Box 28
Edgewater, Maryland, USA 24037
E-mail: jordanth@si.edu

[2]*Present address:*
National Oceanographic Atmospheric Administration
National Marine Fisheries Service - Restoration Center
410 Severn Avenue, Suite 107A
Annapolis, Maryland, USA 21403

[3]*Present address:*
ENVIRON International Corporation
214 Carnegie Center
Princeton, New Jersey, USA 08540-6284

[4]*The Nature Conservancy of Delaware*
110 West 10th Street, Suite 1107
Wilmington, Delaware, USA 19801

[5]*Present address:*
Delaware Department of Natural Resources and Environmental Control
Division of Water Resources
820 Silver Lake Blvd., Suite 220
Dover, Delaware, USA 19904

Abstract: One beneficial service of wetland ecosystems is the improvement of water quality through nitrogen (N) removal. However, one important N-removal process, denitrification, can produce the atmospheric pollutant nitrous oxide (N_2O). Wetland biogeochemical functions, such as N processing, can be assessed by the hydrogeomorphic (HGM) approach using a suite of simple field observations made in a single visit to a wetland. HGM assessments score functions on a scale of 0–1 where 1 equals the functionality of an undisturbed reference standard wetland and 0 equals the functionality of a completely degraded wetland. We compared seasonal measurements of potential denitrification, N_2O emissions, and related soil characteristics to HGM assessments of nine non-tidal riverine wetlands and seven flats wetlands in the Nanticoke River watershed in Delaware and Maryland, USA. Denitrification potential, measured as denitrification enzyme activity (DEA), was higher in riverine wetlands than in flats. DEA increased with increases in percent water-filled pore space, pH, ammonium concentration, and the percentages of N and organic carbon. DEA decreased with increases in oxidation-reduction potential (E_h) and water-table depth. The difference in DEA between riverine and flats wetlands was attributable to the differences in the correlated soil characteristics. N_2O emission rates were higher on average in riverine wetlands than in flats, but the difference was not statistically significant. N_2O emission rates were generally less predictable than DEA and showed only weak correlations with pH, water-table depth, and the percentage of water-filled pore space when data from riverine wetlands and flats were combined. HGM biogeochemistry function scores ranged from 0.18 to 1 for the riverine wetlands and from 0.24 to 0.98 for the flats. The scores did not correlate with N_2O emission or DEA, except for summer DEA in flats, which increased with increasing score. Wetland alterations that increase soil moisture relative to reference standard conditions decrease biogeochemistry and hydrology function scores but increase DEA. Biogeochemistry function scores would more closely reflect denitrification potential if the scoring incorporated measurements of soil characteristics that correlate with DEA.

Key Words: Chesapeake Bay, Delaware, denitrification, flats, HGM, Maryland, nitrous oxide, riverine, wetland assessment

INTRODUCTION

In recent decades, human activities have increased discharges of nitrogen (N) from watersheds, causing problems in coastal ecosystems throughout the world (e.g., Turner and Rabelais 1991, Nixon 1995, Howarth et al. 1996, Jordan and Weller 1996, Cloern 2001). In Chesapeake Bay, for example, increased N discharge from the watershed has stimulated excessive phytoplankton production (Boynton et al. 1982, Malone et al. 1986, 1988, Correll 1987, Jordan et al. 1991a, 1991b, Gallegos et al. 1992, Boesch et al. 2001) that has contributed to the demise of submerged aquatic vegetation (Kemp et al. 1983) and an increase in the extent of hypoxic waters (Taft et al. 1980, Officer et al. 1984). Likewise, increasing N releases from the Mississippi River have led to the formation of an extensive hypoxic dead zone in the Gulf of Mexico (Turner and Rabelais 1991).

N discharged from watersheds can be removed by wetlands, which can accumulate N in sediments and biomass or convert N to gaseous forms via denitrification (e.g., Richardson 1989). Comparing N removal by wetlands, lakes, and rivers, Saunders and Kalff (2001) found that wetlands removed the greatest proportion of their N loads, primarily due to denitrification, but with removal enhanced by aquatic plants. They found that N removal in wetlands ranged up to 130 g N m^{-2} yr^{-1}, almost double the removal rate in lakes. Denitrification may be especially important for N removal by wetlands because denitrification is not limited by the N storage capacity within the wetland. Moreover, waterlogged wetland soils can provide optimal conditions for denitrification, which requires nitrate, organic carbon, and an absence of oxygen. Wetland restoration can reduce N discharges from agricultural watersheds (e.g., Jordan et al. 1999, 2003), and widespread restoration of wetlands has been suggested as part of a plan for reducing nitrogen releases from the Mississippi River basin (Mitsch et al. 2001).

Despite its potential importance, denitrification in wetlands is poorly quantified over large spatial scales. Denitrification is difficult to quantify due to its high spatial and temporal variability and because the N_2 produced by denitrification is difficult to measure in the presence of ambient concentrations of atmospheric N_2 (Tiedje et al. 1989). Denitrification can be assessed with surrogate measurements, measurements of potential denitrification, and indicators or correlates of denitrification (Tiedje et al. 1989). However, denitrification assessments are rarely extrapolated to the spatial scales of whole watersheds.

While denitrification is a potentially important N sink, it is also a source of atmospheric nitrous oxide (N_2O). The recent increase in atmospheric N_2O contributes to global warming (Abrahamson 1989) and the destruction of stratospheric ozone (Bolin et al. 1983). A recent review found much uncertainty about the importance of N_2O production in riparian wetlands, with the ratio of N_2:N_2O production ranging from 99:1 to 1:500 and with proportionally more N_2O production at lower pH (Groffman et al. 2000). The tradeoff between N removal and N_2O production via denitrification in wetlands requires further research.

There is a need to assess N processing, as well as other wetland functions over large spatial scales. One assessment technique is the hydrogeomorphic (HGM) method (Brinson et al. 1995, 2003, Whigham et al. 1999, Rheinhardt et al. 2002, Whigham et al. 2007). The HGM method computes functional capacity scores based on a suite of simple field observations made in a single visit to a wetland site. The scores are normalized relative to observations made in reference wetlands selected to represent the range of conditions of wetlands in the study area, varying from least to most degraded from human impacts. The HGM produces scores for wetland functions such as habitat, plant community, hydrology, and biogeochemistry. The biogeochemistry function is meant to reflect the wetland's ability to perform nutrient-processing functions such as denitrification (e.g., Findlay et al. 2002). HGM or other methods (Tiner et al. 2000, Fennessy et al. 2004, Tiner 2004, Weller et al. 2007) may provide a way of rapidly assessing the relative potential to support denitrification and N_2O emissions that could also be used for extrapolating estimates of these rates over large spatial scales.

This study is part of a larger assessment of the condition of non-tidal riverine and flat wetlands in the entire drainage basin of the Nanticoke River, a tributary of Chesapeake Bay (Weller et al. 2007, Whigham et al. 2007). This paper compares HGM variable and function scores with measurements of denitrification potential, N_2O emission, and a suite of soil characteristics, including temperature, per-

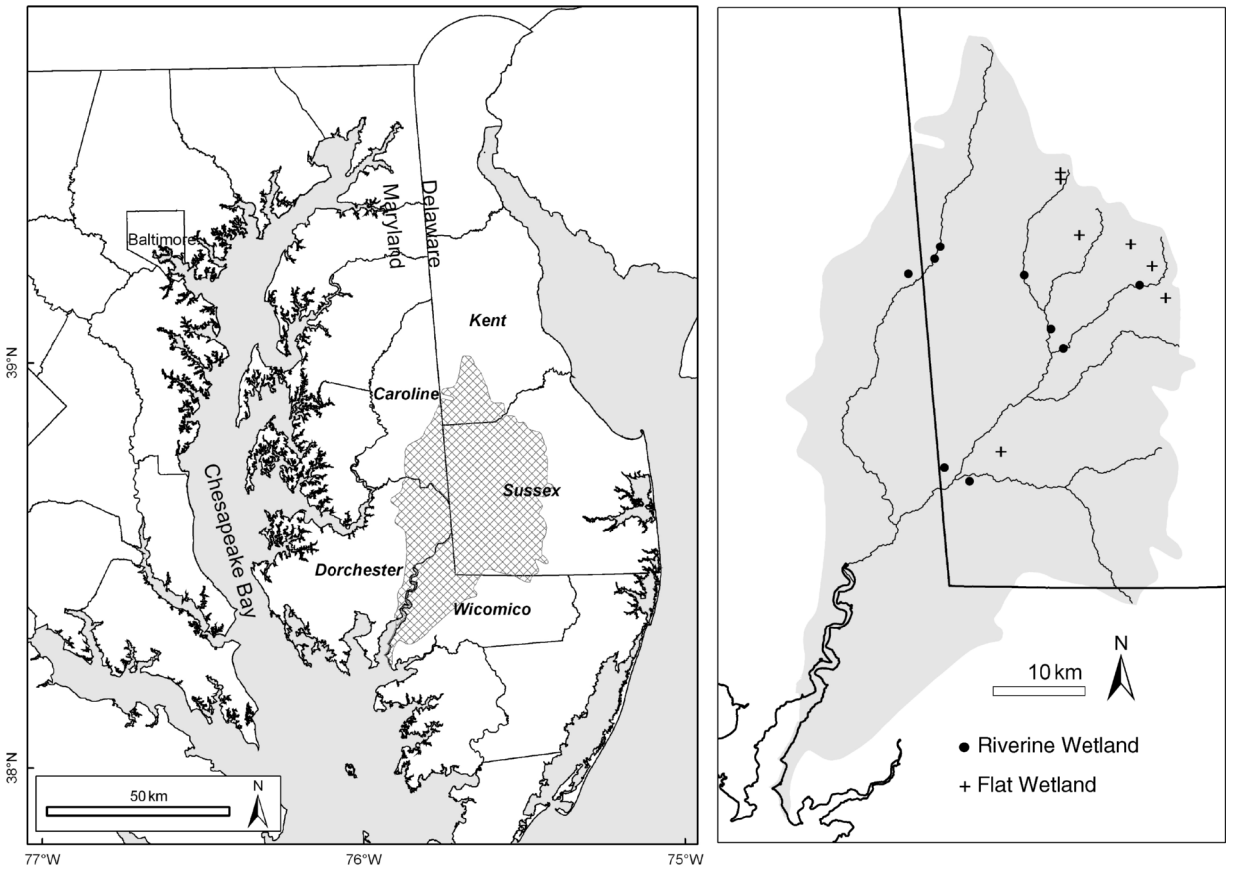

Figure 1. Left: The Nanticoke River watershed (cross-hatched area) on the Delmarva Peninsula in Maryland and Delaware near Chesapeake Bay. Right: The locations of the riverine and flat study wetlands and the major streams in the Nanticoke River watershed.

cent water-filled pore space, percent C, percent N, pH, ammonium concentration, water-table depth, and E_h. The goals are to test possible indicators of denitrification and N_2O emission and to evaluate the utility of HGM scores for assessment of these functions and extrapolating to larger spatial scales.

Our research addresses five questions. 1) Which soil characteristics are the best predictors of denitrification potential and N_2O flux? 2) Can soil characteristics serve as surrogate measurements of denitrification potential and N_2O flux? 3) How do denitrification potentials and N_2O fluxes differ among different HGM classes of freshwater non-tidal wetlands? 4) What wetland characteristics indicate the greatest potential for denitrification functions? 5) Can HGM scores be used to estimate wetland denitrification potential and N_2O flux?

METHODS

Study Sites

We studied non-tidal wetlands of the Nanticoke River watershed on the Delmarva Peninsula on the eastern shore of Chesapeake Bay (Figure 1). The non-tidal wetlands of the Nanticoke River watershed fall mainly into two types: riverine wetlands, which are associated with streams; and flats, which are poorly drained flat lands often located in the headwater and interfluve landscape positions. The assessment of ecological condition of these wetlands (Whigham et al. 2003) used 25 riverine wetlands and 19 flats as reference sites to establish the range of ecological conditions from least to most disturbed. The present study focused on 16 of these reference wetlands, nine riverine and seven flats (Figure 1), which spanned the full range of disturbance levels. The wetlands were all originally forested, but the most disturbed flat was cleared of trees by logging. Flats are often ditched and used for pine plantations in the Nanticoke watershed. Thus, forestry and drainage ditches are the most common sources of disturbance to flats. At the most disturbed riverine wetland, alterations of the adjacent stream channel caused increased flooding, which killed most of the trees. However, riverine wetlands were more commonly disturbed by artificially increased drainage. Our study wetlands

Table 1. Variable scoring criteria used for field observations of flats. The criteria and scores shown are applicable to the hydrology and biogeochemistry FCI scores used in this paper. Other HGM criteria and scores (see Whigham et al. 2003, 2007) are omitted.

Variable (Symbol)	Score	Criteria
Tree Basal Area	1.0	Area $\geq$ 25 m^2 ha^{-1}
(V_{TBA})	0.1–1.0	Area / 25 m^2 ha^{-1}
	0.1	Area $\leq$ 2.5 m^2 ha^{-1}
Tree Density	1.0	Density $\geq$ 350 stems ha^{-1}
(V_{TDEN})	0.1–1.0	Density / 350 stems ha^{-1}
	0.1	Density $\leq$ 35 stems ha^{-1}
Tree Snags	1.0	Standing dead trees $\geq$ 23 stems ha^{-1}
(V_{SNAG})	0.1	Standing dead trees $\leq$ 15 stems ha^{-1}
Fill	1.0	No fill sediment added to assessment area
(V_{FILL})	0.75	Percentage of area covered by fill $\leq$ 10%
	0.5	Percentage of area covered by fill $>$ 10% and $\leq$ 50%
Drainage	1.0	No evidence of drainage ditches in the area
(V_{DRAIN})	0.1–1.0	Proportion of assessment area not affected by ditches
Microtopo-graphy	1.0	No topographic alteration from forestry*
(V_{MICRO})	0.75	Presence of one kind of topographic alteration*
	0.5	Presence of two kinds of topographic alteration*

*Types of topographic alteration by forestry: logging roads, skidder trails, windrows, bedding planted to pine.

also included relatively undisturbed flats and riverine wetlands.

Functional Assessments

The hydrogeomorphic (HGM) method (Whigham et al. 1999, 2003, Rheinhardt et al. 2002) was used for assessment of the ecological functioning of the wetlands. The HGM method calculates various functional capacity index (FCI) scores based on several variable scores. Variable scores are derived from field observations of a 1-ha assessment area around an assessment point in the wetland. Observations of tree, shrub, and herbaceous species and measurements of tree basal area, microtopography, and hydrologic conditions are made within the assessment area (Whigham et al. 2003, 2007). The FCI and variable scores establish a normalized range of quality ratings ranging from 0–1, where 1 represents the highest possible quality, which is considered to be the least disturbed condition present among wetlands in the region. The scores are standardized from reference wetlands that are chosen to represent a broad range of alteration from undisturbed conditions.

Table 2. Variable scoring criteria used for field observations of riverine wetlands. The criteria and scores shown are applicable to the hydrology and biogeochemistry FCI scores used in this paper. Other HGM criteria and scores (see Whigham et al. 2003, 2007) are omitted.

Variable (Symbol)	Score	Criteria
Tree Basal Area	1.0	Area $\geq$ 35.6 m^2 ha^{-1}
(V_{TBA})	0.1–1.0	Area / 35.6 m^2 ha^{-1}
Floodplain	1.0	No alterations to the floodplain
($V_{FLOODPLAIN}$)	0.25	$>$ 10% but $\leq$ 75% area altered to increase or decrease flooding
Stream In	1.0	No channelization, dams, or road crossing in assessment area
($V_{STREAMIN}$)	0.1	Channelization of stream with levees reducing flooding
Stream Out	1.0	No channelization, dams, or road crossings near assessment area
($V_{STREAMOUT}$)	0.5	Minimal stream alteration near assessment area
	0.1	Major channelization with levees near assessment area

Different criteria were used to calculate HGM scores for flats and riverine wetlands. The following functions were scored for both wetland types: hydrology, biogeochemistry, plant community, and habitat (Whigham et al. 2007). A landscape FCI score was also calculated for riverine wetlands. In this study, we are most interested in the biogeochemistry function, which could reflect N processing in the wetlands. The hydrology function is also relevant because it is used to calculate the biogeochemistry function.

The biogeochemistry FCI score was derived from six variable scores for flats (Table 1) and four variable scores for riverine wetlands (Table 2). The only variable shared by the biogeochemistry functions of the two wetland types relates to tree basal area. However, scoring criteria for this variable differ between the two wetland types. Some variable scores are based on quantitative field measurements,

such as tree basal area, while other scores rely on estimates, such as the percentages of area covered by fill or affected by ditches, and other scores rely on observations of presence or absence of specific disturbances, such as stream channelization or logging roads (Tables 1 and 2).

The FCI scores for hydrology and biogeochemistry were calculated from variable scores as follows (Tables 1 and 2 give variable definitions).

For Flats:

$$\text{Hydrology FCI} = 0.25 * V_{FILL} + 0.75 * V_{DRAIN}$$

$$\text{Biogeochemistry FCI} = (V_{MICRO} + ((V_{SNAG} + V_{TBA} + V_{TDEN}) / 3)) / 2 * \text{Hydrology FCI}$$

For Riverine Wetlands:

$$\text{Hydrology FCI} = \text{SQRT}(((V_{STREAMIN} + (2 * V_{FLOODPLAIN})) / 3) * V_{STREAMOUT})$$

$$\text{Biogeochemistry FCI} = V_{TBA} * \text{Hydrology FCI}$$

Measuring Soil Characteristics and N Processes

We sampled five replicate locations within the dominant vegetation cover inside the HGM assessment area of each wetland in spring (March–May), summer (June–July), and fall (September–October) of 2000. At each sampling location, we made in situ measurements of nitrous oxide (N_2O) efflux, oxidation-reduction potential (E_h), water-table (WT) depth, and soil temperature at 5 cm ($Temp_5$). We also collected soil cores to a depth of 10 cm by pressing a sharp-edged, 4-cm-diameter aluminum cylinder into the soil after removing the litter layer. One core from each sampling location was cleared of large roots, homogenized, and subsampled for analysis of denitrification enzyme activity (DEA), total organic carbon (%C), total nitrogen (%N), pH, and adsorbed plus dissolved (2 M KCl extractable) ammonium (NH_4^+). Another core from each location was analyzed for percent water-filled pore space (%WFPS).

N_2O efflux to the atmosphere was measured in situ from the rate of accumulation of N_2O within chambers placed over the soil (Livingston and Hutchinson 1995). We used cylindrical clear acrylic chambers (25-cm diameter $\times$ 15-cm height), each inserted 2–5 cm into the soil and then closed with a 2.5-cm stopper placed in a central hole in the flat acrylic top. If the chambers were in direct sunlight, they were loosely covered with reflective mylar. Immediately after installing the chamber and again after about 24 hours, a 10-ml gas sample was withdrawn from each chamber with a syringe inserted through a septum fitted in the stopper. Each gas sample was injected into an evacuated septum-covered vial for transport back to the laboratory and analysis by gas chromatography with electron capture detection. After gas sampling, the height of the air space in each chamber was measured so the volume of enclosed air could be calculated. At times, water covered the wetland soil, but usually, the air in the chamber was in direct contact with the soil surface.

Soil E_h was measured in situ with platinum electrodes (Faulkner 1989). The electrodes were made by inserting a 15-mm length of 18-gauge platinum wire into the end of a 1-m length of 10-gauge insulated copper wire and covering all but 5 mm of the platinum with insulation. The exposed platinum tip was inserted 5 cm into the soil for E_h measurements. The opposite end of the copper wire was connected to a wire from a Calomel (saturated KCl) reference electrode and pH meter. The reference electrode was inserted into the soil near the platinum electrode. If necessary, the soil was moistened to ensure good contact with the reference electrode. The pH meter was switched to mV, and the value was recorded after the drift of the reading had decreased to 1 mV/15sec. The mV reading was converted to E_h by adding 250 mV. Prior to use, the electrodes were tested using saturated solutions of quinhydrone (0.1 g/50 ml) in pH 4 and pH 7 buffers. Electrodes were rejected if they did not produce readings within 10 mV of 41 mV at pH 7 and 218 mV at pH 4.

Other in situ measurements were made as follows. When the wetland soil was not covered with water, water-table (WT) depth was measured by digging a hole $\geq$ 40 cm deep and measuring the distance from the soil surface to the water that seeped into the hole after about one hour. When the wetland soil was covered with water, WT depth was measured as the depth of water above the soil surface expressed a negative number. Soil temperature 5 cm below the soil surface ($Temp_5$) was measured with an Omega model 871 temperature probe.

Denitrification enzyme activity (DEA) was measured as the rate of N_2O production by soil incubated in a solution of glucose, nitrate, and chloramphenicol under an atmosphere of N_2 and acetylene (Tiedje et al. 1989). This assay optimizes denitrification rates by adding excess glucose and nitrate while excluding oxygen. Adding chloramphenicol inhibits protein synthesis to block production of new denitrification enzymes. Adding acetylene blocks nitrous oxide reduction, thereby making N_2O the end product of denitrification. Thus, the rate of N_2O production in this assay is related to the original concentrations of denitrifica-

tion enzymes (nitrate-, nitrite-, and nitric oxide-reductases) and represents a maximum potential for denitrification with the enzyme stocks present in the soil. Some authors refer to this measurement as denitrification potential (e.g., Maag et al. 1997, Hill and Cardaci 2004).

To measure DEA, a weighed amount of about 25 g wet weight of fresh soil was taken from each core sample and placed in a 125-ml Erlenmeyer flask containing 25 ml of a solution of 1 mM glucose, 1 mM KNO_3, and 1 g l^{-1} chloramphenicol. The flask was flushed with high purity N_2 and then closed with a stopper fitted with a septum. Then, 11 ml of acetylene was injected with a syringe inserted through the septum. We used acetylene produced by reacting calcium carbide with water because commercially available bottled acetylene gas contains acetone. The soils were incubated for 2 hours at 20°C, and then 10 ml of headspace gas was transferred by syringe from the flask to an evacuated septum-covered vial for analysis.

We analyzed N_2O using a Shimadzu GC-14A gas chromatograph (GC) with Porapak-Q columns and an electron capture detector. The first column (1 m) separated N_2O from water and acetylene, which were back flushed out of the column after the N_2O passed through. The second column (3 m) separated N_2O from carbon dioxide and other gases. Vials used to collect gas samples for analysis were loaded onto an O-I-Analytical 4632 automated sampling system that injected samples into the GC. For each batch of analyses, the GC was calibrated using commercially available standard gas mixtures. The detection limit was about 0.1 ppm nitrous oxide, and the analytical error was less than 10% in the range of concentrations that we typically measured (1–10 ppm).

Other soil characteristics were analyzed in subsamples of cores. Total nitrogen and total organic carbon were analyzed in dried, ground samples with a Perkin Elmer Model 2400 Series II CHNS/O Analyzer. Soil pH was measured by shaking 10 g of fresh soil in 20 ml of distilled water for 2 hours and measuring the pH of the supernatant with a pH meter. Adsorbed plus dissolved ammonium (NH_4^+) was first extracted by shaking a weighed amount of fresh soil equivalent to about 20 g dry weight in 80 ml of 2 M KCl for one hour. The extractant was then filtered with Whatman 42 filter paper and analyzed for ammonium with an Astoria-Pacific International Model 300 automated colorimetric analysis system. The colorimetric analysis reacted ammonium with salicylate and hypochlorite in a buffered alkaline solution in the presence of sodium nitroferricyanide (Astoria-Pacific International method A303-S021).

We used separate cores for measuring the percentage of the pore space in the soil that was filled with water (percent water filled pore space, %WFPS). When taking the core samples, compaction of the soil was avoided by carefully twisting the sharpened coring cylinder to sever roots as the cylinder was inserted. The bottom of the fresh core was trimmed flush with the bottom of the 10-cm coring cylinder. If the core was less than 10 cm long, its length was measured so the volume of the core could be calculated. The core was then extruded and wrapped in aluminum foil with the ends of the core exposed. The wrapped core was weighed wet, oven dried, and reweighed. The aluminum foil wrapping was also weighed, so the wet and dry weights of the core could be calculated. The dry material in the core was then ground in a Wiley Mill. The density of the dried ground material was measured by placing a weighed 15–20 g subsample in a 250-ml graduated cylinder containing 100 ml of isopropyl alcohol solution (50% v/v) and then recording the volume of solution displaced by the solids. The total volume of solids was calculated by multiplying the total dry weight of the core by the density of the solids. The total pore space was calculated by subtracting the volume of solids from the total volume of the core. The percentage of the total pore space occupied by water was considered the %WFPS.

RESULTS

N Processes and Soil Characteristics

DEA, N_2O flux, and soil characteristics generally differed between flats and riverine wetlands and, in some cases, differed among seasons (Table 3). Compared to flats, riverine wetlands had significantly higher DEA, %N, pH, and NH_4^+ concentration and significantly lower E_h. N_2O flux was greater on average in riverine wetlands than in flats, but the difference was not statistically significant ($p = 0.07$).

WT depth and %WFPS differed between wetland types and among seasons (Table 3). Riverine wetlands tended to be wetter than flats, while spring tended to be wetter than summer and fall. Thus, %WFPS drops to lower averages in flats than in riverine wetlands during summer and fall (wetland type X season interaction $p = 0.068$). Similarly, average WT depths are generally lower in flats than in riverine wetlands and show a greater but not statistically significant seasonal decrease in flats than in riverine wetlands during summer and fall (wetland type × season interaction $p = 0.075$). In

Table 3. Seasonal means ± standard errors (number of wetlands in parentheses) for flats and riverine wetlands. Replicate measurements within wetland and season were first averaged. The means of these averages are shown. Asterisks indicate the statistical significance of differences between flats and riverine wetlands as tested by ANOVA of averages of replicates within wetlands with factors including wetland type, season, and their interaction. Interactions of wetland type and season were not significant. Units are as follows: N_2O fluxes are μg N m^{-2} day^{-1}; DEA is per weight of dry soil mg N kg^{-1} day^{-1}; and NH_4^+ is μg N g^{-1} dry soil. WT depths ≥ 40 cm were recorded as 40 cm. ND indicates no data.

	Type	Spring	Summer	Fall
N_2O flux	Flat	3.8 ± 4.3 (5)	11 ± 6.5 (7)	19 ± 12 (7)
	Riv.	64 ± 48 (6)	24 ± 18 (8)	83 ± 43 (8)
Log (DEA)	Flat	−0.48 ± 0.22 (5)	−1.0 ± 0.25 (6)	−0.68 ± 0.12 (7)
	Riv.**	0.20 ± 0.16 (7)	0.30 ± 0.22 (9)	−0.027 ± 0.14 (9)
E_h (mV)	Flat	ND	640 ± 17 (7)	580 ± 38 (4)
	Riv.**	ND	330 ± 63 (9)	240 ± 18 (7)
%N	Flat	0.75 ± 0.20 (6)	0.64 ± 0.15 (7)	0.63 ± 0.15 (7)
	Riv.*	0.86 ± 0.11 (8)	1.0 ± 0.12 (8)	0.96 ± 0.12 (9)
%C	Flat	14 ± 3.8 (6)	12 ± 2.6 (7)	12 ± 2.7 (7)
	Riv.	15 ± 2.1 (8)	18 ± 3.3 (8)	17 ± 3.4 (9)
pH	Flat	3.3 ± 0.053 (7)	3.3 ± 0.088 (7)	3.3 ± 0.065 (7)
	Riv.**	4.3 ± 0.26 (8)	4.1 ± 0.24 (9)	4.2 ± 0.21 (9)
Log (NH_4^+)	Flat	0.71 ± 0.12 (7)	0.66 ± 0.059 (7)	0.66 ± 0.11 (7)
	Riv.**	1.1 ± 0.12 (9)	1.2 ± 0.067 (9)	1.2 ± 0.11 (9)
%WFPS	Flat	79 ± 7.2 (6)	62 ± 4.5 (6)	66 ± 5.3 (7)
	Riv.**	79 ± 4.2 (9)	83 ± 4.2 (8)	85 ± 3.9 (9)
WT depth cm	Flat	12 ± 2.0 (3)	40 ± 0 (7)	31 ± 5.3 (7)
	Riv.**	0.61 ± 6.8 (6)	0.022 ± 5.8 (9)	9.0 ± 6.0 (9)
$Temp_5$ (°C)	Flat	11 ± 0.46 (5)	26 ± 1.5 (7)	19 ± 1.2 (7)
	Riv.*	11 ± 1.2 (6)	25 ± 0.31 (9)	15 ± 0.53 (9)

* $0.01 < p \leq 0.05$.
** $p \leq 0.01$.

the summer, WT depths in the flats were all greater than 40 cm, the maximum limit of the WT depth measurement. WT depths in flats were never less than 10 cm. Thus, the WT was always below the depth of our 10-cm core samples in flats. In contrast, the WT was often within the depth of core samples in the riverine wetlands. Sometimes, the soil at riverine wetlands was flooded (i.e., WT depth was < 0). The wetter conditions in riverine wetlands ultimately may be responsible for many of the differences between riverine wetlands and flats.

Differences in WT depth among seasons may have been affected by the amounts of precipitation during our study periods. Based on measurements at Vienna, Maryland, in the Nanticoke River watershed, precipitation during our study was about normal (30-year average amount) in the spring, about twice normal in the summer, and about half normal in the fall (Maryland State Climatologist, www.atmos.umd.edu). Thus, conditions may have been wetter than normal during the summer we studied and drier than normal during the fall we studied.

There were correlations among many of the variables we measured (Table 4). For example, WT depth was significantly correlated with all of the other variables measured, and %WFPS was significantly correlated with all other variables except %N and %C. Because WT depth and %WFPS reflect the degree of water saturation, it is not surprising that these measures correlate with many other soil characteristics. E_h is strongly influenced by soil moisture and correlated with all the variables we measured except N_2O flux. NH_4^+ concentration and pH also correlated with most of the other variables. In contrast, $Temp_5$ correlated only with WT depth, %WFPS, and E_h, probably reflecting the seasonality of soil moisture.

The strongest correlation observed was between %C and %N (Table 4), probably because these elements are both components of soil organic matter. However, the relationship between these elements was different in flats than in riverine wetlands (Figure 2). At lower levels of C, the C:N ratio was higher in flats than in riverine wetlands. When the soil had less than 20 moles of C per dry kg, C:N ratios in flats clustered in two groups, one with C:N ranging from about 24–34 and another with C:N ranging from about 17–23. In contrast, C:N ratios in riverine wetlands were lower, ranging from about 12–18 when the soil had less than 20 moles of C per dry kg. However, when the soil had

Table 4. Pearson correlations (r) among variables. The number of observations in the analysis ranged from 108 for E_h vs. %WFPS to 234 for pH vs. log(NH_4^+).

	N_2O flux	E_h	WT depth	log(NH_4^+)	pH	%N	%C	%WFPS	$Temp_5$
log(DEA)	0.11	−0.66**	−0.60**	0.56**	0.55**	0.53**	0.43**	−0.38**	−0.01
$Temp_5$	−0.18	0.35**	−0.28**	−0.13	−0.13	−0.09	−0.07	−0.16*	
%WFPS	0.20**	−0.69**	−0.60**	0.29**	0.57**	0.09	0.06		
%C	0.13	−0.38**	−0.35**	0.52**	−0.03	0.94**			
%N	0.15	−0.45**	−0.35**	0.52**	0.07				
pH	0.17*	−0.58**	−0.59**	0.42**					
log(NH_4^+)	0.12	−0.68**	−0.52**						
WT depth	−0.18*	0.70**							
E_h	−0.15								

* $0.01 < p \leq 0.05$.
** $p \leq 0.01$.

higher levels of C, the C:N ratios in flats and riverine wetlands both converged in the range of about 17–25. The differences in C:N ratios suggest qualitative differences in the soil organic matter in the two types of wetlands.

N_2O flux correlated with only three of the variables we measured: %WFPS, pH, and WT depth (Table 4). Those significant correlations with N_2O flux were weak, with $r \leq 0.20$. Apparently, the control of N_2O flux is not linked in a simple manner to the factors we investigated, nor did N_2O flux correlate significantly with DEA (Table 4), although the three highest N_2O fluxes occurred in riverine wetland soils with higher than average DEA (Figure 3).

Unlike N_2O flux, DEA correlated with most of the variables we measured (Table 4), suggesting that denitrification rates may be mechanistically linked to the soil characteristics we studied. In order from strongest to weakest correlation, the variables significantly correlated with DEA included E_h, WT depth, NH_4^+, pH, %N, %C, and %WFPS.

DEA increased with decreasing WT depth (Figure 4), with the highest DEA levels observed only when the water table was within the depth of our core samples (10 cm) or when the soil surface was submerged. DEA in our core samples was about ten times lower when the water table was below the depth of the core than when it was within 10 cm of the surface.

DEA increased with rising pH in a manner that suggests a threshold for the pH effect at about pH 3.7 (Figure 5). When pH was less than 3.7, DEA was often less than 0.5 mg N kg^{-1} day^{-1} and ranged up to only 6 mg N kg^{-1} day^{-1}. However, when pH was greater than 3.7, DEA was usually greater than 0.5 mg N kg^{-1} day^{-1} and ranged up to about 30 mg N kg^{-1} day^{-1}. Riverine wetland soils had the widest range of pH (3–7.5), while all but one soil sample from the flats had pH less than 3.8.

DEA decreased with increasing E_h (Figure 6), as would be expected due the inhibition of denitrification by oxygen. The rate of DEA decrease with rising E_h was greater for soils with lower than average %N or %C. In riverine wetland soils, E_h had a wider range (20–660 mV) and reached lower values (20 mV) than in flats soils.

To understand the interrelationships of DEA and the observed soil characteristics (Table 3), we constructed general linear statistical models (GLM, SAS Institute, Inc. 2004) with log (DEA) as the dependent variable. The independent variables included the classification variables season, wetland type (i.e., riverine or flat), and wetland site nested in wetland type, which were entered into the models after the continuous independent variables (measurements such as E_h, pH, and %N) to test whether variance in DEA that was not related to soil characteristics could be related to the classification variables. In preliminary analyses, we entered the main effects of single continuous variables first, then the two-way interactions of all continuous variables, then the classification variables, and finally the two-way interactions of season and the continuous variables. Preliminary analyses showed that the effects of %N and %C were indistinguishable because these two variables are so tightly correlated. Therefore, in subsequent analyses we omitted %C, noting that effects attributed to %N could also be attributed to %C.

A simplified model, omitting non-significant factors (Type I $p > 0.05$), accounted for 78% of the variance of log(DEA) and included E_h, %N, pH, the interaction of E_h and %N, and wetland site (Table 5). The effects of E_h, pH, and %N have been described (Figures 5 and 6). The effects of wetland

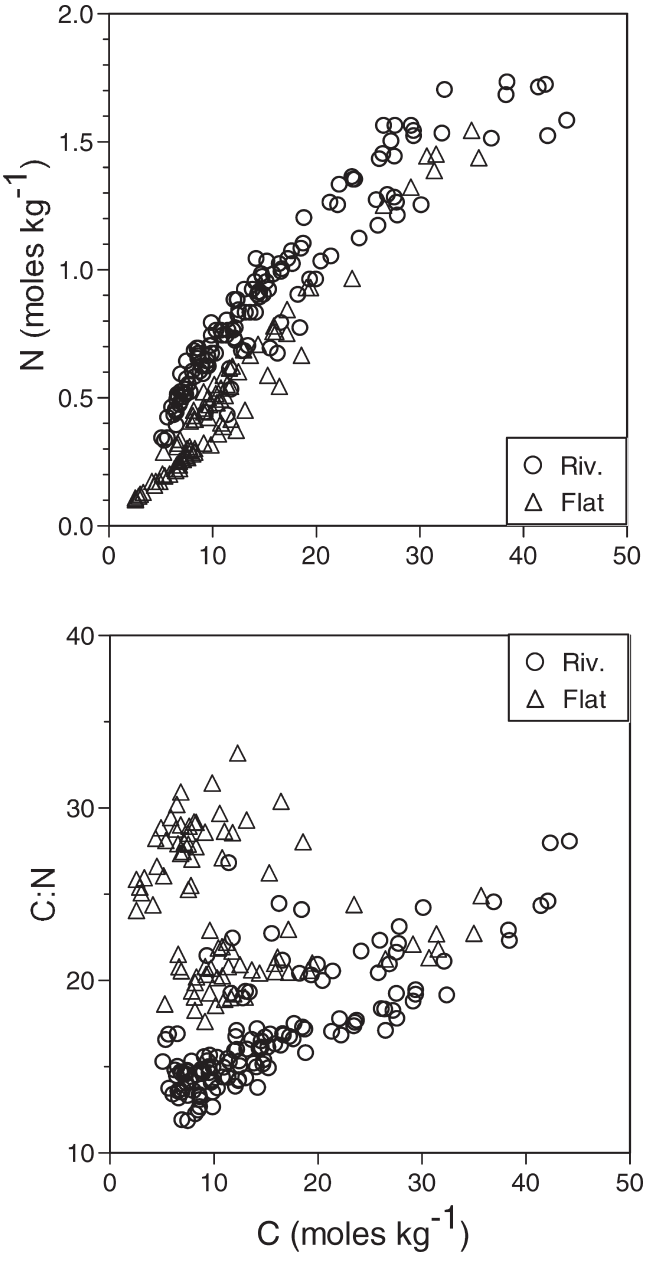

Figure 2. Upper panel: Moles of N per kg dry sediment versus moles of C per kg dry sediment in riverine (circles) and flats (triangles) wetlands. Lower panel: Atomic C:N ratio versus moles of C per kg dry sediment in riverine (circles) and flats (triangles) wetlands. Individual replicates from all seasons are plotted.

type, season, and the interactions of season with continuous variables were not significant. Therefore, the observed differences in log(DEA) between flats and riverine wetlands (Table 1) could be attributed to differences in E_h, pH, and %N. The effect of wetland site represents the differences in log(DEA) among the wetlands that could not be attributed to differences in E_h, pH, and %N. A model omitting the effects of site could still account for 67% of the variance in log(DEA).

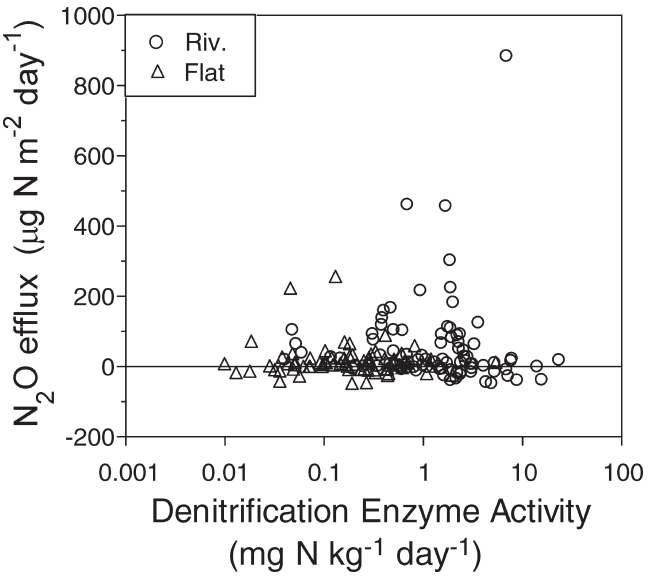

Figure 3. N_2O efflux (μg N m^{-2} day^{-1}) versus DEA (mg N kg^{-1} dry sediment day^{-1}) in riverine (circles) and flats (triangles) wetlands. DEA is plotted on a log scale. Individual replicates from all seasons are plotted.

Comparing N Processes to HGM Assessments

HGM scores indicate that our study wetlands differ greatly in their degree of alteration from undisturbed conditions, as do other wetlands in the Nanticoke River watershed. For the flats, bio-

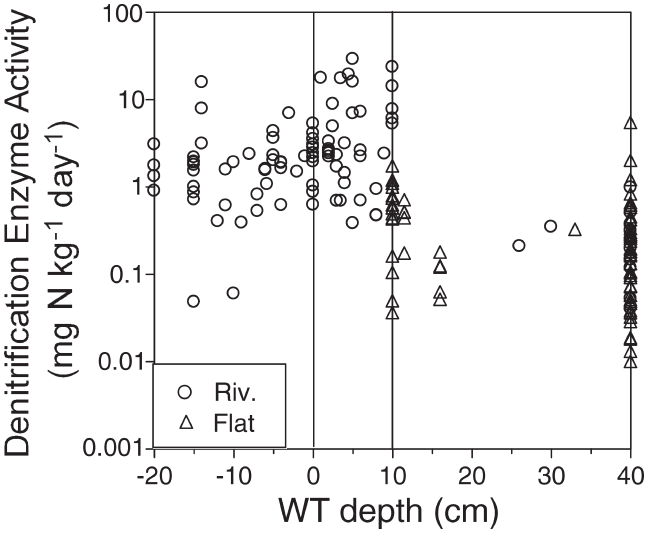

Figure 4. DEA (mg N kg^{-1} dry sediment day^{-1}) versus WT depth (cm) in riverine (circles) and flat (triangles) wetlands. DEA is plotted on a log scale. Vertical lines show the depth range of the core samples. Individual replicates from all seasons are plotted.

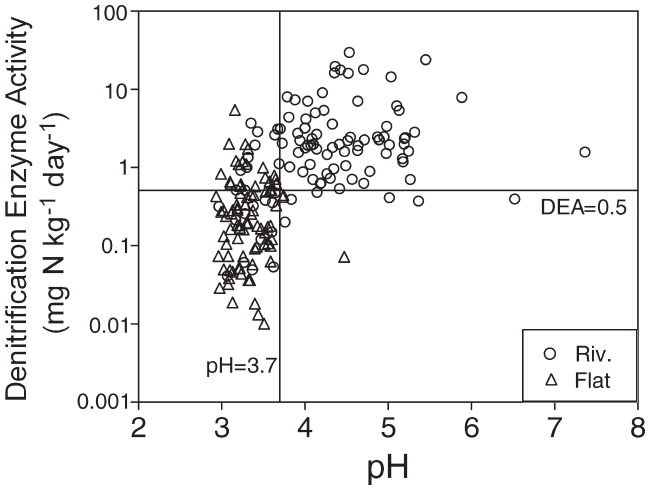

Figure 5. DEA (mg N kg^{-1} dry sediment day^{-1}) versus pH in riverine (circles) and flat (triangles) wetlands. DEA is plotted on a log scale. Individual replicates from all seasons are plotted. Guidelines indicate pH = 3.7 and DEA = 0.5 mg N kg^{-1} day^{-1}.

geochemistry FCI scores ranged from 0.24 to 0.98, and hydrology FCI scores ranged from 0.5 to 1 (Table 6). For the riverine wetlands, biogeochemistry FCI scores ranged from 0.18 to 1 and hydrology FCI scores ranged from 0.14 to 1 (Table 7).

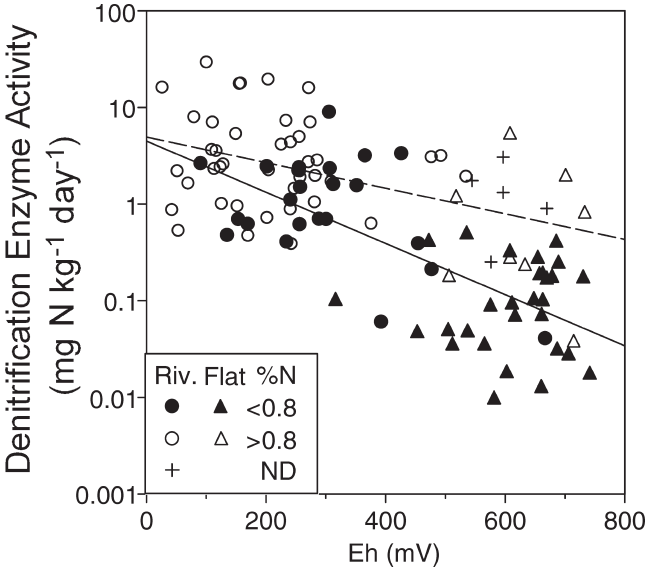

Figure 6. DEA (mg N kg^{-1} dry sediment day^{-1}) versus E_h (mV) in riverine (circles) and flats (triangles) wetlands, with %N < 0.8 (filled symbols) and > 0.8 (open symbols). Crosses indicate riverine DEA when no data are available for %N. DEA is plotted on a log scale. Lines are fit by linear regression separately for data with %N < 0.8 (solid line) and %N > 0.8 (dashed line). Individual replicates from all seasons are plotted.

Table 5. Percentages of variance explained by linear statistical models that relate log(DEA) to various factors. Models were fit with the GLM procedure of the Statistical Analysis System (SAS Institute, Inc. 2004). Each percentage of variance explained is for a model that includes the factor on the line and all the factors on previous lines. According to the *F* statistic generated by the GLM analysis, all the factors were highly statistically significant ($p \leq 0.01$).

Factor	% Variance Explained
E_h	44
%N	60
pH	65
$E_h \times$ %N	67
Site	78

The rankings of biogeochemistry and hydrology scores were similar because hydrology scores were used in calculating biogeochemistry scores. However, the rankings were not identical because some variables used in calculating biogeochemistry scores were not used in calculating hydrology scores. Thus, the rankings of biogeochemistry scores were altered relative to hydrology scores due to the variable scores for tree basal area in riverine wetlands and due to the variable scores for tree snags and microtopography in flats.

Using correlation analysis, we tested whether the HGM biogeochemistry scores for the wetland sites would be useful for predicting the denitrification potential or the N_2O flux at the site. We compared scores for flats and riverine wetlands separately because different criteria were used to score the two types of wetlands. HGM scores were compared to seasonal averages of log(DEA) and N_2O flux. Averages were computed by first averaging replicate measurements within wetland sites and sampling dates and then averaging these means by site and season. Usually, there was only one sampling date per site per season.

DEA decreased significantly with decreasing biogeochemistry score for flats in summer ($r = 0.84$, $p = 0.036$) but not in other seasons (Figure 7). The summer correlation may be due to the tendency for DEA to decrease with decreasing soil wetness (Table 4). Lower biogeochemistry scores (<0.6) were associated with increased artificial drainage due to ditching (Table 6), which is common in flats of the Nanticoke watershed. Ditching should decrease %WFPS and increase WT depth, especially in summer and fall, when %WFPS is generally lowest and WT depth highest (Table 3). Thus, correlations between biogeochemistry scores and DEA might be strongest in summer and fall. However, no signifi-

Table 6. Flats HGM FCI scores and variable scores in order of descending biogeochemistry FCI score.

Site	Biogeochemistry FCI*	Hydrology FCI[t]	Microtopography	Tree Snags	Tree Basal Area	Tree Density	Fill	Drainage
F16	0.98	1.00	1.00	1.0	1.0	0.9	1.00	1.00
F17	0.93	0.93	1.00	1.0	1.0	1.0	1.00	0.90
F2	0.59	0.81	0.75	0.1	1.0	1.0	1.00	0.75
F4	0.50	0.50	1.00	1.0	1.0	1.0	0.50	0.50
F10	0.45	0.63	0.75	0.1	1.0	1.0	1.00	0.50
F3	0.29	0.56	0.50	1.0	0.2	0.4	0.75	0.50
F12	0.24	0.81	0.50	0.1	0.1	0.1	1.00	0.75

* Biogeochemistry FCI = $(V_{MICRO} + ((V_{SNAG} + V_{TBA} + V_{TDEN}) / 3)) / 2$ * Hydrology FCI.
[t] Hydrology FCI = 0.25 * V_{FILL} + 0.75 * V_{DRAIN}.

cant correlation was observed in fall. Moreover, in summer, when the correlation was significant, %WFPS and WT depth did not show a markedly different pattern than in fall (Table 3).

In the riverine wetlands, DEA did not correlate significantly with the biogeochemistry score in any season (Figure 8). Low biogeochemistry scores in riverine wetlands were associated with alterations in drainage due to ditching or due to blockage of surface channels. These alterations could cause either decreases or increases in soil wetness. In one of our study wetlands (R17), alterations decreased drainage, which could increase soil wetness and DEA. This wetland had the lowest biogeochemistry and hydrology scores (Table 7) but moderately high DEA (Figure 8). Even if we disregard this wetland, biogeochemistry score could not be used to predict DEA in riverine wetlands.

The lack of correlations between DEA and biogeochemistry FCI scores contrasts with the abundance of correlations between DEA and soil characteristics (Table 4). However, the correlations with soil characteristics considered data from both flats and riverine wetlands in all seasons, whereas our correlation between DEA and FCI scores considered different wetland types and seasons separately. Some of the variance in DEA and correlated soil characteristics is accounted for by separating wetland type and season. For example, DEA, E_h, %N, pH, NH_4^+, %WFPS, WT depth, and $Temp_5$ differ significantly between flats and riverine wetlands (Table 3). Therefore, correlations between soil characteristics and DEA are less evident if the data for the two wetland types are analyzed separately. Nevertheless, there are significant correlations between soil characteristics and DEA even when data for different wetland types and seasons are analyzed separately (Table 8). For flats, %C and %N are positively correlated with DEA in each season, although the correlation with %C is not significant in spring. Also, in flats, DEA shows the expected negative correlation with WT depth in spring, although not in other seasons. Correlations in riverine wetlands differ seasonally and differ from those in flats. In riverine wetlands pH and NH_4^+, were significantly positively correlated with DEA in spring and fall. In summer in riverine wetlands, only $Temp_5$ and E_h are correlated with DEA. In fall in riverine wetlands, DEA correlated with a suite of interrelated soil char-

Table 7. Riverine wetlands HGM FCI scores and variable scores in order of descending biogeochemistry FCI score.

Site	Biogeochemistry FCI*	Hydrology FCI[t]	Tree Basal Area	Stream In	Stream Out	Floodplain
R16	1.00	1.00	1.00	1.0	1.0	1.00
R7	0.71	0.71	1.00	1.0	0.5	1.00
R8	0.71	0.71	1.00	1.0	0.5	1.00
R13	0.71	0.71	1.00	1.0	0.5	1.00
R19	0.71	0.71	1.00	1.0	0.5	1.00
R4	0.15	0.32	0.46	0.1	0.5	0.25
R5	0.10	0.14	0.74	0.1	0.1	0.25
R18	0.069	0.14	0.49	0.1	0.1	0.25
R17	0.031	0.14	0.22	0.1	0.1	0.25

* Biogeochemistry FCI = V_{TBA} * Hydrology FCI.
[t] Hydrology FCI = SQRT $(((V_{STREAMIN} + (2 * V_{FLOODPLAIN})) / 3) * V_{STREAMOUT})$.

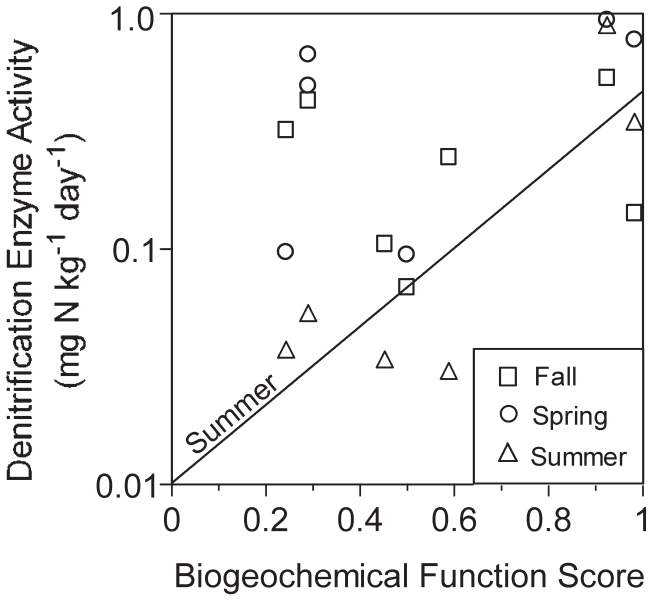

Figure 7. DEA (mg N kg^{-1} dry sediment day^{-1}) versus biogeochemical FCI score in flats during fall (squares), spring (circles), and summer (triangles). Data points are averages by wetland site and season. The line for summer is fit by linear regression.

acteristics (Table 8) as it did when data from all seasons and both wetland types were combined (Table 4). Thus, while DEA cannot be predicted from biogeochemistry FCI scores, it can be predicted from soil characteristics, even within wetland type and season.

To make our measurements of soil characteristics more analogous to FCI scores, we averaged seasonal mean values to produce one mean of each measurement per wetland (Table 9). Comparing these means among wetlands, we found that mean DEA is significantly correlated ($p < 0.05$) with mean %N and %C in flats, and with mean %WFPS, NH_4^+, and E_h in riverine wetlands. However, statistical models using both mean %N and %WFPS as independent variables provide the best predictions of mean log DEA in both flats and riverine wetlands (Table 10). A model combining data from both flats and riverine wetlands revealed a significant interaction between wetland type and the effect of %WFPS. Separate models for flats and riverine are more analogous to the HGM assessments, which consider the wetland types independently. Linear equations using parameters from the separate models (Table 10) can be used to assess wetland denitrification potential more effectively than biogeochemistry FCI scores.

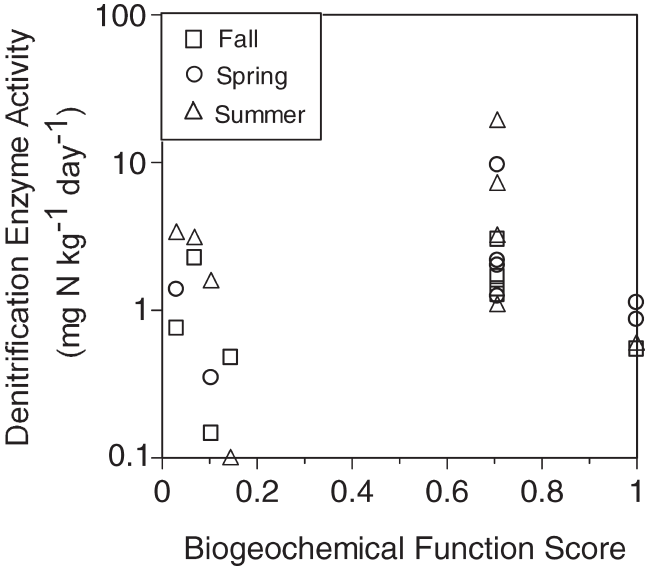

Figure 8. DEA (mg N kg^{-1} dry sediment day^{-1}) versus biogeochemical FCI score in riverine wetlands during fall (squares), spring (circles), and summer (triangles). Data points are averages by wetland site and season.

Biogeochemistry FCI scores did not correlate with N_2O efflux in either type of wetland in any season. This is consistent with the lack of strong correlation of N_2O efflux with any of the soil characteristics we observed. Similarly, N_2O efflux could generally not be predicted from any soil characteristics when data from different wetland types and seasons were analyzed separately. The only exceptions were significant negative correlations between N_2O efflux and %C, %N, and NH_4^+ in flats in spring only and a significant positive correlation between N_2O efflux and %N in riverine wetlands in fall only.

DISCUSSION

Denitrification requires an absence of oxygen and supplies of organic C and nitrate, so soil characteristics related to these requirements often correlate with DEA (Table 4). Absence of oxygen in wetland soils is usually due to a combination of respiration and water-saturation. Respiration consumes oxygen faster than it can be replaced in waterlogged soils because oxygen diffuses more slowly through water-filled soil pores than through gas-filled pores. Thus, DEA often correlates with %WFPS (Pennock et al. 1992, Ambus and Christensen 1993, Flite et al. 2001), WT depth (Groffman et al. 1996a), or duration of flooding (Pinay et al 2002). Likewise, we found correlations of DEA with %WFPS and WT depth (Table 4, Figure 4). We also found a correlation between DEA and pH (Table 4, Figure 5), which may reflect the pH tolerance of denitrifying bacteria or an association between pH and wetness. Waterlogged soils with near neutral pH may become more acid and less able to support denitrification as they dry (van Oorschot et al. 2000).

Table 8. Pearson correlations (r) with log(DEA) by wetland type and season.

	Flats			Riverine		
	Spring	Summer	Fall	Spring	Summer	Fall
$Temp_5$	0.31	0.29	0.33	0.044	0.44**	−0.25
%WFPS	−0.001	−0.11	0.14	0.18	0.25	0.61**
%C	0.31	0.63**	0.49**	0.29	0.16	0.44**
%N	0.50**	0.69**	0.53**	0.41	0.32	0.39**
pH	−0.014	−0.17	0.26	0.59**	0.17	0.49**
$Log(NH_4^+)$	0.11	0.43	−0.03	0.55**	0.26	0.51**
WT depth	−0.92**	ND	0.001	0.34	−0.16	−0.68**
E_h	ND	−0.0004	0.16	ND	−0.50**	−0.11

* $0.01 < p \leq 0.05$.
** $p \leq 0.01$.

DEA also correlates with respiration (Groffman et al. 1996a), which consumes oxygen and other electron acceptors. Once oxygen is exhausted, respiration uses alternate electron acceptors including nitrate, nitrite, and nitrous oxide; the electron acceptors of denitrification. The consumption of electron acceptors drives down the E_h. Hence low E_h is an indicator of microbial activity and an absence of oxygen, and low E_h is also a correlate of DEA (Pennock et al. 1992). E_h was the single variable most closely correlated to DEA in our study (Table 4, Figure 6).

Because denitrification requires organic carbon, DEA correlates with several measurements of organic carbon availability. Our study and others found that the percentage of organic C correlates with DEA (Groffman et al. 1996a, Hill and Cardaci 2004, Hill et al. 2004). Findlay et al. (2002) suggested that percentage of organic carbon could be a useful indicator of denitrification potential in wetland soils. Other studies found correlations between DEA and water extractable organic C (Ambus and Christensen 1993), extractable available organic C (Pinay et al. 1993), mineralizable organic C (Maag et al. 1997), and anaerobically mineralizable organic C (Hill and Cardaci 2004). Hill and Cardaci (2004) concluded that both the quantity and quality of organic C correlated with DEA, but they found no single predictor of DEA.

DEA also correlates with several variables related to nitrogen supply. Some studies show positive correlations with nitrate concentrations (Ambus and

Table 9. Average DEA (mg N kg^{-1} day^{-1}), %WFPS, %N, %C, pH, NH_4^+ (μg N g^{-1}), E_h (mV), and WT depth (cm) for each flat and riverine wetland site, listed in descending order of DEA.

Site	DEA	%WFPS	%N	%C	pH	NH_4^+	E_h	WT depth
Riverine								
R19	6.8	91	0.93	15	4.8	28	180	4.6
R8	2.8	82	1.5	27	4.2	18	320	−6.9
R13	2.7	87	1.2	29	3.9	20	250	−3.1
R18	2.7	91	0.78	12	4.5	18	270	1.6
R17	1.5	77	1.0	17	4.4	20	170	−2.2
R7	1.2	92	0.57	8.0	5.4	8.1	300	−2.1
R16*	0.69	84	0.89	19	3.9	30	200	−6.1
R5	0.43	72	0.82	11	3.6	6.3	620	17
R4	0.22	64	0.82	12	3.2	5.7	650	23
Flats								
F17	0.76	62	1.5	29	3.2	8.8	590	30
F16*	0.34	78	0.79	13	3.2	5.2	670	40
F3	0.24	85	0.49	7.3	3.6	3.1	640	21
F12	0.11	75	0.41	9.9	3.3	2.6	630	32
F2	0.086	49	0.60	11	3.2	6.0	670	40
F4	0.080	60	0.44	11	3.3	7.9	620	40
F10	0.060	77	0.28	6.6	3.4	3.3	520	25

* Wetlands with biogeochemistry FCI scores closest to 1.

Table 10. Parameter estimates and significance levels from linear models predicting $\log_{10}$ DEA from %WFPS and %N averaged to one value per wetland.

	Estimate	*p*
Riverine ($r^2 = 0.81$, n = 9)		
Intercept	−3.79	0.0030
%WFPS	0.0389	0.0041
%N	0.792	0.0496
Flats ($r^2 = 0.94$, n = 7)		
Intercept	−2.35	0.0017
%WFPS	0.0135	0.0291
%N	0.954	0.0014

Christensen 1993, Pinay et al. 1993, 2000), but nitrate concentrations in our wetlands were often undetectable. In soils with low or variable oxygen concentrations, nitrate may be depleted by denitrification and replenished by nitrification. Thus, DEA may correlate with other measurements of N supply, such as NH_4^+ concentration (Pinay et al 1993), %N, and N mineralization potential (Groffman et al. 1996a, Pinay et al. 2000). Similarly, we found correlations with NH_4^+ and %N (Table 4).

Although other studies have also reported correlates of DEA, our study is unusual in simultaneously examining multiple correlates in several different wetlands belonging to two wetland classes. By comparing multiple correlates, we were able to establish that E_h provided the strongest correlation and that %N or %C interacted with E_h. Those factors, combined in a statistical model with pH, predicted DEA better than other combinations of correlates. We also found that the effect of wetland class (flat or riverine) on DEA could be attributed entirely to differences in E_h, %N, and pH. Adding other correlates, such as %WFPS or WT depth, to the statistical model did not improve predictions. However, when we averaged measurements to produce one mean value per wetland, we found that the best statistical predictions of mean DEA were obtained from models using both mean %N and mean %WFPS as independent variables (Table 10).

DEA is a measure of potential denitrification. Actual denitrification is difficult to measure due its spatial and temporal variability and because N_2 produced by denitrification is difficult to measure against the background N_2 concentrations in situ. Pinay et al. (1993) found that DEA ranged from 1.3–20 times the rate of actual denitrification measured by the acetylene inhibition method in intact cores of wetland soil.

DEA is highly variable. Other studies report ranges from nearly zero to various maximum rates. For example, reported maxima range from 150 ng N g^{-1} dry soil hr^{-1} (Pinay et al. 2002) to 3,600 ng N g^{-1} dry soil hr^{-1} (Findlay et al. 2002), with many maxima in between (Flite et al. 2001, Clement et al. 2002, Hill et al. 2004). By comparison, the highest DEA values we found were about 2,000 ng N g^{-1} dry soil hr^{-1}. Because of the log-normal distribution of DEA values, the maxima are much higher than the geometric means. Our seasonal geometric means ranged from 4.2–14 ng N g^{-1} dry soil hr^{-1} in flats and 31–83 ng N g^{-1} dry soil hr^{-1} in riverine wetlands. By comparison, Hunter and Faulkner (2001) reported means of 657 ng N g^{-1} dry soil hr^{-1} in natural wetlands and 167 ng N g^{-1} dry soil hr^{-1} in restored wetlands.

The average and maximum rates of N_2O fluxes that we observed were lower than many others reported. For example, the maximum rate we observed was about 890 μg N_2O-N m^{-2} d^{-1} in a riverine wetland (Figure 3), while Weller et al. (1994) found maximum fluxes of 2,300 μg N_2O-N m^{-2} d^{-1} in riparian forest, and Davidsson and Leonardson (1997) found maximum rates of 15,000 and 8,500 μg N_2O-N m^{-2} d^{-1} for flooded and drained pastures, respectively. We found seasonal average flux rates ranging from 3.8 μg N_2O-N m^{-2} d^{-1} for flats in spring to 83 μg N_2O-N m^{-2} d^{-1} for riverine wetlands in fall (Table 3), while Hefting et al. (2003) found rates averaging 5,500 μg N_2O-N m^{-2} d^{-1} in riparian forest and 550–1,100 in riparian grassland. The lower rates in the wetlands we studied suggest that these wetlands may be relatively unimportant sources of atmospheric N_2O compared to other wetlands.

The N_2O fluxes we measured were only a small fraction of the potential denitrification rates measured as DEA. For comparison, we converted DEA from units per weight of dry soil to units per m^2, assuming that DEA in the top 10 cm of soil sampled by our cores represented the total DEA for the soil column. This assumption would underestimate DEA for the entire soil column, but most of the DEA may be in the top 10 cm because DEA usually declines rapidly with depth in the soil (Ambus and Lowrance 1991, Groffman et al. 1996b). Average summer DEA ranged from 5,500 μg N m^{-2} d^{-1} in flats to 63,100 μg N m^{-2} d^{-1} in riverine wetlands. This is 500 to 2,600 times the summer N_2O-N flux in flats and riverine wetlands, respectively. Actual denitrification is generally much lower than potential denitrification as estimated by DEA (e.g., Pinay et al. 1993). Also, the ratio of N_2:N_2O produced by denitrification is often much greater than 1, although the ratio varies so widely that it cannot

be used to predict N_2 production from measurements of N_2O production (Groffman et al. 2000).

In contrast to DEA, we found that N_2O efflux rates were very unpredictable (Table 4), having only weak correlations with %WFPS ($r^2 = 0.04$) and WT depth ($r^2 = 0.03$). Others have also found that the highest N_2O efflux rates are observed when soils are moist (Velthof et al. 1996) or when %WFPS exceeds 30% (Garcia-Montiel et al. 2001) or 50% (Hefting et al. 2003). N_2O efflux rates can also correlate with concentrations of NO_3^- (Keller and Reiners 1995, Mellilo et al. 2001), NH_4^+, or organic C (Velthof et al. 1996), or with rates of net N mineralization (Matson and Vitousek 1995, Garcia-Montiel et al. 2001) or net nitrification (Riley and Vitousek 1995). Unpredictability of N_2O efflux rates may be related to high spatial (Weller et al. 1994, Velthof et al. 1996) and temporal variability (Jordan et al. 1998).

HGM FCI scores might be expected to reflect denitrification potential because denitrification is strongly influenced by hydrology and geomorphology. For example, Johnston et al. (2001) compared riverbed, levee, and backwater wetland sediments and found that nutrient dynamics were related to geomorphology, with backwater sediments having the highest denitrification potential. Findlay et al. (2002) compared fringe, sheltered, and enclosed freshwater tidal wetlands and found systematic differences in DEA among those three morphological types. Clement et al. (2002) compared a topo-hydro-sequence of riparian wetland soils and found that topography was the most important correlate with denitrification rates. Our study showed that riverine wetlands had significantly higher denitrification potential than did flats (Table 3), possibly reflecting the hydrogeomorphic differences between these two classes of wetlands. The importance of hydrology is also suggested by the correlations of DEA with variables related to soil wetness (%WFPS, WT depth, E_h, and pH). However, within our wetland classes, biogeochemistry and hydrology FCI scores were poor predictors of DEA. Similarly, the variables measured to calculate the biogeochemistry FCI score (Tables 1 and 2) were not useful for predicting DEA. DEA correlated with the biogeochemistry score only for flats in the summer (Figure 7).

The development of HGM was stimulated by the need to assess wetland function over large spatial scales (Whigham et al. 2003). Correlations between HGM scores and DEA or N_2O efflux would have provided a means of extrapolating estimates of these rates over large scales. Another approach to scaling up wetland assessments is to use remotely sensed landscape indicators. Weller et al. (2007) found several correlations between HGM function scores and 48 landscape variables based on remotely sensed data, such as land cover and stream density within specified distances of the wetland assessment point. Thus, landscape data can be used to extrapolate HGM assessments to larger spatial scales. However, a preliminary analysis showed no clear correlations between DEA or N_2O efflux and any of the landscape variables used by Weller et al. (2007). Therefore, neither HGM FCI scores nor the landscape variables are apparently of much value in extrapolating estimates of DEA or N_2O efflux to large spatial scales.

Why are HGM FCI scores such poor predictors of DEA? One possibility is that wetland disturbances could either increase or decrease wetness compared to the relatively undisturbed conditions of the reference standard wetlands. One of our riverine wetlands was altered in a manner that would increase flooding, while our other riverine wetlands experienced increased drainage. Any alteration to the hydrology decreases the FCI scores for hydrology and biogeochemistry, but DEA generally increases with increased wetness. Thus, a low FCI score could mean that DEA is either lower or higher than the typical DEA of reference standard wetlands, and depending on the direction of disturbances, DEA might be either positively or negatively correlated with FCI scores.

Scoring different wetland types separately may also limit the correlation between FCI scores and DEA. Among the wetlands we studied, much of the variance in DEA is linked to the wetland type, with riverine wetlands having higher DEA than do flats (Table 3, Figure 7). Others have also found that DEA differs among wetland types more than within wetland types (Johnston et al. 2001, Findlay et al. 2002). However, we found significant correlations between certain soil characteristics and DEA even when the two wetland types were analyzed separately (Tables 8 and 9). This suggests that FCI scores of biogeochemical function could be improved by incorporating measurements of selected soil characteristics.

It is probably unrealistic to use a single FCI score to rate all biogeochemical functions, including N and P transformation and retention, carbon sequestration, and many others. Ideally, a separate FCI score should be developed just for denitrification. Several soil parameters may serve as easy-to-measure indicators of DEA that could be incorporated into denitrification FCI scores. Findlay et al. (2002) based a wetland function score directly on DEA measurements but noted that the laborious DEA measurements may be impractical for large

numbers of assessments. They suggested that soil organic matter or moisture content might be useful indicators of DEA. Hefting et al. (2004) compared 13 riparian wetlands and found that WT depth was a prime determinant of N dynamics, with ammonification dominant when WT depths were less than 10 cm, denitrification dominant when WT depths were 10–30 cm, and nitrification dominant when WT depths were greater than 30 cm.

Our results suggest that DEA indicators may include moisture-related variables such as WT depth, %WFPS, pH, or E_h. E_h closely correlated with DEA when data from both wetland types were combined (Table 4) but did not correlate consistently when data from different wetland types and seasons were considered separately (Table 8). When wetland types were considered separately, %N was correlated with DEA in all seasons in flats, while in riverine wetlands, various soil characteristics correlated with DEA in different seasons. No single DEA indicator stands out as the best for both wetland types in all seasons, suggesting that multiple indicators would be preferable. Regressions using both %N and %WFPS provided the best predictions of DEA averaged by wetland. As indicators, %N and %C have the advantage of staying relatively constant through the seasons. Analysis of %N requires the use of either chemical digestion or an elemental analyzer, so %N is more difficult to measure than %C, which may be measured by loss of weight on ignition or estimated from bulk density. WT depth, pH, and E_h vary with season and antecedent rainfall but are simple to measure in the field. %WFPS also varies with season and rainfall and is laborious to measure, although the measurement does not require specialized instrumentation.

To develop an HGM score for denitrification potential as represented by DEA, we would need to identify reference DEA values typical of the least and most disturbed wetlands. The average DEA for wetlands with biogeochemistry FCI scores closest to 1 (Table 9) could be defined as the reference standard DEA, representative of the least disturbed conditions. Although the biogeochemistry FCI scores were poor predictors of DEA, a score close to 1 suggests that the wetland was minimally disturbed. Note that defining the wetlands with the highest FCI scores as reference standards would result in the reference standard DEA being lower than the average DEA in one of the seven flats and six of the nine riverine wetlands (Table 9). DEA values for highly disturbed conditions could be set equal to the lowest DEA value observed (e.g., 0.01 mg N kg^{-1} day^{-1}, Figure 5), reasoning that a worst-case alteration of wetland condition could reduce DEA almost to zero (zero DEA cannot be represented by our statistical models of the log of DEA). In wetlands to be assessed, average %N and %WFPS could be used to predict average DEA, which would be compared to reference standard DEA. The difference between the predicted DEA and the reference standard DEA could be scaled from 0 to 1, using the difference between DEA under the most and least disturbed conditions. This would result in a DEA FCI score of the difference between DEA in the assessment wetland and DEA under the least disturbed conditions. It is important to note that the DEA FCI score represents the degree of alteration from undisturbed conditions. Thus, a low DEA FCI score could mean that DEA is either higher or lower than DEA in the reference standard wetland, assuming that disturbances can either increase or decrease %N or %WFPS.

The utility of a DEA FCI score may be limited if disturbances can either increase or decrease DEA. In such a case, the FCI score by itself could not be used to evaluate the potential ecosystem service of denitrification in individual wetlands or to extrapolate potential denitrification to larger spatial scales. However, DEA predicted from indicators such as %N and %WFPS could be used for these purposes. Scoring to evaluate ecosystem disturbance should be distinguished from scoring to evaluate ecosystem service because undisturbed conditions may not support the maximal rates of some desirable functions or ecosystem services.

DEA is an indicator of potential denitrification, not a measurement of actual denitrification or of the ecosystem service of N removal from water. We found that riverine wetlands had higher DEA than flats, suggesting a relationship between hydrogeomorphology and DEA. Actual dentrification rates may also be higher in riverine wetlands than in flats because flood water and ground water can carry nitrate to riverine wetlands from upstream sources such as croplands or developed lands. In contrast, flats are often on drainage divides and therefore not positioned to intercept nitrate from other sources in the watershed. However, flats at high positions in watersheds could still remove N from atmospheric deposition, which is an important source of N loading. Also, flats make up 72% of the wetland area in the Nanticoke watershed while riverine wetlands only account for 12% (Tiner 2005, terrene and lotic wetlands, respectively). Therefore, flats may be important N sinks in the Nanticoke watershed even if they remove less N per area than do riverine wetlands.

Our study suggests that the present formulation of the biogeochemistry FCI score does not adequately reflect the potential ecosystem service of N removal via denitrification. FCI scoring formulas could be improved by incorporating data on several easy-to-measure soil properties, such as WT depth, %WFPS, pH, E_h, %N, or %C. A linear model combining measurements of E_h, pH, and %N provided the best predictions of individual DEA measurements in our study wetlands. Average DEA was best predicted by a model using means of both %N and %WFPS as independent variables.

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