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Linkages between organic matter mineralization and denitrification in eight riparian wetlands

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Abstract. Denitrification (N_2 production) and oxygen consumption rates were measured at ambient field nitrate concentrations during summer in sediments from eight wetlands (mixed hardwood swamps, cedar swamps, heath dominated shrub wetland, herbaceous peatland, and a wetland lacking live vegetation) and two streams. The study sites included wetlands in undisturbed watersheds and in watersheds with considerable agricultural and/or sewage treatment effluent input. Denitrification rates measured in intact cores of water-saturated sediment ranged from ≤ 20 to 260 μmol N m^{-2} h^{-1} among the three undisturbed wetlands and were less variable (180 to 260 μmol N m^{-2} h^{-1}) among the four disturbed wetlands. Denitrification rates increased when nitrate concentrations in the overlying water were increased experimentally (1 up to 770 μM), indicating that nitrate was an important factor controlling denitrification rates. However, rates of nitrate uptake from the overlying water were not a good predictor of denitrification rates because nitrification in the sediments also supplied nitrate for denitrification. Regardless of the dominant vegetation, pH, or degree of disturbance, denitrification rates were best correlated with sediment oxygen consumption rates (r^2 = 0.912) indicating a relationship between denitrification and organic matter mineralization and/or sediment nitrification rates. Rates of denitrification in the wetland sediments were similar to those in adjacent stream sediments. Rates of denitrification in these wetlands were within the range of rates previously reported for water-saturated wetland sediments and flooded soils using whole core ^{15}N techniques that quantify coupled nitrification/denitrification, and were higher than rates reported from aerobic (non-saturated) wetland sediments using acetylene block methods.

Introduction

Nitrogen cycling in wetlands has received considerable attention (e.g., Valiela & Teal 1979; Dierberg & Brezonik 1983; Bowden 1986), in part, because of the potential of wetlands to decrease pollutant inputs of nitrogen to downstream surface and groundwater. Several studies have shown that freshwater wetlands are a "sink" for natural and anthropogenic N inputs (e.g., Tilton & Kadlec 1979; Hemond 1983; Gersberg et al. 1984) with N removal efficiencies ranging from 20% to over 70% (see review by Nixon & Lee 1986). Vegetative growth, immobilization by microbes, and burial in the sediments can retain nitrogen for various periods of time (Peterjohn & Correll 1984; Verhoeven 1986; Bowden 1987), however, denitrification (bacterial reduction of nitrate or nitrite to gaseous N) is the major process by which nitrogen is removed permanently from wetlands and downstream ecosystems.

While many measurements of denitrification have been made using sediments from freshwater wetlands, few measurements have been made at ambient field conditions (see review by Bowden 1987). The actual contribution of denitrification to N removal in wetlands, therefore, is difficult to assess based on existing data. Kaplan et al. (1979) measured N_2 production using *in situ* domes in a saltmarsh, but such direct measurements have not been made in freshwater wetlands. Numerous studies have estimated denitrification in freshwater wetlands from nitrogen mass balance calculations (e.g., Dierberg & Brezonik 1983; Brinson et al. 1984; Bowden 1986). Others have measured potential denitrification rates after nitrate additions to homogenized sediment slurries (e.g., Muller et al. 1980; Gordon et al. 1986; Westermann & Ahring 1987; Koerselman et al. 1989) or to whole cores (Dierberg & Brezonik 1983). Interpretation of measurements from sediment slurries, even if nitrate is not added (Hemond 1983; Westermann & Ahring 1987; Koerselman et al. 1989), is difficult because the coupling of denitrification to other N and C cycling processes in many soils and sediments depends on the fine scale structure of organic matter, water content and oxygen concentrations (Patrick & Reddy 1976; Myrold & Tiedje 1985; Parkin 1987. When whole cores have been used, samples usually have been incubated with acetylene (e.g., Dierberg & Brezonik 1983; Urban et al. 1988; Zak & Grigal 1991; Merrill & Zak 1992) which inhibits nitrification (Hynes & Knowles 1978). Nitrification of mineralized ammonia is an important source of nitrate for denitrification in wetlands as demonstrated by measurements of ^{15}N–N_2 production from whole cores following ^{15}N–NH_4^+ additions (Patrick & Reddy 1976; DeBusk & Reddy 1987; Reddy et al. 1989). When denitrification is coupled closely to nitrification, incubations with acetylene can markedly underestimate denitrification rates (Kemp et al. 1990; Seitzinger et al. 1993).

Freshwater wetlands include a broad range of ecosystems that differ not only in their vegetational composition, but also in their hydrology, pH, soil organic content, organic matter mineralization rates, and inputs of anthropogenic N (Mitsch & Gosselink 1986). All of these factors may influence the temporal and spatial distribution of denitrification rates within and among wetlands. Previous studies of denitrification in wetlands generally have focussed on the effect of one or more factors within a single wetland (e.g., Patrick & Reddy 1976; Hemond 1983; Gordon et al. 1986). Few studies have compared denitrification rates across a range of wetland types; those that have, have measured potential denitrification rates (nitrate amended anaerobic sediment slurries) (Muller et al. 1980; Jorgensen & Richter 1992).

In the present study, denitrification (N_2 production) was measured in eight wetlands during summer using intact sediment cores without nitrate amendments to: (1) compare denitrification rates among wetlands with different dominant vegetation that were either located in undisturbed watersheds or in areas receiving inputs of N from sewage and/or agricultural sources (disturbed), (2) compare denitrification rates in wetlands with similar dominant vegetation from undisturbed and disturbed watersheds, (3) provide insight into factors controlling denitrification rates across a broad range of wetlands, and (4) compare denitrification rates in wetland sediments with adjacent stream sediments.

Methods

Study sites

Eight riparian wetlands were chosen for denitrification studies based on their degree of anthropogenic N inputs and dominant vegetation. Seven wetlands were in the southern New Jersey Pinelands National Reserve region (Fig. 1), an area with generally sandy soils (Tedrow 1979) and naturally acidic streams (Morgan 1984); one wetland was in the Pocono Mountain region of north-eastern Pennsylvania.

Nitrogen loading rates to the eight study wetlands were not quantified. Three wetlands had no development in the surrounding forested watershed and no known anthropogenic N inputs other than atmospheric deposition (termed undisturbed) (Table 1). The dominant vegetation in these wetlands were either Atlantic White-cedar (*Chamaecyparis thyoides*), mixed hardwoods (primarily *Acer rubrum*), or heath dominated shrubs (primarily *Rhododendron canadense* and *Vaccinium corymbosum*). The streams adjacent to these wetlands have low nitrate concentrations (≤ 1 μM), and are acidic, brown-water streams, with pHs between 4 and 5.

Four wetlands had extensive agricultural fields directly surrounding them (termed disturbed) (Table 1); two of these wetlands also received nutrient inputs from a sewage treatment plant that discharged into Hammonton Creek approximately 5 km upstream. Nitrate concentrations (> 50 μM) and pH (5.5 to 6.5) were elevated in the streams in these disturbed watersheds compared to streams in the undisturbed watersheds (Durand & Zimmer 1982) (Table 1). The dominant vegetation in the disturbed wetlands was either Atlantic White-cedar (*Chamaecyparis thyoides*), mixed hardwoods (primarily *Acer rubrum*), or, in the herbaceous peatland, *Polygonum arifolium* (Table 1). One wetland appeared to be highly disturbed based on the dominance of dead plant material over live plants (listed as unvegetated).

The eighth wetland was located in a watershed with limited agricultural activity and was bordered by a small campground (termed intermediate disturbance) (Table 1). *Chamaecyparis thyoides* was the dominant vegetation in this wetland.

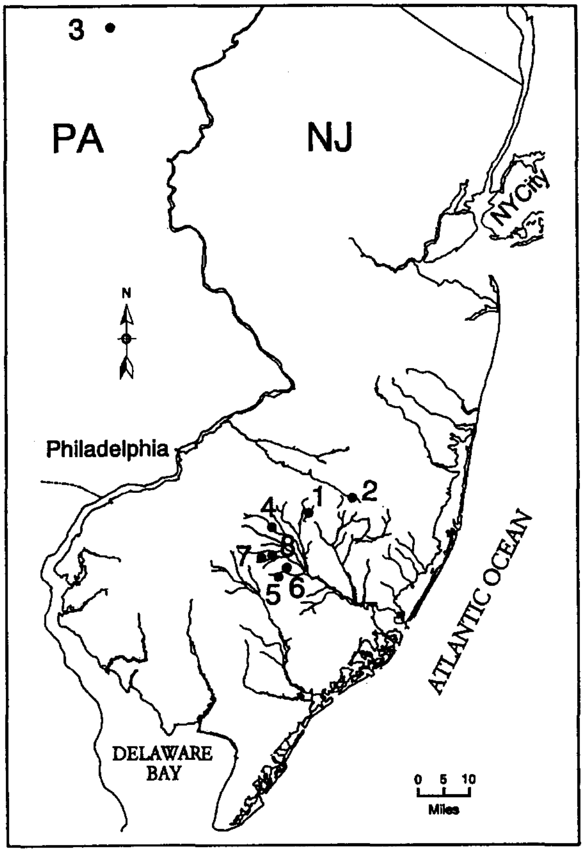

Fig. 1. Location of wetlands in New Jersey and Pennsylvania where studies of denitrification were conducted. Undisturbed: cedar swamp (1), mixed hardwood (2), heath (3); intermediate disturbance: cedar swamp (4); disturbed: cedar swamp (5), herbaceous (6), mixed hardwood (7), unvegetated (8).

Sample collection

A number of factors which would be expected to affect denitrification rates, such as water saturation of sediments (Davidson & Swank 1986; Groffman & Tiedje 1988; Groffman et al. 1991) and temperature (Knowles 1982; Westermann & Ahring 1987) vary spatially and temporally in these wetlands. For example, the forested and heath sediments vary spatially from relatively dry hummock sites around the root of trees and shrubs, to depressions, which often have standing water. To facilitate comparison of denitrification rates among the various wetlands, all measurements were made during summer (23 °C) with water-saturated sediment and aerobic overlying water as described below. The incubation conditions are most representative of late spring or

Table 1. Characteristics of wetland study sites and adjacent streams.

Wetland	Dominant vegetation	Latitude	Longitude	Stream basin	Watershed use	Wetland sediment TKN mg/gds	Stream			
							width (m)	depth (m)	NO_3 (µM)	pH
Undisturbed										
Cedar swamp	*Chamaecyparis thyoides*	N39 47 15	W74 38 30	Skit Brook	forested	15.7	2	1.5	1	4.8
Mixed hardwood	*Acer rubrum*	N39 52 45	W74 29 58	McDonalds Branch	forested	13.2	1.3	0.7	< 1	4.5
Heath	*Rhododendron canadense*	N41 5 59	W75 26 26	Unnamed	forested	7.9	1.3	0.5	< 1	4.3
Intermediate disturbance										
Cedar swamp	*Chamaecyparis thyoides*	N39 44 43	W74 45 40	Mullica River	forested/ camground	11.8	1000*	1.2	1	4.9
Disturbed										
Cedar swamp	*Chamaecyparis thyoides*	N39 38 03	W74 43 15	Hammonton Creek	agricultural/ residential	19.6	5	1.5	130	6.5
Herbaceous	*Polygonum arifolium*	N39 38 03	W74 43 05	Hammonton Creek	agricultural/ residential	n.m.	5	1.5	130	6.5
Mixed hardwood	*Acer rubrum*	N39 38 03	W74 43 05	Great Swamp Branch	agricultural	31.9	4	1.4	60	5.5
Unvegetated		N39 40 23	W74 48 45	Great Swamp Branch	agricultural	18.2	4	1.6	55	5.5

* Very wide section of river, depth near swamp.

summer when the water table is high, and/or the streams flood the adjacent wetlands, due to heavy rainfall. Sediments cores (6.7 cm diameter, 6 cm deep) from the five forested and one heath wetland were collected from depressions with standing water; oxygen concentrations in the standing water, measured at the time of core collection, were near saturation. The depressions were estimated visually to cover approximately 30% of the wetland surface. Few or no rooted plants were growing in the upper 6 cm of sediment in the depressions in the forested wetlands. In the heath wetland, *Sphagnum* sp. was growing in the depressions and was included in the sediment cores. There was little variation in sediment topography in the herbaceous and the unvegetated wetland compared to the forested wetlands. Sediment cores collected from these two wetlands did not include the larger herbaceous or woody plants, and thus the potential effect of oxygen release from their roots on denitrification rates (Reddy et at. 1989) was not measured.

Duplicate cores from all eight wetlands were collected within 5 m of each other and within 50 m of the stream edge of the wetland using plastic coring tubes. Sediment cores also were collected from the stream bottom near the disturbed and undisturbed cedar swamp study sites for comparison with rates in those wetland sediments. The stream sediments were collected from areas with obvious organic matter deposition.

Denitrification measurements

Denitrification rates (N_2 production), sediment-overlying water nitrate and ammonia fluxes, and sediment oxygen consumption rates were measured using modifications of techniques previously used for submerged sediments in estuaries, lakes and rivers (Gardner et al. 1987; Seitzinger 1988 and 1993; Nowicki & Oviatt 1990). Briefly, denitrification was measured as production of N_2 from intact sediment cores (6.7 cm diameter, 6 cm deep) at the ambient nitrate concentrations found in the adjacent stream. Sediment cores were incubated in gas-tight glass chambers, in the dark, at 23 ± 2 °C, with an overlying water (~600 ml) and gas phase (~70 ml) that had been sparged with a mixture of 79% He and 21% O_2 to decrease the background N_2 concentration, and thus permit detection of N_2 production due to denitrification. The water over the cores was changed every three to five days with freshly sparged (He/O_2) water collected from streams adjacent to each wetland. The water was stirred slowly to facilitate the equilibration of dissolved gases with the overlying gas phase. The gas phase in the chambers was flushed with the He/O_2 mixture as needed between water changes to maintain oxygen concentrations in the overlying water above 50% saturation.

Duplicate samples (50 μl) of the gas phase were taken from each chamber through sampling ports using a He-flushed gas-tight syringe, at approximately 24-h intervals beginning 24-h after the water was changed. Samples were analyzed for N_2 and O_2 concentration by gas chromatography (Schimadzu, Model GC-8A equipped with a thermal conductivity detector and 2 m $\times$ 0.318 cm o.d. stainless steel columns packed with 45/60 mesh Molecular Sieve 5A, He carrier gas flow rate 25 ml/min). The average N_2 production and O_2 consumption rates for each core were calculated based on the change in N_2 or O_2 concentration over two to four separate ~24-h intervals, the volume of gas phase in each chamber, the surface area of sediment and the incubation interval.

Initially the flux of N_2 out of saturated sediments is due to a combination of N_2 production due to denitrification and re-equilibration of N_2 originally dissolved in the interstitial water with the low-N_2 overlying water. Previous experiments with estuarine sediments showed that the N_2 initially dissolved in the pore waters became equilibrated with the low-N_2 overlying water in about 10 d (Seitzinger 1993). The first N_2 flux measurements were made after 10 d in the present experiment, which was sufficient to deplete the N_2 initially dissolved in the interstitial waters. Depletion of initial N_2 was demonstrated by N_2 fluxes which were below the level of detection ($\leq$ 20 μmol N m^{-2} h^{-1}) from the undisturbed cedar swamp wetland and adjacent stream sediments after 10 d, and by the constancy of the N_2 flux after 10 d from cores with measurable denitrification rates (see Results).

A potential short-coming of this technique is the 10 d pre-incubation time, during which conditions in the sediments could change and affect denitrification and/or organic matter decomposition rates. Organic matter decomposition rates, measured by oxygen consumption and CO_2 production rates, in sediments from an undisturbed cedar swamp were measured daily up to 8 d after field collection and did not change (Sue Watts, unpubl. data). Recent improvements in the N_2-flux method make it possible to measure denitrification rates with only 2–3 d of pre-incubation (Nowicki 1993); application of this modification in various subtidal sediments demonstrated that denitrification rates measured after 3–5 days incubation did not differ statistically from those measured after 7–11 d (Nowicki 1993). In addition, denitrification rates in Boston Harbor and Massachusetts Bay Sediments were comparable when measured with a stoichiometric method and after 3 d pre-incubation with the modified N_2-flux method (Giblin et al. 1992). The modified N_2-flux method recently has been used in cedar swamp sediments that were not water-saturated; N_2 fluxes did not change between days 3 and 8 (longer times have not been tested) (Sue Watts, unpubl. data). Comparisons of *in situ* and laboratory measured denitrification rates in wetland sediments are needed.

The effect of nitrate concentration in the overlying water on denitrification rates was examined in three of the wetlands: disturbed and undisturbed cedar swamp, and undisturbed heath wetland. After denitrification rates were measured at the ambient stream nitrate concentration, the nitrate concentration in the water placed over the cores was increased (up to 770 μM with KNO_3 amendments) and denitrification rates were again measured.

Sediment-water nutrient fluxes

The rate of uptake or release of NO_3^- and NH_4^+ to/from the overlying water by the wetland sediments was calculated based on initial water samples from each chamber after the water was changed over a core and final samples taken just before the water was changed again. Controls consisted of water incubated without sediment. Samples were filtered through pre-rinsed glass fiber filters (Whatman 934-AH) and analyzed for nitrite plus nitrate (Technicon 1977) and ammonia (Solorzano 1969).

Results

Denitrification rates at ambient field nitrate concentrations

Denitrification rates (N_2 production) were significantly different ($\alpha = 0.05$) among the three undisturbed wetlands, and ranged from an average of ≤ 20 μmol N m^{-2} h^{-1} in the cedar swamp to 260 μmol N m^{-2} h^{-1} in the heath wetland (Fig. 2a). Average denitrification rates in duplicate cores from a wetland were similar; there was no consistent increase or decrease in denitrification rates over time in cores, although rates varied from day to day. Rates of oxygen consumption in the undisturbed wetlands ranged from –980 μmol O m^{-2} h^{-1} to –3750 μmol O m^{-2} h^{-1}, with lowest rates in the cedar swamp and highest rates in the heath wetland (Table 2). Nitrate concentrations in the overlying water were ≤ 1 μM, and there was little or no net flux of nitrate between the sediments and overlying water (Table 2).

The denitrification rate in the cedar swamp with an intermediate level of anthropogenic N input was 60 μmol N m^{-2} h^{-1} (data not shown) and the oxygen consumption rate was –1420 μmol O m^{-2} h^{-1} (Table 2). The nitrate concentration in the overlying water was 1 μM and these was little net flux of nitrate across the sediment-water interface (Table 2).

Denitrification rates in the four wetlands receiving considerable inputs of anthropogenic nutrients were similar and ranged from an average of 185 μmol N m^{-2} h^{-1} in the cedar swamp to 255 μmol N m^{-2} h^{-1} in the mixed hardwood wetland (Fig. 2b). Oxygen uptake rates ranged from –2350 μmol O m^{-2} h^{-1} in a cedar swamp core to –6150 μmol O m^{-2} h^{-1} in a core from the unvegetated area (Table 2). Nitrate concentrations in the stream water incubated over the cores were high compared to the undisturbed sites, with concentrations ranging from 55 μM to 130 μM. There was a net flux of nitrate into the sediments from the overlying water with the highest uptake rates (–135 μmol N m^{-2} h^{-1}) in a core from the herbaceous (*Polygonum*) wetland.

Denitrification rates were ≤ 20 μmol N m^{-2} h^{-1} in the stream sediments, adjacent to the undisturbed cedar swamp. In the stream sediments adjacent to the disturbed cedar swamp and herbaceous peatland, denitrification rates were 250 and 405 μmol N m^{-2} h^{-1} in the two cores.

Table 2. Overlying water nitrate concentrations, sediment oxygen consumption rates and sediment-overlying water nitrate and ammonia fluxes in sediment cores from wetlands and two adjacent streams in undisturbed (forested) watersheds and disturbed watersheds (extensive agricultural and/or residential development). Summer measurements in water-saturated conditions with ambient stream nitrate concentrations in overlying water. Positive numbers indicate a net flux from sediments to overlying water, negative numbers indicate a net flux from the overlying water to the sediments. n.m. = not measured.

Vegetation type	NO_3^-, µM	O_2 flux (µmol) O m^{-2} h^{-1}	NO_3^- flux (µmol) N m^{-2} h^{-1}	NH_4^+ flux (µmol) N m^{-2} h^{-1}
Undisturbed wetlands				
Cedar swamp	1	–1220	< –5	n.m.
	1	–980	< –5	n.m.
Mixed hardwood	< 1	–2610	< –5	5
	< 1	–1980	< –5	10
Heath	< 1	–3250	< –5	35
	< 1	–3760	< –5	50
Intermediate disturbance				
Cedar swamp	1	–1420	< –5	35
Disturbed wetlands				
Cedar Swamp	130	–2350	–25	n.m.
	130	–3030	< –5	n.m.
Herbaceous	130	–2590	–90	n.m.
(*Polygonum*)	130	–3060	–135	n.m.
Mixed hardwood	60	–5030	–45	10
	60	–3740	< –5	30
Unvegetated	55	–6150	–95	345
	55	–5850	–115	455
Stream sediments				
Skit Brook	1	–1870	< –5	n.m.
adjacent to undisturbed cedar swamp	1	–820	< –5	n.m.
Hammonton Creek	130	–2440	–60	n.m.
adjacent to disturbed cedar swamp	130	–2840	–15	n.m.

Effect of increasing nitrate concentrations of denitrification rates

Denitrification rates increased when nitrate concentrations in the overlying water were increased (Fig. 3). In two of the three wetlands (undisturbed cedar swamp and heath wetland), the increase in the denitrification rate was equal

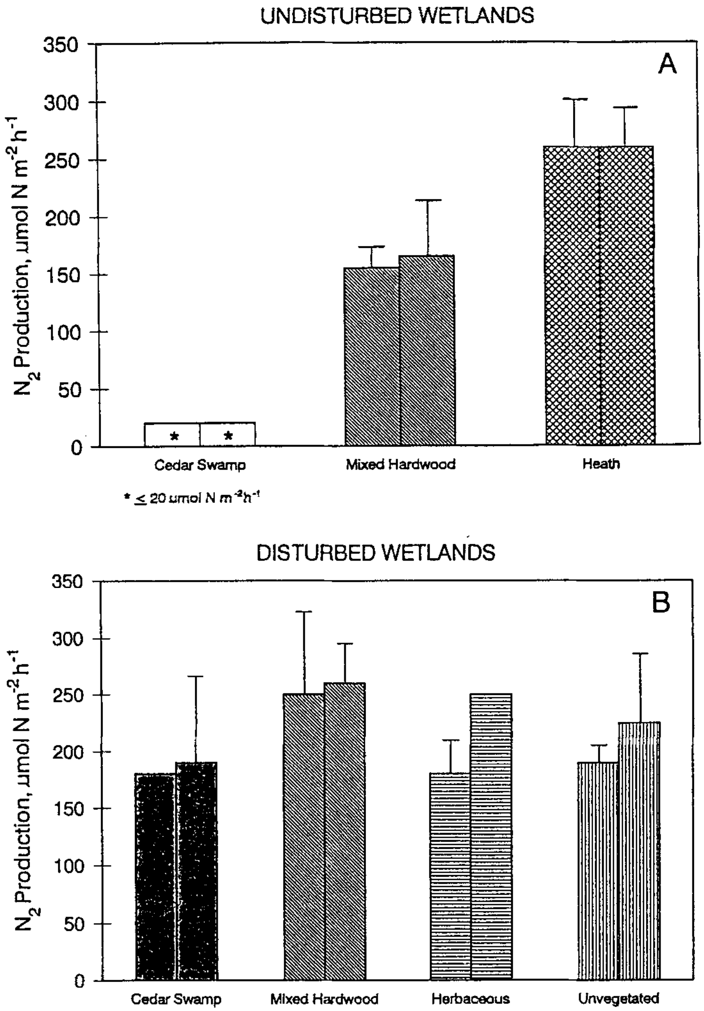

Fig. 2. Denitrification (N_2 production) rates (average ± S.D.) in duplicate cores collected from: A) each of three wetlands in undisturbed watersheds, and B) each of four wetlands in disturbed watersheds with agricultural fields directly surrounding the wetland and/or with sewage treatment plant discharge to the stream (no S.D. is indicated for two of these cores because only one flux measurement was made).

to the increase in the rate of nitrate flux into the sediments when the nitrate concentration was increased (Fig. 4). In the disturbed cedar swamp, the increase (~100 μmol m^{-2} h^{-1}) in denitrification was less than the increase (~300 μmol $m^{-2\ -1}$) in the uptake of nitrate, indicating that processes in addition to denitrification (e.g., assimilatory nitrate reduction) were also utilizing nitrate, or that end products of denitrification other than N_2 (e.g., N_2O) were produced. The undisturbed heath wetland sediments showed the greatest response to increasing nitrate concentrations (Fig. 3).

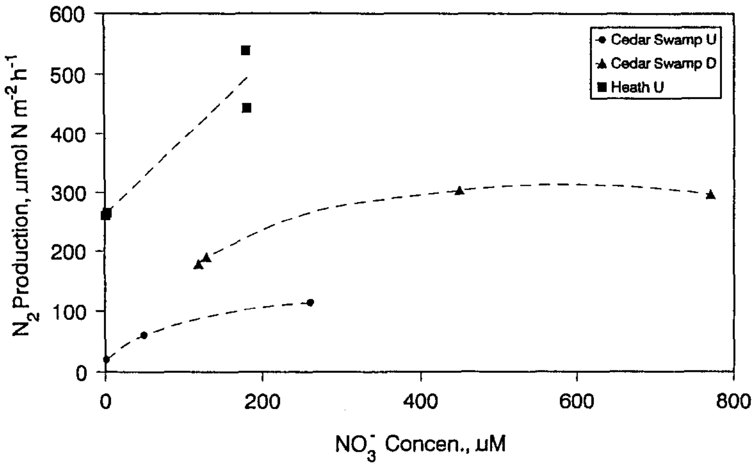

Fig. 3. Denitrification (N_2 production) rates as a function of nitrate concentration in the water overlying the sediments: cedar swamp undisturbed (U) and disturbed (D), and heath dominated wetland. Dashed lines are drawn to guide the eye.

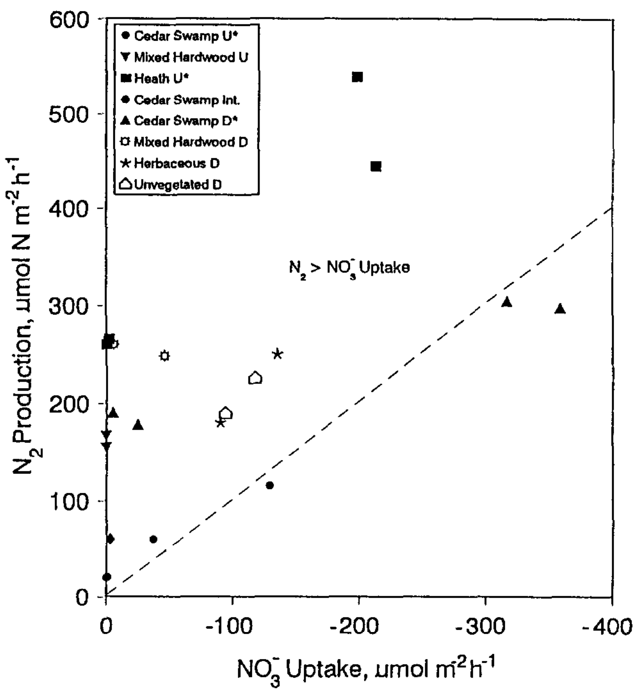

Fig. 4. Denitrification (N_2 production) rates as a function of the rate of nitrate uptake by the sediments from the overlying water. Data from cores incubated with ambient stream nitrate concentration and, if measured, with increased nitrate concentrations (*) are shown. Line is the 1:1 ratio between denitrification and nitrate uptake; points above the line represent sediments in which denitrification rates were greater than net nitrate flux into sediments from overlying water. U, Int., and D refer to undisturbed, intermediate level of disturbance, and disturbed wetlands, respectively.

Discussion

Denitrification rates

Denitrification rates in the three undisturbed wetlands with different dominant vegetation varied by more than an order of magnitude (≤ 20 μmol N m^{-2} h^{-1} to 260 μmol N m^{-2} h^{-1}) (Fig. 2a). The highest rates occurred in the heath wetland, intermediate rates in the mixed hardwood swamp and lowest rates in the cedar swamp sediments. Some studies have concluded that denitrification rates are low in acidic environments (Bartlett et al. 1970; Muller et al. 1980). However, denitrifying bacteria can be very active in strongly acidic environments as demonstrated by the high denitrification rates measured in the low pH (≤ 4.5) mixed hardwood and heath wetlands in the current study. While not directly comparable, high denitrification capacities have been reported in acidic (pH ≤ 4.4) tropical rain forest soils (Tiedje et al. 1982) as well. The wide range in denitrification rates among the three undisturbed wetlands was unexpected given the similarity in incubation conditions including nitrate concentration and pH in the overlying water (Table 1 and 2), water-saturated sediments, and temperature. Denitrification rates in the four disturbed wetlands with different dominant vegetation were consistently high (180 to 250 μmol N m^{-2} h^{-1}) (Fig. 2b).

Denitrification rates in the wetlands with similar dominant vegetation were higher when inputs of anthropogenic N were high, relative to denitrification rates in undisturbed wetlands. For example, average denitrification rates in the cedar swamps from an undisturbed watershed, moderately disturbed, and disturbed watershed were ≤ 20 (Fig. 2a), 60 (not plotted), and 185 (Fig. 2b) μmol N m^{-2} h^{-1}, respectively. Similarly, average denitrification rates were significantly higher ($\alpha = 0.05$) in the disturbed hardwood swamp (255 ± 10 μmol N m^{-2} h^{-1}) (average ± S. E. for duplicate cores) relative to the undisturbed hardwood swamp (160 ± 10 μmol N m^{-2} h^{-1}). This is consistent with experimental studies in which denitrification rates were higher after additions of sewage or fertilizer N directly to cypress domes (Dierberg & Brezonik 1983) and to a wetland in Australia (Brodrick et al. 1988).

Many riparian wetlands throughout the US and Europe have been destroyed. Reconstruction of riparian wetlands has been considered as a way to enhance nutrient removal and decrease nutrient concentrations in stream and river water. While wetlands may increase the temporal and spatial contact between the water and sediments and thus increase the total amount of nitrogen removed by denitrification, the rates of denitrification per unit area of stream bottom or wetland area may not differ greatly. Denitrification rates were not significantly different in the water-saturated wetland sediments relative to sandy sediments from the adjacent streams where there was noticeable organic matter deposition. Denitrification rates were ≤ 20 μmol m^{-2} h^{-1} in sediment cores in the undisturbed cedar swamp and from the adjacent stream. Rates were not statistically different ($\alpha = 0.05$) in the disturbed cedar swamp

(185 ± 10 μmol m^{-2} h^{-1}) or herbaceous peatland (215 ± 50 μmol m^{-2} h^{-1}) sediments relative to the adjacent stream (330 ± 110 μmol m^{-2} h^{-1}). Denitrification measurements across the range of sediment types and hydrological conditions within wetlands and streams are needed.

Factors controlling denitrification rates

Two factors that appear to control the rates of denitrification in these wetlands when the sediments are water-saturated are nitrate and organic matter mineralization rates: the two may be related. Nitrate often controls denitrification rates in wetlands (e.g., Hemond 1983; Westermann & Ahring 1987; Koerselman et al. 1989; Merrill & Zak 1992). In the current study, when nitrate concentrations in the overlying water were increased, denitrification rates increased (Fig. 3). However, except for the undisturbed cedar swamp, nitrate in the overlying water did not appear to be the major source of nitrate supporting denitrification at ambient stream nitrate concentrations. For example, nitrate uptake by the sediments accounted for less than 20% of the nitrate needed to support the measured denitrification rates (at ambient stream nitrate concentrations) in five of the eight wetlands (undisturbed mixed hardwood and heath wetlands, cedar swamp (intermediate), and disturbed cedar and mixed hardwood swamps) (Fig. 4). In two wetlands, the disturbed herbaceous and unvegetated wetlands, nitrate in the overlying water accounted for ~ 50% of the nitrate needed to support the measured denitrification. Other potential sources of nitrate include groundwater and nitrification of mineralized ammonia in the sediments. Substantial amounts of nitrate may enter the disturbed wetlands in groundwater or surface water runoff, given the high rates of fertilizer N added to agricultural fields in these areas (Durand & Zimmer 1982). Sediment cores were incubated in the lab for 10 d before denitrification measurements were made, which makes it unlikely that nitrate from groundwater directly supported the measured denitrification rates, although groundwater may supply additional NO_3^- for denitrification in the field, particularly in the disturbed watersheds. Nitrification of NH_4^+ released during mineralization of organic nitrogen appears to be the dominant nitrate source supporting the denitrification rates measured.

Denitrification rates were highly correlated (r^2 = 0.912) with sediment oxygen consumption rates regardless of the dominant vegetation, pH, or degree of disturbance (Fig. 5). This correlation has been demonstrated in a variety of submerged estuarine sediments as sell (Seitzinger 1990). There are a number of possible explanations for this correlation. The correlation with O_2 consumption rates may reflect control of denitrification by the availability of electron donors (organic C), and/or nitrification linked to organic N mineralization (ammonification) rates. While there is no direct evidence that demonstrates which, if either, of these is responsible for the observed correlation, control of denitrification by nitrification linked to organic N mineralization seems the most probable. This is based on the findings that

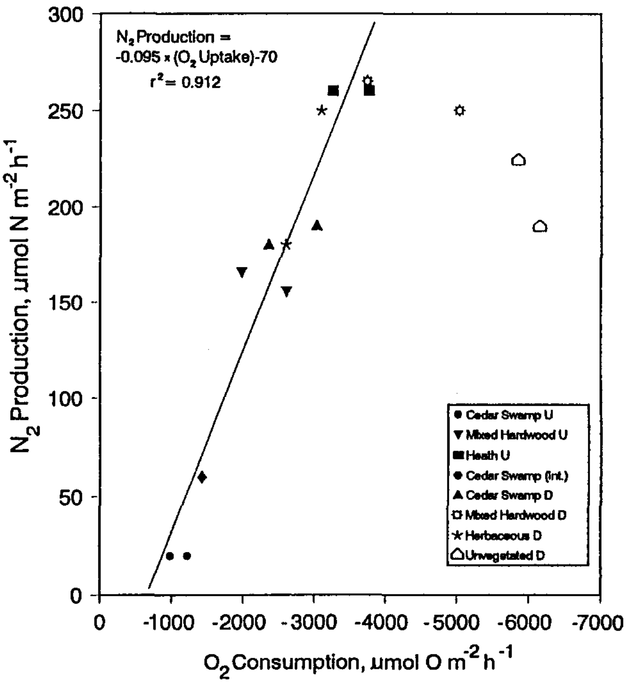

Fig. 5. Denitrification (N_2 production) rates measured at ambient stream nitrate concentrations as a function of sediment oxygen consumption rates. Results of linear regression analysis; data from wetland without vegetation were not included in regression. U. Int., and D refer to undisturbed, intermediate level of disturbance, and disturbed wetlands, respectively.

nitrate controls denitrification rates and that the major source of nitrate for denitrification is nitrification of mineralized ammonia (this study) and previous studies which demonstrate that addition of organic carbon (electron donors, e.g., glucose) alone to wetland sediments generally does not increase denitrification rates (Gordon et al. 1986; Westermann & Ahring 1987; Merrill & Zak 1992).

Oxidation of organic matter via denitrification was estimated to account for a substantial portion (30%) or the organic matter oxidized in the wetland sediments in the current study. This was calculated using the slope of the regression line from Fig. 5, a ratio of 276:106 (atoms) of oxygen consumed to carbon oxidized, and a ratio of 106: 84.8 of carbon oxidized to N_2 produced (Richards 1965).

In addition to N_2, N_2O can be an end product of denitrification (Knowles 1982). N_2O fluxes were not measured in the current study (due to instrumentation problems). Total denitrification rates may have been underestimated if N_2O fluxes were significant relative to the N_2 fluxes. N_2O accounted for 25% or less of gaseous N losses in a mixed hardwood swamp in Michigan (Merrill & Zak 1992) and two bogs in Minnesota and Canada (Urban et al.

1988) and 80% or more of gaseous N fluxes in bogs in Massachusetts and Minnesota (Hemond 1983; Urban 1983 cited in Urban et al. 1988).

Comparison with previous studies

A wide range of denitrification rates has been measured using sediments from freshwater wetlands (Table 3). Comparison of denitrification rates is somewhat difficult given the variety of methods used. To facilitate comparison of denitrification rates measured with slurries to rates in whole cores, I applied the rates measured in slurry experiments to a 1 cm depth of sediment (and in some cases assumed sediment densities). Potential denitrification rates measured in sediments highly enriched with nitrate (slurries or whole cores) range from 1 to 1110 μmol N m^{-2} h^{-1} (Table 3). As expected, rates measured without nitrate amendments, in either anaerobic sediment slurries or whole cores which were not water-saturated, are considerably lower (generally < 1 μmol m^{-2} h^{-1}) than potential rates (with nitrate amendment). Denitrification rates in water-saturated cores (< 20 to 365 μmol m^{-2} h^{-1}) are usually substantially higher than those measured in unsaturated cores (all without nitrate amendments). This pattern is similar to that found in forest soils; denitrification rates were lower in well drained aerobic soils relative to poorly drained soils (Groffman et al. 1993).

The lower denitrification rates in the wetland sediments that are not water-saturated relative to those that are, may be due to a number of factors. While a large portion of mineralized ammonia can be nitrified in aerobic sediments (not water-saturated) (e.g., Merrill & Zak 1992), the coupling of nitrification and denitrification may be limited by the extent of anaerobic "microniches," such as those surrounding organic matter aggregates (Sexstone et al. 1985; Parkin 1987). This contrasts with water-saturated sediments that are anoxic except for a thin (few mm) aerobic surface layer (Revsbech et al. 1980) or aerobic zone surrounding roots of some vascular plants (Reddy et al. 1989). High denitrification rates in such sediments can be supported by efficient nitrification of ammonia that diffuses through the interstitial water to the aerobic sediment layer; the nitrate is subsequently denitrified when it diffuses back down into the anaerobic zone (Patrick & Reddy 1976; DeBusk & Reddy 1987). This is analogous to N cycling in submerged sediments in many lakes and estuaries where nitrification of mineralized NH_4^+ in the aerobic surface few mm of sediments is coupled closely to denitrification (Jenkins & Kemp 1984; Gardner et al. 1987; Seitzinger 1988).

Lower denitrification rates in non-saturated relative to saturated sediments also may be due to differences in the methods used to measure denitrification. The acetylene block method was used in the non-saturated sediment studies; this method has been shown to underestimate denitrification rates in lake and estuarine sediments when nitrification and denitrification are closely coupled (because acetylene also blocks nitrification) (Kemp et al. 1990; Seitzinger et al. 1993). The denitrification rates in the water-saturated

Table 3. Denitrification rates measured by a variety of methods in wetland sediments. When rates were reported by authors in volume units, rates per m^{-2} were calculated for a 1-cm depth interval.

Wetland type	Location	Denitrification rate µmol N m^{-2} h^{-1}	Comments	Reference
No nitrate amendment				
Acetylene block in slurries				
Alder swamp	Denmark	0.42	1	Westermann & Ahring 1987
Fen	The Netherlands	negligible		Koerselman et al. 1989
Bog	MA	< 0.8		Hemond 1983
Acetylene block with whole cores; non-water saturated				
Mixed hardwood	MN	0.2–24	2	Zak & Grigal 1991
Mixed hardwood	MI	0.04–0.3	2	Merrill & Zak 1992
Bogs	Canada & MN	0.01–0.2	3	Urban et al. 1988
Mixed hardwood	RI	negligible	4	Groffman et al. 1991
		4	5	Groffman et al. 1991
^{15}N–NH_4 *coupled nitrification/denitrification with whole cores; water saturated*				
Cypress swamp	FL	180	6	DeBusk & Reddy 1987
Pontederia in marsh sediment	FL	365	7	Reddy et al. 1989
Juncus in marsh sediment	FL	305		Reddy et al. 1989
Flooded soils		330	8	Patrick & Reddy 1976
Whole core N_2 flux; water saturated				
Cedar swamp	NJ	< 20	9	This study
Mixed hardwood	NJ	160	9	This study
Heath	PA	260	9	This study
Cedar swamp	NJ	60	10	This study
Cedar swamp	NJ	185	11	This study
Mixed hardwood	NJ	255	11	This study
Herbaceous	NJ	215	11	This study
Unvegetated	NJ	205	11	This study

Table 3. (Continued).

Wetland type	Location	Dentrification rate mmol N m^{-2} h^{-1}	Comments	Reference
Nitrate amendment (Denitrification potentials)				
Acetylene block in slurries				
Alder swamp	Denmark	33	1	Westermann & Ahring 1987
Fen	The Netherlands	4–85	1	Koerselman et al. 1989
Mires (8)	Finland	11–1110	1	Muller et al. 1980
Everglades marsh	FL	12–395	1	Gordon et al. 1986
Acetylene block with whole cores				
Cypress swamp	FL	1–16	12	Dierberg & Brezonik 1983
Mixed hardwood	RI	110	4	Groffman et al. 1991
		415	5	Groffman et al. 1991
Other methods; slurries				
Marsh	MA	115–310	13; 1	Bartlett et al. 1979
Phragmites marsh	Denmark	150–165	14	Andersen & Hansen 1982

1 – calculated for 1 cm sediment depth; 2 – 10-cm deep core; 3 – *in situ* dome; 4 – aerobic; 5 – anaerobic; 6 – ^{15}N–NH_4 added to surface water; 7 – ^{15}N–NH_4 added to root zone; 8 – ^{15}N–NH_4 added to soil; 9 – undisturbed; 10 – intermediately disturbed; 11 – disturbed; 12 – plus NO_3 mass balance; 13 – manometric; 14 – NO_3 loss, slurries

sediments were measured with either ^{15}N–NH_4^+ or by N_2-flux methods, both of which capture coupled nitrification/denitrification.

The current study was not designed to assess the importance of denitrification as a sink for N at the ecosystem scale. Such an evaluation would require measurements of N inputs, as well as denitrification measurements over seasonal cycles, across the range of sediment microhabitats (e.g. depressions and hummocks) and degree of water saturation. The denitrification rates measured in the current study are most representative of late spring or summer when the water table is high, and/or the streams flood the adjacent wetlands, due to heavy rainfall. However, given the above limitations, it is perhaps still useful to compare the denitrification rates in the water-saturated sediments with available information on N inputs. Atmospheric deposition, N_2-fixation, groundwater, surface water runoff, and streamwater are some possible N sources (Bowden 1987). Atmospheric deposition of N was estimated to be approximately 1 g N m^{-2} y^{-1} (Morris 1991), which if evenly distributed throughout the year, would be 8 μmol m^{-2} h^{-1}. Denitrification rates measured in all the wetlands, with the possible exception of the undisturbed cedar swamp, were considerably greater than the estimated atmospheric deposition. N_2-fixation rates in various wetlands range from undetectable to 12 g N m^{-2} y^{-1} (summarized by Bowden 1987), or up to 360 μmol N m^{-2} h^{-1}, assuming a 100 d active season. While N_2-fixation rates are spatially and temporally highly variable in wetlands, it is possible that the unexpectedly high denitrification rates in the undisturbed heath or mixed hardwood wetland (260 and 160 μmol N m^{-2} h^{-1}, respectively) were ultimately supported by high inputs of N to the wetlands from N_2-fixation. The wetlands from disturbed watersheds receive additional N inputs in runoff and groundwater from the agricultural fields adjacent to their upland perimeter; as much as 17 g N m^{-2} y^{-1} fertilizer N are added to those fields and less than 10% is removed during harvest (Durand & Zimmer 1982). Thus, it is also plausible that the disturbed wetlands received N inputs sufficient to account for the measured denitrification rates.

Denitrification (N_2 production) rates in eight wetlands incubated with water-saturated sediments and aerobic overlying water were correlated with sediment oxygen consumption rates, regardless of the degree of anthropogenic N loading, pH or dominant vegetation. Some of the highest and lowest denitrification rates occurred in low pH (< 5) wetlands. Nitrification in the sediments linked to organic nitrogen mineralization appears to be an important factor controlling rates of denitrification in these water-saturated wetland sediments. Rates of denitrification were within the range of rates previously reported for water-saturated wetland sediments and flooded soils, calculated using whole core ^{15}N techniques that quantify coupled nitrification/denitrification, and were higher than rates reported from aerobic (non-saturated) wetland sediments using the acetylene block method.

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References

Andersen FO & Hansen JI (1982) Nitrogen cycling and microbial decomposition in sediments with *Phragmites australis* (poaceae). Hydrobio. Bull. 16: 11–19

Bartlett, MS, Brown LC, Hanes NB & Nickerson NH (1979) Denitrification in freshwater wetland soil. J. Environ. Qual. 8: 460–464

Bowden, WB (1987) The biogeochemistry of nitrogen in freshwater wetlands. Biogeochem. 4: 313–348

———. 1986. Nitrification, nitrate reduction, and nitrogen immobilization in a tidal freshwater marsh sediment. Ecology 67: 88–89

Brinson MM, Bradshaw HD & Kane ES (1984) Nutrient assimilative capacity of an alluvial floodplain swamp. J. Appl. Ecol. 21: 1041–1058

Brodrick SJ, Cullen P & Maher W (1988) Denitrification in a natural wetland receiving secondary treated effluent. Water Res. 22: 431–440

DeBusk WF & Reddy KR (1987) Removal of floodwater nitrogen in a cypress swamp receiving primary wastewater effluent. Hydrobiologia 153: 79–86

Davidson EA & Swank WT (1986) Environmental parameters regulating gaseous nitrogen losses from two forested ecosystems via nitrification and denitrification. Appl. Environ. Microbio. 52: 1287–1292

Dierberg FE & Brezonik PL (1983) Nitrogen and phosphorus mass balances in natural and sewage-enriched cypress domes. J. Appl. Ecol. 20: 323–337

Durand JB & Zimmer BJ (1982) Part I. Pinelands surface water quality. Final Report. 27-4668 SNJ DEP, DWR, Pinelands, 196 pp

Gardner WS, Nalepa TF & Malczyk JM (1987) Nitrogen mineralization and denitrification in Lake Michigan sediments. Limnol. Oceanogr. 32: 1226–1238

Gersberg RM, Elkins BV & Goldman CR (1984) Use of artificial wetlands to remove nitrogen from wastewater. J. Water Poll. Control. Fed. 56: 152–156

Giblin AE, Hopkinson CS & Tucker J (1992) Metabolism and nutrient cycling in Boston Harbor sediments. MWRA Environm. Quality Dept. Tech. Rep. Series No. 92-1, Massachusetts Water Resources Authority, Boston, MA, 42 pp

Gordon AS, Cooper WJ & Scheidt DJ (1986) Denitrification in marl and peat sediments in the Florida Everglades. Appl. Environ. Microbiol. 52: 987–991

Groffman PM & Tiedje JM (1988) Denitrification hysteresis during wetting and drying cycles in soil. Soil Sci. Soc. Am. J. 52: 1626–1629

Groffman PM, Axelrod EA, Lemunyon JL & Sullivan WM (1991) Denitrification in grass and forest vegetated filter strips. J. Environ. Qual. 20: 671–674

Groffman PM, Zak DR, Christensen S, Mosier A & Tiedje JM (1993) Early spring nitrogen dynamics in a temperate forest landscape. Ecology 74: 1579–1592

Hemond HF (1983) The nitrogen budget of Thoreau's bog. Ecology 64: 99–109

Hynes RK & Knowles R (1978) Inhibition by acetylene of ammonia oxidation in *Nitrosomonas europaea*. FEMS Microbiol. Lett. 4: 319–321
Jenkins MC & Kemp WM (1984) The coupling of nitrification and denitrification in two estuarine sediments. Limnol. Oceanogr. 29: 609–619
Jorgensen RG & Richter GM (1992) Composition of carbon fractions and potential denitrification in drained peat soils. J. Soil Sci. 43: 347–358
Kaplan WA, Valiela I & Teal JM (1979) Denitrification in a salt marsh ecosystem. Limnol. Oceanogr. 24: 726–734
Kemp WM, Sampou P, Caffrey J & Mayer M (1990) Ammonium recycling versus denitrification in Chesapeake Bay sediments. Limnol. Oceanogr. 35: 1545–1563
Knowles R (1982) Denitrification. Microbiol. Rev. 46: 43–70
Koerselman W, De Caluwe H & Kieskamp WM (1989) Denitrification and dinitrogen fixation in two quaking fens in the Vechtplassen area, the Netherlands. Biogeochem. 8: 153–165
Merrill AG & Zak DR (1992) Factors controlling denitrification rates in upland and swamp forests. Can. J. For. Res. 22: 1597–1604
Mitsch WJ & Gosselink JG (1986) Wetlands. Van Nostrand Reinhold Co. Inc., p 537
Morgan MD (1984) Acidification of headwater streams in the New Jersey Pinelands: a re-evaluation. Limnol. Oceanogr. 29: 1259–1266
Morris JT (1991) Effects of nitrogen loading on wetland ecosystems with particular reference to atmospheric deposition. Annu. Rev. Ecol. Syst. 22: 257–279
Muller MM, V Sudman V & Skujins J (1980) Denitrification in low pH spodosols and peats determined with the acetylene inhibition method. Appl. Environ. Microbio. 40: 235–239
Myrold DD & Tiedje JM (1985) Diffusional constraints on denitrification in soil. Soil Sci. Soc. Am. J. 49: 651–657
Nixon S & Lee V (1986) Wetlands and Water Quality. Final Report. Dept. Army. Technical Report Y-86-2. 229 pp
Nowicki BL & Oviatt CA (1990) Are estuaries traps for anthropogenic nutrients? Evidence from estuarine mesocosms. Mar. Ecol. Prog. Ser. 66: 131–146
Nowicki BL (1994) The effect of temperature, oxygen, salinity and nutrient enrichment on estuarine denitrification rates measured with a modified nitrogen gas flux technique. Estuar. Coastal Shelf Sci. 38(2): 137–156
Parkin TB (1987) Soil microsites as a source of denitrification variability. Soil Sci. Soc. Am. J. 51: 1194–1199
Patrick WH & Reddy KR (1976) Denitrification reactions in flooded soils and water bottoms: dependence on oxygen supply and ammonium diffusion. J. Environ. Qual. 4: 469–471
Peterjohn WT & Correll DL (1984) Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65: 1466–1475
Reddy KR, Patrick WH Jr, Lindau CW (1989) Nitrification-denitrification at the plant root-sediment interface in wetlands. Limnol. Oceanogr. 34: 1004–1013
Revsbech NP, Sorensen J, Blackburn TH & Lomholt JP (1980) Distribution of oxygen in marine sediments measured with microelectrodes. Limnol. Oceanogr. 25: 403–411
Richards F (1965) Anoxic basins and fjords. In: Riley JP & Skirrow G (Eds), Chemical Oceanography, Vol. 1 (pp 611–645). Academic Press
Seitzinger SP, Nielsen LP, Caffrey J & Christensen PB (1993) Denitrification measurements in aquatic sediments: a comparison of three methods. Biogeochemistry 23: 147–167
Seitzinger SP (1993) Denitrification and nitrification rates in aquatic sediments. In: Kemp PF, Sherr BF, Sherr EB & Cole JJ (Eds), Handbook of Methods in Aquatic Microbiol Ecol. (pp 633–641). Lewis
Seitzinger SP (1988) Denitrification in freshwater and coastal marine ecosystems: ecological and geochemical significance. Limnol. Oceanogr. 33: 702–724
Seitzinger SP (1990) Denitrification in aquatic sediments. In: Revsbech NP & Sorensen J (Eds), Denitrification in Soil and Sediment (pp 301–322). Plenum Press
Sexstone AJ, Revsbech NP, Parkin TB & Tiedje JM (1985) Direct measurement of oxygen profiles and denitrification rates in soil aggregates. Soil Sci. Soc. Am. J. 49: 645–651

Solorzano L (1969) Determination of ammonia in natural waters by the phenylhypochlorite method. Limnol. Oceanogr. 14: 799–801

Technicon. (1977) Nitrate and nitrite in water and seawater. Method. No. 158-71W/A. Technicon Industrial Systems, Tarytown, NY. 4 pp

Tedrow JL (1979) Development of Pine Barrens soils. In: Forman RT (Ed), Pine Barrens: Ecosystems and landscape (pp 61–79). Academic

Tiedje JM, Sexstone AJ, Myrold DD & Robinson JA (1982) Denitrification: ecological niches, competition and survival. Antonie van Leeuwenhoek 48: 569–583

Tilton DL & Kadlec RH (1979) The utilization of a fresh-water wetland for nutrient removal from secondarily treated waste water effluent. J. Environ. Qual. 8: 328–334

Urban, N. R. (1983) The nitrogen cycle in a forested bog watershed in northern Minnesota. M. S. thesis, Univ. Minnesota. 359 pp

Urban NR, Eisenreich SJ & Bayley SE (1988) The relative importance of denitrification and nitrate assimilation in midcontinental bogs. Limnol. Oceangr. 33: 1611–1617

Valiela I & Teal JM (1979) The nitrogen budget of a salt marsh ecosystem. Nature 280: 652–656

Verhoeven JTA (1986) Nutrient dynamics in minerotrophic peat mires. Aquatic Botany 25: 117–137

Westermann P & Ahring BK (1987) Dynamics of methane production, sulfate reduction, and denitrification in a permanently waterlogged alder swamp. Appl. Environ. Microbio. 53: 2554–2559

Zak DR & Grigal DF (1991) Nitrogen mineralization, nitrification and denitrification in upland and wetland ecosystems. Oecologia 88: 189–196