AN ABSTRACT OF THE THESIS OF

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William H. Emmingham

Managing riparian buffer zones is a potentially important approach to protecting streams from agricultural pollution. This study was conducted to determine if a pasture, a hybrid poplar (*Populus trichocarpa* x *deltoides*) stand, or a native oak (*Quercus garryana*) forest, had the greatest potential to serve as a nutrient buffer zone. The effects of fertilizer treatments and vegetation type on denitrification and vegetative uptake were investigated in the Willamette Valley riparian area of Oak Creek, near Corvallis, Oregon. Field and potential denitrification rates measured in the pasture and poplar stand were between 2 and 83 times greater than in the native forest. Two possible explanations exist: (1) lack of a readily degradable C source may be limiting denitrification in the organic C rich native forest plots, or (2) denitrifying microbial populations may be smaller in the native forest due to a lack of soil NO_3^-. While field denitrification rates peaked in the winter and were at a minimum in the summer, denitrification potentials, a reflection of the site's accumulative *in situ* denitrification over time, were greatest

in the fall, suggesting that more favorable conditions for actual denitrification may occur during this season. Vegetative uptake of N (as measured by litterfall N) was greatest in the native oak forest, with values 1.5 and 2 times greater than poplar and pasture sites, respectively, and primarily occurred from early spring through summer. To optimize nutrient removal rates, vegetation in riparian buffer zones should be able to take up entering excess nutrients as well as provide a readily degradable C source for denitrifying microorganisms. Because the native oak forest took up more N and the pasture and poplar sites denitrified more N, an integrated riparian buffer area with all three vegetation types may serve as the best riparian nutrient removal solution. In areas devoid of native forest, establishment of a poplar plantation can provide for significant uptake and good denitrification potential in a relatively short time.

Denitrification and Vegetative Uptake in a Pasture, Poplar and Native Oak Riparian Buffer Area

by

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INTRODUCTION

Background

Riparian areas can protect stream water quality from upland agricultural sources of pollution (Lowrance et al., 1984). Complex interactions between soil, water, and vegetation, can prevent nutrients from entering the stream system. Because of their location between land and stream, riparian zones are unique because their hydrology is typified by the merging of flow from upslope lands with inchannel flow, concentrating and integrating water from vast areas. Soils are unique since they have formed during continuous flooding and drying cycles. And finally, vegetation in these areas is unique, having adapted to the dynamic hydrologic and edaphic conditions.

Riparian buffer zones, also referred to as vegetative filter strips, are stream-side strips or bands of planted or natural vegetation that are capable of removing pollutants from surface runoff, subsurface flow, and shallow groundwater (Dillaha et al., 1986; Welsch, 1991; Environmental Protection Agency, 1993). Pollutants, such as sediments, suspended solids, and nutrients, are removed by deposition, absorption, adsorption, plant uptake, and denitrification (Dillaha et al., 1986; Welsch, 1991). Critical to the effectiveness of the buffer zone is the slowing down

of concentrated flows to create more uniform, shallow, sheet flow to allow for sediment deposition and soil infiltration (Dillaha et al., 1986; Welsch, 1991; Environmental Protection Agency, 1993; Schultz et al., 1994).

Lowrance, et al. (1984), Peterjohn and Correll (1984), Jacobs and Gilliam (1985), and Pinay and Decamps (1988), have shown that as nitrate-enriched groundwater passes through the riparian zone, nitrate levels are diminished. The primary removal mechanism appears to be denitrification (Jacobs and Gilliam, 1985). However, the vegetation also plays an important role by removing substantial amounts of nutrients (Lowrance, 1992) and by providing a source of carbon for soil denitrifiers. Of these two mechanisms, nitrogen removal by denitrification has a more long-term benefit to the system than plant uptake since nitrogen remained on site as plant biomass (Groffman et al., 1992). If marketable plants such as hybrid poplar are planted in riparian zones, nitrogen taken up by these plants may be removed permanently upon harvest.

Nitrogen is an important plant nutrient, functioning as a component of chlorophyll, amino acids, enzymes and other proteins, DNA, RNA, vitamins and hormones. Nitrogen also plays a role in the stimulation of root development and activity, carbohydrate utilization and the uptake of other plant nutrients. Without an adequate supply of N, plants are slow-growing and stunted and will develop chlorosis, or a yellow appearance. (Tisdale, et al., 1993; Stevenson and Cole, 1999)

However, too much N in the environment can lead to impacts on human health and degradation of environmental quality. Methemoglobinemia, a condition

where the bloodstream is unable to circulate oxygen, is caused by elevated levels of nitrate in drinking water supplies. Rural groundwater wells are at most risk from contamination due to over fertilization. (Stevenson and Cole, 1999) Eutrophication is the major environmental concern when too much nitrogen is present in the soil and can runoff into surface waters. It occurs when excess nutrients, primarily phosphates and nitrates, enter a river or lake causing large algal blooms. The surficial algal blooms in turn inhibit light penetration into the stream and consume excess oxygen during decomposition, thus creating anoxic conditions ("Eutrophication," 1999; "Inland water ecosystem," 1999).

Nitrogen can exist in many forms, with each fulfilling an important ecological roll. All soil nitrogen is ultimately supplied by the atmosphere, through nitrogen fixation (Figure 1). Total annual global fixation has been estimated at 44-200 x 10^{12}, 60 x 10^{12}, and 0.5-30 x 10^{12} g N, for biological, industrial, and electrical sources, respectively (Perry, 1994). Nitrogen is lost from soils by vegetative uptake, leaching, volatilization, and denitrification (Tisdale et al., 1993; Foth and Ellis, 1997; Stevenson and Cole, 1999). Total annual global losses of N have been estimated at 13-40 x 10^{12}, and 59-459 x 10^{12} g N from leaching and denitrification, respectively (Perry, 1994), thus global nitrogen additions and losses are generally in equilibrium (Foth and Ellis, 1997). Within soils, nitrogen is converted to its diverse forms, primarily through microbially mediated processes. Mineralization occurs when organic nitrogen is converted to mineral forms of nitrogen (NO_3^-, NH_4^+); immobilization is the reverse process (Figure 2). Because nitrate is negatively

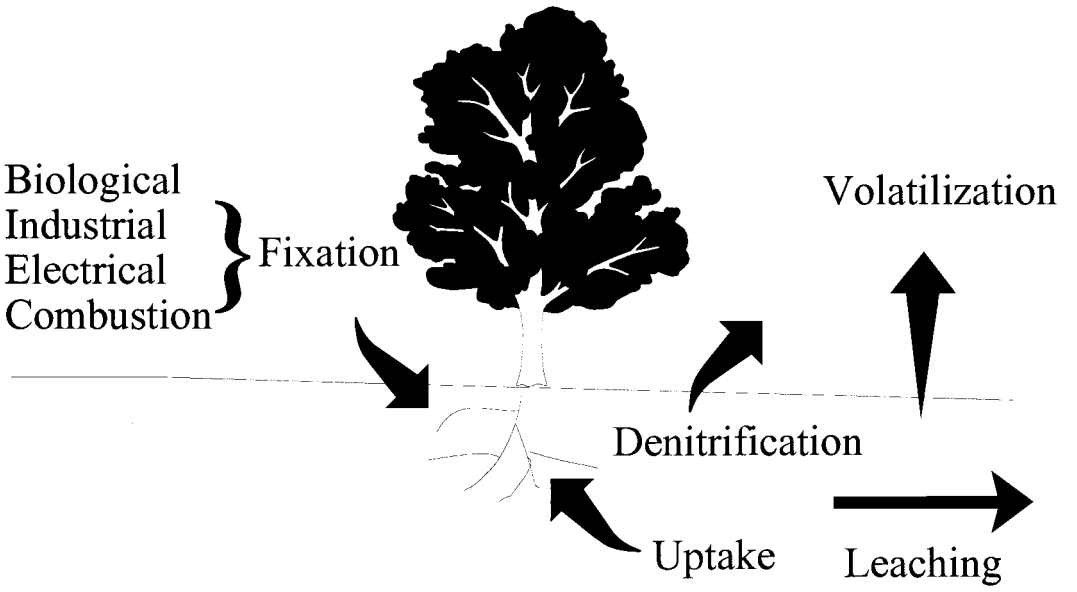


Figure 1. Nitrogen additions and losses from the soil environment.

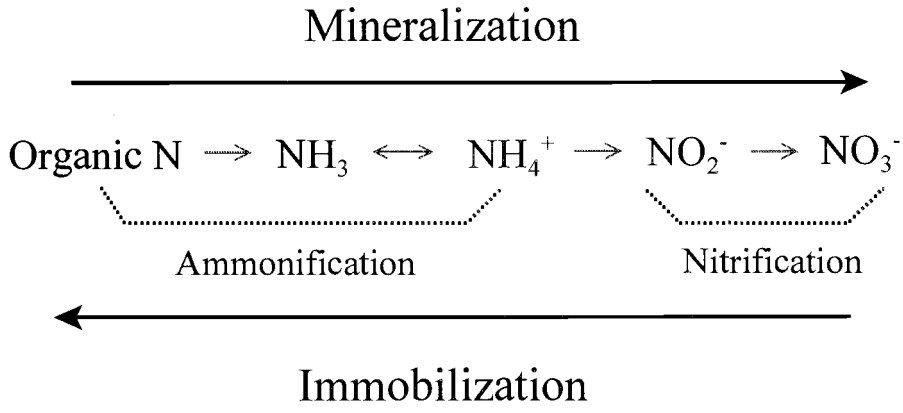


Figure 2. Nitrogen conversion pathways in the soil environment.

Figure 3. Reduction of nitrate via denitrification.

charged and cannot bind to the negatively charged soil particles, it stays in solution and is easily leached (Tan, 1994). Unless it is taken up by plants or denitrified, nitrate-nitrogen is the form of nitrogen that causes the most aquatic environmental damage.

Microbial reduction of nitrate via denitrification is one pathway by which excess nitrates can be removed from soils (Figure 3). Denitrification requires very specific conditions before it can occur. These include the presence of denitrifying organisms, anaerobic conditions, an abundant NO_3^- supply, a carbon source, and appropriate soil pH and temperature conditions (Firestone, 1982; Paul and Clark, 1989; Davidson, et al., 1990; Tisdale, et al., 1993).

Most denitrifying bacteria are heterotrophs, deriving their growth energy and obtaining cell carbon from organic substrates (Firestone, 1982; Paul and Clark, 1989). Most are aerobic bacteria that function in an anaerobic environment only in the presence of N oxides, using the N oxides as electron acceptors during respiration, instead of oxygen (Firestone, 1982). Many genera of bacteria are capable of denitrifying but common genera include *Pseudomonas, Alcaligenes,* and *Bacillus* (Firestone, 1982; Paul and Clark, 1989; Tisdale, et al., 1993). Some forest soils are thought to be devoid of denitrifying bacteria (Davidson, et al., 1990) but riparian forests, such as those in this study, are known to have significant levels of denitrifying populations (Davidson and Swank, 1986; McClellan, 1987).

The anaerobic conditions required for denitrification are usually created when soils become saturated following precipitation or flooding events. Water in

the soil pores limits the diffusivity of oxygen in the soil environment. Therefore any characteristic that impacts the soil moisture content, such as soil texture and structure, will potentially affect denitrification. An abundance of carbon can also impact soil aeration by increasing oxygen demand causing anaerobiosis (Davidson, et al., 1990).

Denitrification requires that sufficient concentrations of nitrate be available. In most pollution remediation work, a source of nitrates is usually not a limiting factor. However, nitrates can be removed by other methods, such as through plant uptake, immobilization, and leaching, so competition may cause nitrate limiting conditions.

Temperature and pH are also factors influencing denitrification rates. At temperatures above 20° C, denitrification increases exponentially with increasing temperature according to the Arrhenius equation. At temperatures below 20° C, denitrification increases linearly with temperature (Firestone, 1982). Maximum and minimum temperatures for denitrification are 75° and 5° C, respectively (Paul and Clark, 1989). Optimal denitrification rates occur in neutral soils of pH 6 to 8. Denitrification decreases below pH 5 and is essentially nonexistent below pH 4 (Paul and Clark, 1989).

Traditionally, denitrification is assessed by measuring actual rates in the field or by measuring denitrification potentials. Field denitrification rates are conducted *in situ* using methods that minimize experimental disturbance (Tiedje, et al., 1989). Denitrification potentials are measured using the denitrifying enzyme

assay (DEA). This assay, which measures denitrifying enzyme activities, is usually conducted under optimal conditions (Tiedje, et al., 1989) which are designed to express the "potential for on-site denitrification at the time of sampling." (Schipper, et al., 1993) Potentials can also be used to determine if certain factors such as carbon or nitrate are limiting denitrification at a site by not including that factor in the analysis (Tiedje, et al., 1989). By using a combination of field rates and potentials, a more complete picture of the system and its N removal capabilities can be determined.

Vegetation affects nitrogen pools directly by taking up nutrients, binding them in biomass, freeing exchange sites in the soil (Fennessy and Cronk, 1997), and pulling up nutrients from depth for surficial cycling (Hanson, et al., 1994). Nutrients reach plant roots by three methods: (1) roots grow into the soil to capture nutrients, (2) nutrients flow toward the roots as the roots take-up water, and (3) decreasing nutrients create a concentration gradient near the root surface, setting up a pathway for diffusion. The rate of plant uptake and the relative mobility of nutrients in the soil solution determine which of these methods predominates. Plant demand for N, P, and K is so high that the flow of nutrients with soil water is usually insufficient and diffusion becomes the primary method of nutrient delivery (Waring and Schlesinger, 1985).

However, plant uptake is not truly a removal method unless the vegetation is harvested and removed. If plant material is not physically removed from the site, nutrients are eventually cycled back into the environment and remain on site

(Hauck and Tanji, 1982). The rate of N cycling and N storage as plant biomass is affected by tissue type, plant type, and age. When trees are actively growing, they tend to take up and sequester more N than other types of vegetation (Waring and Schlesinger, 1985). In trees, the longer-lived woody tissues, as a whole, contain the majority of plant N (Kozlowski, et al., 1991). Lodhiyal and Lodhiyal (1997) reported the standing state of N in 4-year-old *Populus deltoides* as 26.6, 23.6, 35.5, 13.0, and 1.3 % allocated to the bole, branches, foliage, coarse roots, and fine roots, respectively. The lower decomposition rate of woody tissues when compared to grass or herb foliage makes trees a logical choice for sequestering N. Younger trees tend to accumulate higher concentrations of nutrients compared to more mature trees (Kozlowski, et al., 1991) because of the increase in biomass with age (Lodhiyal and Lodhiyal, 1997). Indeed, Boyle (1975) estimated that three 10-year rotations versus one 30-year rotation of *P. tremuloides*, with both rotations using whole-tree harvesting, increased N depletion by 240%.

Uptake varies over the course of a year, depending on the life cycle of the plant species. In western Oregon's Mediterranean climate, for example, deciduous trees such as poplars and oaks leaf out in spring, actively grow through the dry summer and drop their leaves in the fall. Since deciduous trees are basically dormant in the winter, no nutrient uptake occurs during this season. Grasses however germinate or resprout, depending if they are annual or perennial, respectively, in the autumn after the rains begin. Depending on the plant, they could

senesce at the beginning of the summer drought or wait until the following autumn (Hooper and Vitousek, 1997).

Nutrients are brought up from the soil, sometimes from great depths, and cycled through the plant. Thus, plants can act as pumps, removing NO_3^- from groundwater, sequestering it as plant biomass and then returning this nitrogen to the ground as organic N in litter. Organic N is mineralized and either denitrified or immobilized as microbial biomass (Lowrance, 1992; Hanson, et al., 1994). Indeed, surficial denitrification of groundwater NO_3^- is a complicated combination of hydrologic, vegetative, and microbial processes (Hanson, et al., 1994).

Indirectly, vegetation affects microbial processes that potentially have a greater impact on nitrogen pools than plant uptake (Hooper and Vitousek, 1998). In denitrification, organic carbon from plant litter and root exudates is required as an electron donor for energy production and as cellular material for growth (Firestone, 1982). However, plant residues vary in quality and unfortunately little research has been conducted looking at how substrates from natural sources influence denitrification (Beauchamp, et al., 1989). In a comparative study, soils amended with alfalfa produced higher rates of denitrification than those amended with straw. This was thought to be due to the greater extractable C release from the alfalfa and to the higher lignin value of straw (deCatanzaro and Beauchamp, 1985). In other denitrification studies, Schipper, et al. (1994) concluded that the quality of C was a more important factor than the quantity of C in controlling denitrification rates. More specifically, they found that denitrification rates were higher in soils amended

with fresh plant material than in soils amended with the same material after it had been dried. They concluded that this was due to more readily degradable C in fresh litter. McKenney, et al. (1993, 1995) found that the type of plant residue, degree of decomposition and supply of soluble C all affect denitrification rates.

Finally, plants create a feedback loop in N cycling through differences in litter quality and quantity (Nadelhoffer, et al., 1983; Pastor, et al., 1984; Wedin and Tilman, 1990; Zak and Pregitzer, 1990; Hobbie, 1992; Scott and Binkley, 1997). Soil microbes decompose and mineralize plant litter making N available for plant uptake or immobilization by microorganisms. Vegetation from nutrient-poor systems produce nutrient-poor litter that decomposes slowly, thereby delaying nutrient loss.

Objectives and Approach

The objectives of this study were to: (1) quantify denitrification and vegetative uptake in three riparian vegetation types, (2) determine how the vegetation type influences N dynamics and thus which type has the greatest potential to serve as a nutrient buffer zone, and (3) determine the factors limiting denitrification.

The approach taken to accomplish these goals was to install experimental plots in three adjacent riparian vegetation types, a pasture, a hybrid poplar stand on a former pasture, and a native oak forest. Once a season, for one year, vegetation

samples were collected to estimate nutrient uptake and then the plots were fertilized. After fertilization, soil samples were collected in each of the plots. One set of samples was incubated in the field to determine *in situ* denitrification rates. The second set of samples was taken back to the laboratory for quanitification of denitrifying enzyme activity (DEA), in soils amended with nitrate and glucose or with nitrate, and other soil characteristics.

METHODS

Site description and history

The study was conducted on the Oregon State University dairy farm, near Corvallis, Oregon, in the riparian area of Oak Creek during 1994 - 1995. The area immediately adjacent to Oak Creek was mature native forest composed of Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), wild rose (*Rosa spp.*), snowberry (*Symphoricarpos albus*), and poisonoak (*Rhus diversiloba*). Adjacent to the native forest was a pasture used by the dairy farm for grazing. In 1989, the pastured area adjacent to the native forest was planted with hybrid poplar (*P. trichocarpa* x *deltoides*) and again replanted in 1990 following severe damage by mammals. By 1994, the poplar stand was not very uniform, with an average tree height of 6.23 m on a 1.8 x 1.8 m spacing. Crown closure had occurred in a few small patches throughout the stand but a dense understory grass cover predominated. These three distinct vegetation types, native forest, pasture, and hybrid poplar stand, served as the basis of comparison in this study.

In general, the area has a Mediterranean climate, with hot, dry summers and mild, wet winters. Annual rainfall for Corvallis is 108.5 cm, predominantly occurring October through April. The average mean annual temperature is 11.1° C, with a mean annual maximum and minimum temperature of 16.9° and 5.3° C, respectively.

Soils in the study site include a Bashaw clay (very fine, montmorillonitic, mesic Typic Pelloxerert) in the hybrid poplar stand and pasture and a Waldo silty clay loam (fine, mixed, mesic Fluvaquentic Haplaquoll) in the native forest.

Procedures

A sampling strategy was followed to confirm the seasonal pattern of denitrification (Tiedje et al., 1989) predicted for this region. To accomplish this, fertilizer was applied and soil samples were taken for analysis once each season in November, 1994, March, June and October, 1995, which are referred to as fall, winter, spring, and summer, respectively. Because of the time required to complete each sampling, the sampling was divided up into three sampling periods in the fall, and into two periods (generally two consecutive weekends) for the remaining seasons. It was assumed that climatic conditions would not vary substantially between sampling periods in a single season.

To compare nitrogen loss between the pasture, hybrid poplar stand, and native forest, four sets of paired square 16 m^2 plots in each of the three vegetation types were used. One plot in the pair was treated with fertilizer and the other plot served as a control (see Figure 4). The plots were randomly selected in each vegetation type by pulling numbers, corresponding to x-y coordinates, from a bag. Pre-determined rules of selection were followed to control variation between a single pair of plots, i.e. the two plots within the pair had to have similar vegetation

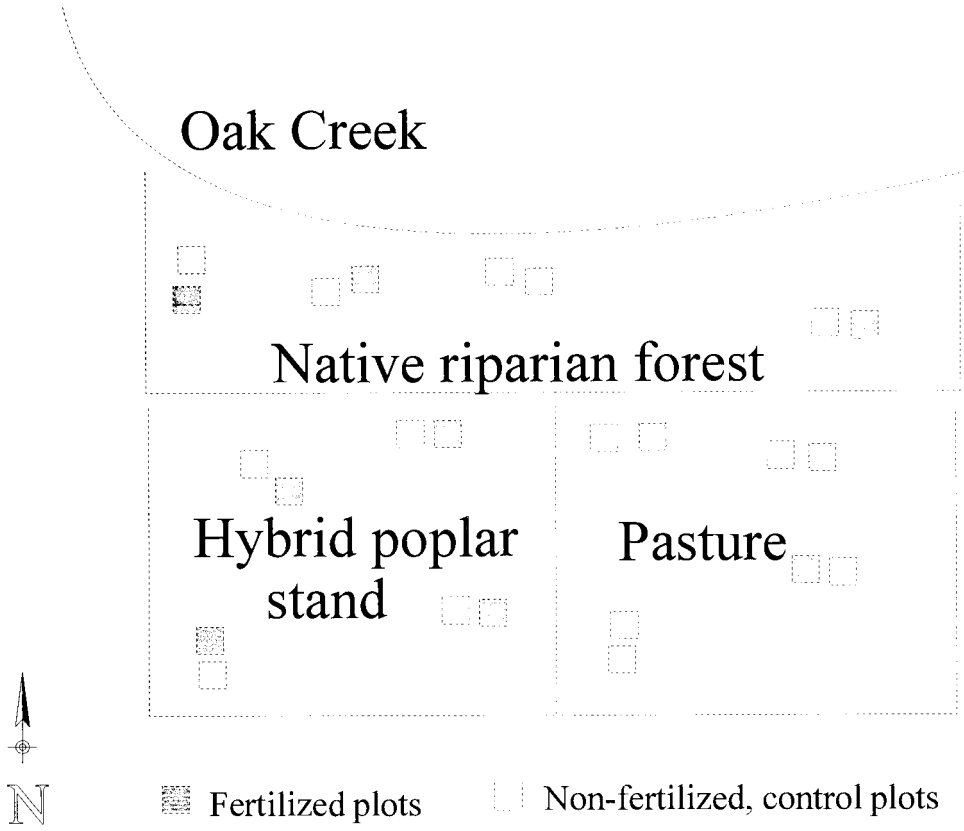


Figure 4. Site layout.

and structure. However, different pairs within a vegetation type were allowed to vary.

Ammonium nitrate (NH_4NO_3) fertilizer was applied to one of the plots in each pair for each season of one year. Granular ammonium nitrate was dissolved in water and applied with a backpack sprayer at a rate of 200 pounds nitrogen/acre/year. The remaining plot in each pair served as the control plot and was sprayed with water from the backpack sprayer.

The day following fertilizer application, soil cores were collected from each of the plots using an Oakfield sampler. The cylindrical cores measured 1.9 cm in diameter with a length of 15 cm. Ten paired soil cores were collected from random locations within each plot, for a total of 20 cores per plot. The two cores in each pair were immediately adjacent to one another to obtain as similar samples as possible. One of the cores from each pair was kept intact and placed into a wide-mouth Mason® jar for *in situ* incubation; the other core was placed into a sealable plastic storage bag to make up a composite soil sample for each plot. Samples were stored in a cooler until being transferred to the laboratory and stored at 5° C. In addition to the core samples, in the hybrid poplar plots soil samples were collected from the 15-30 cm depth to determine if denitrification rates decreased with depth.

Field denitrification rates were determined by the acetylene block method of inhibiting the conversion of nitrous oxide (N_2O) to nitrogen gas (N_2) and measuring the build up of nitrous oxide (Klemedtsson et al., 1977; Yoshinari et al., 1977; Tiedje et al., 1989). The ten in-tact soil cores were placed into the Mason® jars,

sealed, and injected with 10% acetylene (C_2H_2) through a rubber stopper in the lid of the jar, to inhibit the final step in the denitrification process. The acetylene in the headspace was mixed by repeatedly pumping the injection syringe to insure diffusion into the soil cores (Tiedje et al., 1989). The jars were incubated in a 15 cm deep hole directly adjacent to the paired treatment plots. Gas samples of the headspace were taken through the rubber stopper after 2 and 24 hours of incubation and placed into evacuated glass tubes (Vacutainers®). Samples were assayed for nitrous oxide concentration using a Hewlett Packard 5840A (carrier: O_2 free N; oven at 60° C; detector at 325 C; injector at 125 C; flow 100 ml/min) gas chromatograph fitted with an electron capture detector and using a Hewlett Packard 3396 integrator. Gas concentrations were calibrated with known gas standards. All nitrous oxide concentrations were corrected for the amount of N_2O dissolved in water using the Bunsen absorption coefficient (Tiedje, 1982). Soil temperature was measured at each jar incubation site at the beginning and end of each incubation period.

The composite soil samples from each plot were stored at 5° C until processed for ammonium, nitrate, and dissolved organic carbon concentrations, pH, moisture content, and denitrification potential analysis. Average storage time between sample collection and processing was six days.

Ammonium and nitrate concentrations were determined by extracting 10 grams of unsieved field moist soil with 100 milliliters of 2 Molar potassium chloride (KCl), on a rotary shaker for one hour (Keeney and Nelson, 1982). The

samples were allowed to settle for 30 minutes before being filtered and frozen for storage. Thawed samples were analysed with an Alpkem R.F.A Model 300 series. Dissolved organic carbon (DOC) concentrations were determined by extracting 5 grams of unsieved field moist soil with 15 milliliters of water at 22° C on a rotary shaker for one hour. Samples were then centrifuged and the supernatant was frozen for storage. DOC concentrations were measured on a Dormann carbon analyzer. pH was determined by adding 5 grams of dried soil to 50 milliliters of deionized water, mixing for one hour on a rotary shaker, and measuring with an Orion 710A pH meter. Moisture content was determined by drying 10 grams of soil at 70° C for 24 hours.

The denitrifying enzyme assay (DEA, Smith and Tiedje, 1979; Tiedje et al., 1989) was used to estimate both maximum DEA activity and to assess factors limiting denitrification. Five grams of unsieved field moist soil were added to 25 milliliter Erlenmeyer flasks, capped with serum bottle stoppers, and amended with either (a) 1 mM potassium nitrate (KNO_3) or (b) a solution containing 1 mM of both potassium nitrate and glucose. The headspace in the flasks was purged of all oxygen by flushing with argon and then injected with 10% acetylene (C_2H_2). The samples were incubated at 24° C for 2 hours, with gas samples taken at 30 minutes and 2 hours. Samples were stored in evacuated glass tubes (Vacutainers®) and assayed for nitrous oxide concentration as described above. Stimulation of denitrification by C was calculated as the relative increase in denitrification due to amendment with glucose and nitrate versus nitrate only amendments.

To estimate vegetative uptake of nitrogen in the three vegetation types, litter fall was collected (Heilman and Stettler, 1986) and grasses and understory vegetation were clipped from a rectangular plot (1.43 meter^2) at the center of each set of paired plots. The vegetative material was collected immediately preceding each seasonal fertilizer application and was dried at 70° C until it reached a constant weight. The material was then ground in a Wiley mill and analyzed for total Kjeldahl nitrogen (Thomas et al., 1967). Samples were assayed colorimetrically using a Technicon autoanalyzer. Values from each vegetation type were then totaled to develop an annual estimate of uptake.

Statistical analysis

All soil data was analyzed in SAS (SAS Institute, Inc., 1997) using a split plot design and a mixed linear model. The vegetation type, pasture, poplar or native forest, was the main plot factor and the treatment, fertilized or not fertilized, was the subplot factor. All denitrification, dissolved organic carbon, and nitrate analyses were conducted using a logarithmic transformation to correct for heteroscedacity. In all analyses (except denitrification potentials as noted below), each season was analyzed separately. This was done because each season was expected to behave differently, based on differing climatic conditions, and to avoid having to conduct a more complicated repeated measures analysis. Therefore, no comparisons can be made between the seasons.

Denitrification potentials measured on the same plots for each season were compared using a repeated measures procedure within a mixed linear model.

RESULTS

There were no significant differences between the fertilizer treated plots and the control plots for field denitrification (Table 1). With the exception of summer poplar denitrification rates, field denitrification rates (Table 2) exhibited the same pattern throughout the year for the pasture, hybrid poplar stand, and the native forest. Rates were highest in the winter in all three vegetation types, substantially lower in the fall, and minimal in the spring and summer. The pasture and poplar stand had significantly ($p<0.05$) higher denitrification rates than the native forest in the fall and in the winter. During the winter, sampling was conducted over two consecutive weekends. In the interim week soil temperature rose from 4.5°C, on average, to 9.8°C, causing a substantial increase in denitrification (Figure 5.). A separate analysis of each of the two winter sampling periods shows that while denitrification rates increased in all three vegetation types with the increase in soil temperature, the pasture and the hybrid poplar stand denitrification rates were still significantly ($p<0.05$) higher than the native forest rates.

There were no significant differences between the fertilizer treated plots and the control plots for pH, soil moisture content, or temperature (data not shown). pH, moisture content, and soil temperature were the same in all three vegetation types, at each season ($p<0.05$) but they did vary throughout the year. Mean seasonal values for temperature and moisture content are given in Figure 6, including a

Table 1. Mean field denitrification rates (ng N/hr·g) for fertilized and control plots.

		Fertilized plots			Control plots		
Season	Site	Mean	Std Dev	n	Mean	Std Dev	n
Fall	Pasture	0.60	0.60	4	0.23	0.17	4
	Poplar	0.99	1.83	4	0.33	0.10	4
	Native	0.014	0.018	4	0.038	0.038	4
Winter	Pasture	2.63	1.67	4	2.53	2.38	4
	Poplar	4.78	5.18	4	2.35	2.10	3
	Native	0.34	0.36	4	0.41	0.70	4
Spring	Pasture	0.11	0.070	4	0.031	0.018	4
	Poplar	0.06	0.042	4	0.063	0.032	4
	Native	0.021	0.018	4	0.016	0.021	4
Summer	Pasture	0.038	0.038	4	0.040	0.067	4
	Poplar	0.0062	0.0063	4	0	0	4
	Native	0.013	0.024	4	0.019	0.013	4

Table 2. Mean field denitrification rates (ng N/hr·g) and 95% confidence intervals. Means not followed by the same letter are significantly different from each other at the given p-value.

			95% Confidence Intervals			
Season	Site	Mean	Minimum	Maximum	df	p-value
Fall	Pasture	0.25 a	0.047	1.34	9	0.004
	Poplar	0.25 a	0.047	1.34	9	
	Native	0.003 b	0.0007	0.02	9	
Winter	Pasture	1.81 a	0.20	16.87	9	0.047
	Poplar	2.00 a	0.20	20.12	9	
	Native	0.05 b	0.006	0.48	9	
Spring	Pasture	0.046	0.0066	0.33	9	0.09
	Poplar	0.048	0.0068	0.34	9	
	Native	0.003	0.0005	0.023	9	
Summer	Pasture	0.0065	0.0005	0.085	9	0.31
	Poplar	0.0005	0.00004	0.006	9	
	Native	0.0026	0.0002	0.034	9	

Figure 5. Response of denitrification to an increase in soil temperature. The winter sampling was conducted during two weekend sessions in which the soil temperature doubled. Subsequently, denitrification rates increased in all three vegetation types.

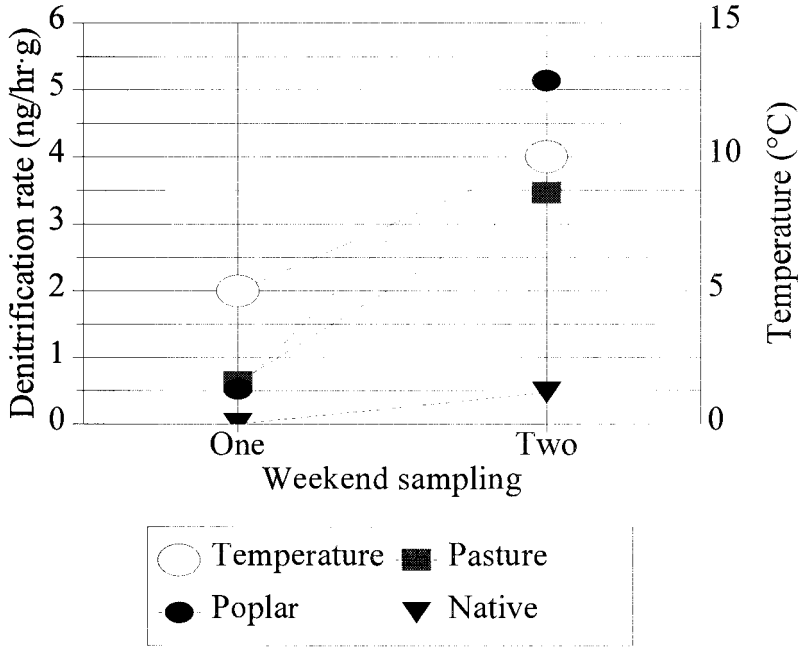
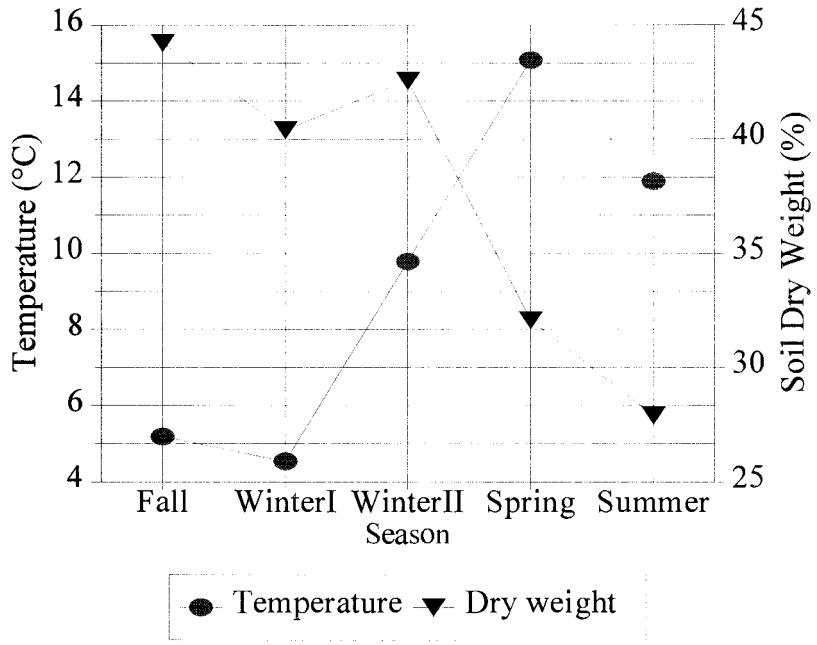


Figure 6. Mean seasonal values of soil temperature and moisture content, expressed as dry weight (%). The largest response in field denitrification occurred when both soil temperature and moisture were high in the second winter sampling.



breakout of the two winter sampling periods. Mean seasonal pH values are given in Table 3.

There were significantly ($p<0.0006$) higher nitrate concentrations in the fertilized plots, regardless of vegetation type, in each season (Table 4). Ammonium concentrations were significantly ($p\leq0.030$) higher in the fertilized plots during the fall, spring, and summer (Table 4). However in the fall, ammonium concentrations were only significantly ($p=0.01$) higher in the fertilized plots for the pasture and native forest (data not shown). Seasonal nitrate and ammonium concentrations for each vegetation type are given in Table 5. Significant ($p<0.025$) differences were observed in dissolved organic carbon (DOC) concentrations in plots with different vegetation (Figure 7). Throughout the year, pasture and poplar plots had lower DOC levels than native forests. With the exception of summer samples, there were no significant differences in DOC in pasture and poplar plots. During the fall, winter, and summer DOC levels were significantly ($p<0.01$) lower in the fertilized plots (Table 6).

In hybrid poplar plots, there were significant ($p<0.05$) differences in nitrate concentrations between top (0-15 cm) and bottom (15-30 cm) samples (Table 7).

Potential denitrification rates were measured by amending samples with either glucose and nitrate or nitrate (Tables 8 and 9). In glucose and nitrate amended soils, significant differences were observed between the vegetation types for all seasons except fall. During the remaining seasons, there were no significant differences between pasture and poplar plots but these were both significantly

Table 3. Mean, minimum and maximum seasonal pH values for the three riparian vegetation types.

		Mean	Minimum	Maximum
Fall				
	Pasture	5.92	5.71	6.24
	Poplar	6.14	5.80	6.37
	Native	6.08	5.90	6.37
Winter				
	Pasture	5.75	5.54	6.06
	Poplar	5.99	5.70	6.25
	Native	5.89	5.77	6.20
Spring				
	Pasture	5.74	5.49	6.17
	Poplar	5.84	5.60	6.05
	Native	5.83	5.67	6.00
Summer				
	Pasture	6.00	5.81	6.25
	Poplar	6.15	5.88	6.36
	Native	6.11	5.92	6.62

Table 4. Mean nitrate and ammonium levels (ppm) for the fertilized and control plots. Means not followed by the same letter are significantly different from each other at the given p-value.

Nitrate (ppm)

			95% Confidence Intervals			
Season	Treatment	Mean	Minimum	Maximum	df	p-value
Fall	Fertilized	0.48 a	0.21	1.09	9	0.0001
	Control	0.043 b	0.019	0.096	9	
Winter	Fertilized	0.69 a	0.18	2.58	9	0.009
	Control	0.062 b	0.016	0.23	9	
Spring	Fertilized	0.40 a	0.27	0.60	9	0.0001
	Control	0.055 b	0.037	0.082	9	
Summer	Fertilized	0.78 a	0.47	1.29	9	0.0001
	Control	0.16 b	0.094	0.26	9	

Ammonium (ppm)

Season	Treatment	Mean	Std Error	df	p-value
Fall	Fertilized	0.20 a	0.031	9	0.030
	Control	0.14 b	0.031	9	
Winter	Fertilized	0.34	0.087	9	0.45
	Control	0.25	0.087	9	
Spring	Fertilized	0.39 a	0.067	9	0.026
	Control	0.20 b	0.067	9	
Summer	Fertilized	0.50 a	0.075	9	0.0014
	Control	0.24 b	0.075	9	

Table 5. Mean nitrate (ppm) and ammonium (ppm) concentrations for the three riparian vegetation types.

	Nitrate	Std Err	df	Ammonium	Std Err	df
Fall						
Pasture	0.20	0.56	9	0.14	0.051	9
Poplar	0.17	0.56	9	0.13	0.051	9
Native	0.087	0.56	9	0.25	0.051	9
Winter						
Pasture	0.54	0.80	9	0.45	0.12	9
Poplar	0.34	0.80	9	0.12	0.12	9
Native	0.048	0.80	9	0.31	0.12	9
Spring						
Pasture	0.19	0.22	9	0.40	0.082	9
Poplar	0.17	0.22	9	0.14	0.082	9
Native	0.10	0.22	9	0.34	0.082	9
Summer						
Pasture	0.56	0.34	9	0.32	0.12	9
Poplar	0.47	0.34	9	0.28	0.12	9
Native	0.16	0.34	9	0.50	0.12	9

Figure 7. Dissolved organic carbon levels for the three vegetation types in each season. Bars represent 95% confidence levels. Bars followed by the same letter are not significantly different from each other ($p<0.025$).

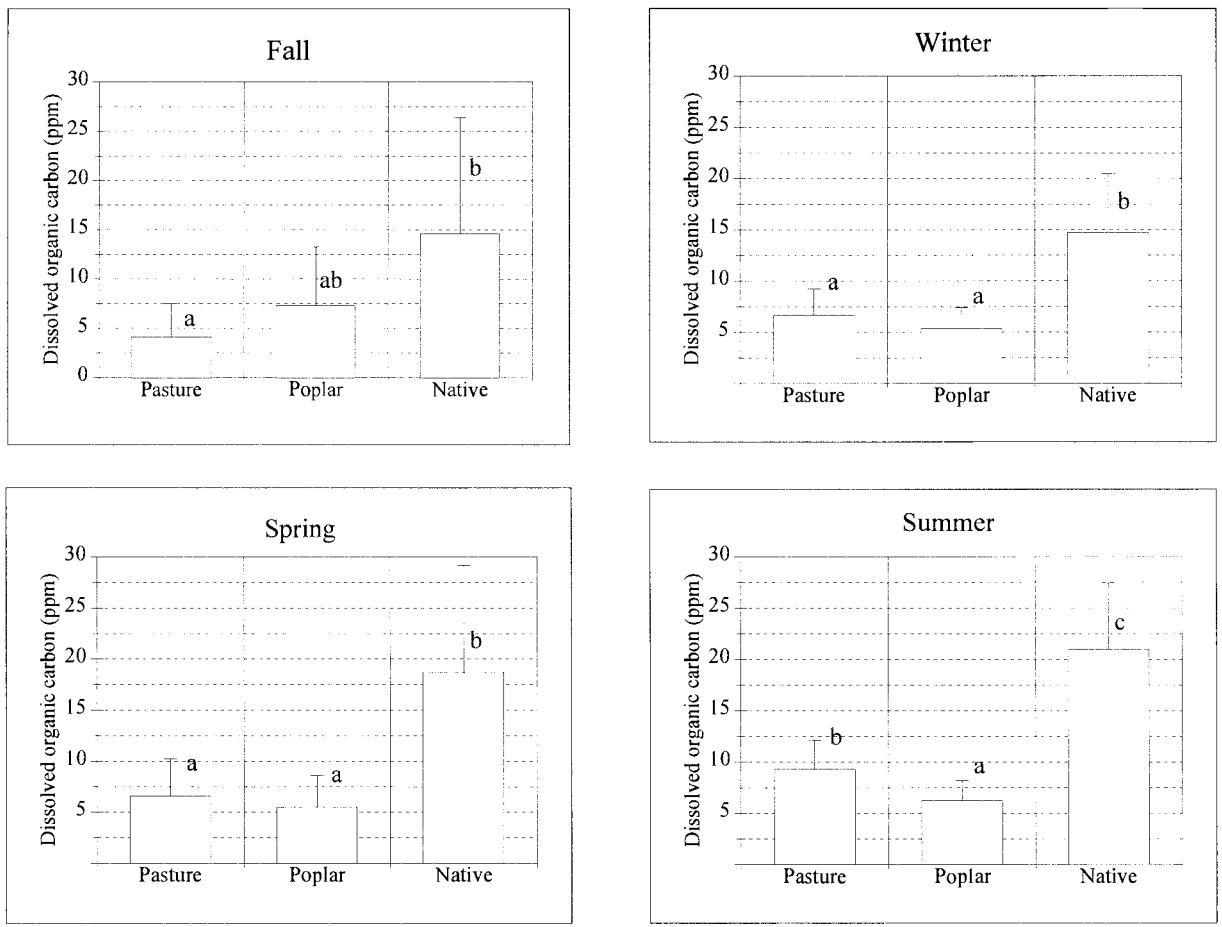


Table 6. Mean dissolved organic carbon levels (ppm) for the fertilized and control plots with 95% confidence intervals. Means not followed by the same letter are significantly different from each other at the given p-value.

			95% Confidence Intervals			
Season	Treatment	Mean	Minimum	Maximum	df	p-value
Fall	Fertilized	6.45 b	4.51	9.23	9	0.006
	Control	8.99 a	6.28	12.86	9	
Winter	Fertilized	6.69 b	5.31	8.43	9	0.01
	Control	9.67 a	7.68	12.19	9	
Spring	Fertilized	7.97	5.98	10.59	9	0.83
	Control	9.70	7.29	12.91	9	
Summer	Fertilized	9.21 b	7.69	11.03	9	0.006
	Control	12.39 a	10.34	14.84	9	

Table 7. Mean nitrate concentrations (ppm) in the surface (0-15 cm) and subsurface (15-30 cm) soil samples (poplar stand only). Means not followed by the same letter are significantly different from each other at the given p-value.

Season	Depth	Mean	Std Error	df	p-value
Fall	Surface	0.45 a	0.12	6	0.025
	Subsurface	0.075 b	0.12	6	
Winter	Surface	0.56 a	0.11	6	0.015
	Subsurface	0.14 b	0.11	6	
Spring	Surface	0.29 a	0.063	6	0.024
	Subsurface	0.041 b	0.063	6	
Summer	Surface	0.67 a	0.12	6	0.017
	Subsurface	0.089 b	0.12	6	

Significant interaction with fertilized plots in winter, spring, and summer.

Table 8. Mean denitrification potentials (ng N/hr·g) and 95% confidence intervals for samples amended with glucose and nitrate. Means not followed by the same letter are significantly different from each other at the given p-value.

			95% Confidence Intervals			
Season	Site	Mean	Minimum	Maximum	df	p-value
Fall	Pasture	102.80	50.23	210.39	5	0.062
	Poplar	88.17	49.13	158.22	5	
	Native	37.70	21.01	67.66	5	
Winter	Pasture	39.40 ab	23.68	65.55	9	0.025
	Poplar	65.40 a	39.31	108.80	9	
	Native	22.25 b	13.37	37.02	9	
Spring	Pasture	61.46 a	42.12	89.68	8	0.026
	Poplar	62.57 a	39.35	99.50	8	
	Native	30.25 b	20.73	44.15	8	
Summer	Pasture	42.44 a	28.70	62.75	9	0.027
	Poplar	53.84 a	36.41	79.62	9	
	Native	24.42 b	16.51	36.11	9	

Table 9. Mean denitrification potentials (ng N/hr·g) and 95% confidence intervals for samples amended with nitrate. Means not followed by the same letter are significantly different from each other at the given p-value.

			95% Confidence Intervals			
Season	Site	Mean	Minimum	Maximum	df	p-value
Fall	Pasture	48.03	0.082	28093.41	1	0.40
	Poplar	49.87	0.55	4513.45	1	
	Native	12.85	0.022	7517.52	1	
Winter	Pasture	38.55 a	27.88	53.29	9	0.0016
	Poplar	33.56 a	24.28	46.39	9	
	Native	14.20 b	10.27	19.64	9	
Spring	Pasture	9.73	5.81	16.29	8	0.52
	Poplar	14.48	7.51	27.94	8	
	Native	12.94	7.73	21.67	8	
Summer	Pasture	8.69	5.28	14.30	9	0.41
	Poplar	12.76	7.75	21.01	9	
	Native	8.74	5.31	14.40	9	

higher than in native forest plots (Table 8). Comparing the denitrification potentials between the vegetation types regardless of season, the glucose and nitrate amended samples show a strong difference ($p=0.0044$) between the vegetation types, with the pasture and hybrid poplar plantation having higher denitrification rates than the native forest (Figure 8). The glucose and nitrate amended samples also show a strong seasonal difference ($p=0.0001$), with the fall having higher denitrification potentials than any other season (Figure 9.)

A seasonal comparison of the nitrate only amended samples revealed a much more complicated picture. When denitrification potentials were measured using nitrate amendments without glucose, denitrification rates were significantly greater in pasture and poplar plots when compared with native forest plots in winter only (Table 9). While there were significant differences between the vegetation types ($p=0.0245$), the fertilized and unfertilized plots ($p=0.0001$), and between the seasons ($p=0.0001$), the seasonal differences depended on which vegetation type the samples were from (Figure 10) or plot fertilization (Figure 11.)

To gauge the effect on potential denitrification rates due to an increase in C, stimulation was calculated and compared for all treatments (Table 10). There was significantly ($p = 0.042$) more stimulation in the pasture soils than in the native soils during the winter. While not significant for all seasons, a consistent trend was that pasture and poplar soils were more stimulated by the addition of C than the native forest soils.

Figure 8. Comparison of glucose and nitrate amended denitrification potentials. Regardless of season, the pasture and poplar soils had higher potential rates than the native forest soils (p = 0.0044).

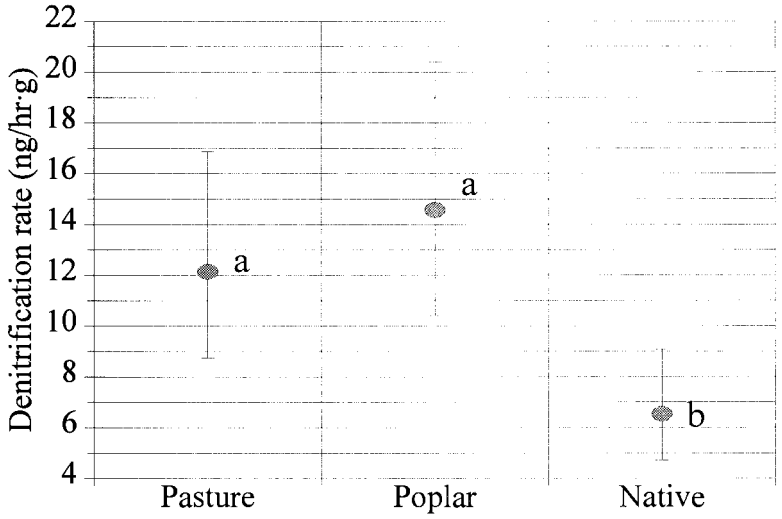


Figure 9. Comparison of glucose and nitrate amended denitrification potentials. Regardless of vegetation type, the fall had the highest potential denitrification rates. Bars followed by the same letter are not significantly different from each other (p = 0.0001).

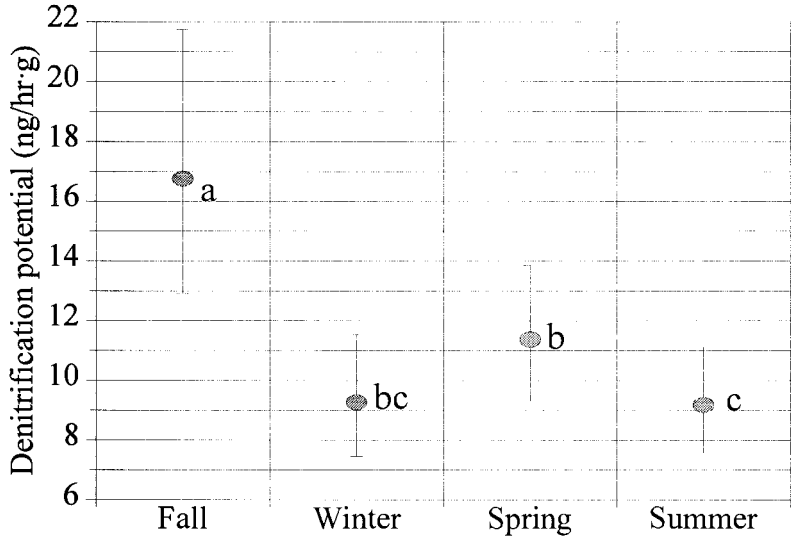


Figure 10. Comparison of nitrate amended denitrification potentials. In the fall and winter, the pature and poplar soils had higher denitrification potentials than the native forest soils.

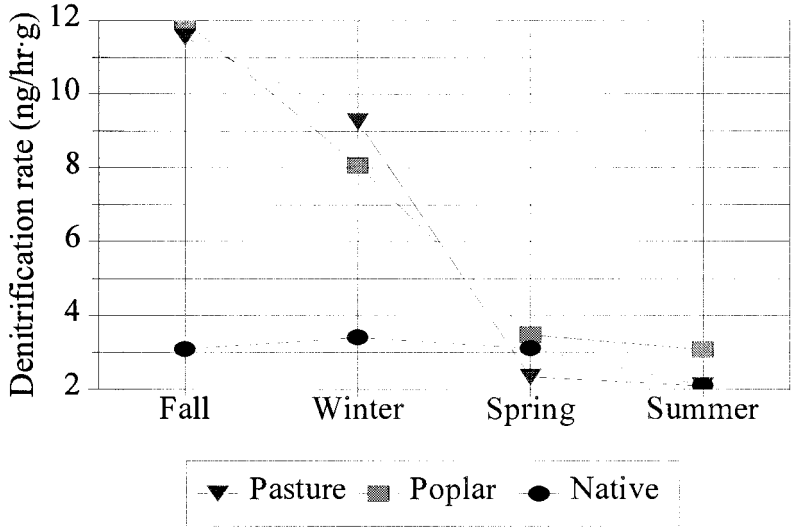


Figure 11. Comparison of nitrate amended denitrification potentials. During the fall, unfertilized soils had higher denitrification potentials than fertilized soils.

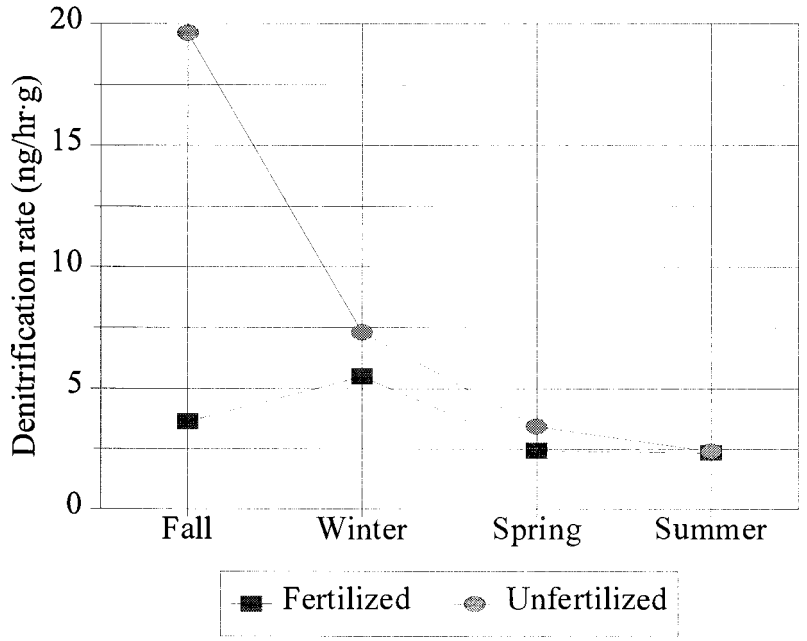


Table 10. Mean stimulation* (%) of denitrification by glucose and nitrate amendments versus nitrate only amendments. Means not followed by the same letter are significantly different from each other at the given p-value.

Season	Site	Mean	Std Error	df	p-value
Fall	Pasture	185	245	1	0.89
	Poplar	255	173	1	
	Native	104	245	1	
Winter	Pasture	8.8	33	9	0.12
	Poplar	110	33	9	
	Native	94	33	9	
Spring	Pasture	589 a	98	8	0.042
	Poplar	428 ab	127	8	
	Native	160 b	98	8	
Summer	Pasture	452	105	9	0.27
	Poplar	388	105	9	
	Native	203	105	9	

*Stimulation was calculated as: Stimulation (%) = [[(Denitrification rate with carbon and nitrate amendments) - (Denitrification rate with nitrate amendments)] ÷ (Denitrification rate with nitrate amendments)] x 100.

When there were sufficient samples to perform the analysis, in the winter and summer, the surface 15 cm of soil in the hybrid poplar stand had significantly ($p<0.05$) higher denitrification potentials, in both the glucose and nitrate, and nitrate only amended samples (Table 11) than the 15-30 cm soil horizon.

Vegetative uptake of nitrogen was greatest ($p=0.0045$) in the native forest (Table 12). Even though the hybrid poplar stand produced as much litter as the native forest, the average nitrogen content in poplar and pasture plant materials was the same and was significantly lower than that in the native vegetation. A comparison of how total nitrogen values changed throughout the year in each of the three vegetation types is shown in Table 13.

Table 11. Mean denitrification potentials (ng N/hr·g) in the surface (0-15 cm) and subsurface (15-30 cm) soil samples (poplar stand only), with 95% confidence intervals. Means not followed by the same letter are significantly different from each other at the given p-value.

Samples amended with glucose and nitrate.

			95% Confidence Intervals			
Season	Depth	Mean	Minimum	Maximum	df	p-value
Fall	Surface	88.17	35.60	216.02	4	0.10
	Subsurface	33.70	13.75	82.57	4	
Winter	Surface	65.40 a	37.79	113.17	6	0.0024
	Subsurface	13.32 b	7.70	23.05	6	
Spring	Surface	62.86	26.95	146.59	2	0.090
	Subsurface	24.51	9.07	66.28	2	
Summer	Surface	53.84 a	24.95	116.22	6	0.035
	Subsurface	16.04 b	7.43	34.62	6	

Samples amended with nitrate.

			95% Confidence Intervals			
Season	Depth	Mean	Minimum	Maximum	df	p-value
Fall	Surface	49.87	1.26	1980	1	0.23
	Subsurface	14.82	0.16	1345	1	
Winter	Surface	33.56 a	22.32	50.48	6	0.0062
	Subsurface	12.67 b	8.42	19.06	6	
Spring	Surface	14.34	1.47	140.41	2	0.073
	Subsurface	0.91	0.075	11.12	2	
Summer	Surface	12.76 a	4.28	38.08	6	0.030
	Subsurface	2.14 b	0.72	6.40	6	

Table 12. A comparison of mean vegetation amounts and mean nitrogen contents. Means not followed by the same letter are significantly different from each other at the given p-value.

	Quantity of vegetative material. (g/sq m)	Average nitrogen content. (% TKN)	Total amount of nitrogen in vegetative material. (g/sq m)
Pasture	237.9 b	1.25 b	2.56 b
Poplar	402.54 a	1.03 b	3.74 b
Native	406.91 a	1.84 a	5.47 a
Std Error	40.64	0.099	0.45
df	9	9	9
P-value	0.026	0.0007	0.0045

Table 13. A comparison of nitrogen content for the various samples collected.

	% TKN
Poplar (grass only)	
March	2.35
June	1.07
Poplar (poplar leaves)	
October - December	0.9
Pasture	
November	1.06
March	2.4
June	1.17
October	0.91
Native (understory only)	
March	3.91
June	1.3
Native (oak leaves)	
October - December	1.42

DISCUSSION

Differences between vegetation types

Denitrification

The pasture and poplar stand had approximately 34 times greater field denitrification rates (Table 2) and approximately double the denitrification potential rates (glucose and NO_3^- amended) (Table 8) than the native riparian oak forest. Others have reported similar results (Table 14) in riparian areas. Ambus and Lowrance (1991) found a much larger response in denitrification to NO_3^- additions than to C additions alone (Table 14). Nitrate and C additions prompted an even greater response in denitrification, but only in the mixed hardwood-pine forest. The large potential denitrification rates in the mixed hardwood-pine forest suggest that there are greater denitrifying populations in the mixed hardwood-pine forest than in the slash pine forest. Groffman et al. (1991) found lower denitrification rates in amended forest soils than in grasslands (Table 14). By comparing denitrification rates in soils amended with NO_3^- and with NO_3^- and glucose, it was apparent that even though organic matter levels were higher in forest soils, they apparently were more C limited than grassland soils (Table 14). However, both forest and grassland soils were significantly limited by soil NO_3^-. Schipper et al. (1993) reports values (Table 14) that are 20 times greater than were measured in my study, however the sites were sprayed with treated effluent. The control site in

Table 14. Comparison of reported denitrification rates for riparian areas. All values reported are from studies that were conducted in riparian zones using comparable methods. Notations are made where denitrification rates are measured in agricultural or domestic waste enriched soils.

Reference		**Laboratory rates** ----------		
Location	**Field**	**No**		
Vegetation type	**Rate**	**Amend**	**NO_3^-**	**C**	**NO_3^- & C**
Ambus and Lowrance, 1991					
Tifton, GA	(μg N_2O-N/kg·d)				
Riparian forest with poorly drained soils					
Slash pine		2	223	2.3	216
Mixed hardwood-pine		1	1402	11	2038
Groffman, et al., 1991					
Kingston, RI	(gN/ha·d)				
Well-drained forest		1.1	1306		2155
Poorly-drained forest		13.1	1402		2951
Tall fescue		1	17208		21702
Reed canary grass		1	15208		15819
Lowrance, 1992					
Tifton, GA	(μg N_2O-N/kg·d)				
Riparian forest		28.95	115.9	29	191.4
Schipper et al., 1993					
New Zealand	(ng N/g·hr)				
Radiata pine forest sprayed with sewage	520		810		
Hanson et al., 1994					
Kingston, RI	(g N/ha·d)				
Hardwood forests:					
Sewage-enriched	58.6		600		
Control	17.3		185		
Lowrance et al., 1995					
Southeastern US	(g N_2O-N/ha·d)				
Restored buffer zone Enriched site					
Zone 1-hardwoods	42.5				
Zone 2-pines	30.4				
Zone 3-grass	68.8				
Present study					
Oak Creek, OR	(g N/ha·d)				
Pasture	22.8		1134		2658
Poplar stand	24.8		1195		2916
Native oak forest	0.63		526		1238

Hanson et al. (1994) did have field rates in their control site that were very similar to those reported in my study (Table 14). Lowrance et al. (1995) found higher levels of denitrification in the grassed area versus the forested area of a restored riparian buffer zone (Table 14). The authors proposed two factors that may have been responsible for this difference: increased availability of N or readily degradable C in the grassed area. From these reports it is clear that both C and NO_3^- are important controlling factors for denitrification.

I found DOC to be significantly higher throughout the year in native riparian forest soils than in pasture and poplar soils (Figure 6).However all three vegetation types showed increased denitrification potentials in NO_3^- and glucose amended soils when compared with NO_3^- amended soils (Table 10). Denitrification stimulation in response to carbon is most dramatic in the spring and summer (Tables 8 and 9). Jacobson and Alexander (1980), deCatanzaro and Beauchamp (1985), McKenney, et al. (1993,1995), and Schipper, et al. (1994), all found that different sources of C affect denitrification rates. Groffman et al. (1991) found unexpectedly higher denitrification potentials in a grassed buffer strip than in riparian forests of red maple and red and white oak. They concluded that soil organic matter was more suitable for denitrification in the grass plots than in the forest plots, even though the forest plots contained higher levels of organic matter. From these results, I conclude that denitrification potentials are at least partially limited by readily degradable C in all vegetation types. However, the degree to which this occurs apparently changes with seasons (Table 10).

An examination of the relative levels of NH_4^+ and NO_3^- in the three vegetation types (Table 5) reveals that, while not statistically significant, the dominant plant-available form of N in the native riparian forest is NH_4^+, in the poplar stand it is NO_3^-, and in the pasture, NO_3^- dominates in fall, winter, and summer, and NH_4^+ dominates in spring. This could mean that NO_3^- is more available for denitrification in the pasture and poplar stand. It is expected that the forest soil would be NH_4^+ rich because forests typically occur on NH_4^+ dominated soils and are thought to be NO_3^- limited for denitrification (Van Miegroet and Johnson, 1993). Perry (1994) also showed that deciduous forests show variation in inorganic-N species dominance with higher NO_3^- concentrations in poplar stands and higher NH_4^+ concentrations in oak stands. However, Griffiths et al. (1997) found that in western Oregon riparian areas, pasture soils were balanced between NO_3^- and NH_4^+ dominance, as with this study, but forest soils were dominated by NO_3^-.

Nitrate dominance in the pasture and poplar soils versus NH_4^+ dominance in the native forest soils could result in larger denitrifying populations in the pasture and poplar soils. Verchot et al. (1998) found that increased N loading on a site over time increased denitrification rates increasing denitrifying microorganism numbers. Groffman et al. (1991) suggested that lower potential denitrification rates in forest soils versus grassland soils were due to smaller and/or less active populations of denitrifiers. Denitrifying organisms have been shown to be restricted under low soil

NO_3^- conditions (< 1 mg N kg^{-1} soil) which I found in unfertilized native forest soils (Jacobson and Alexander, 1980).

Higher NO_3^- values were measured in the fertilized plots (Table 4). However a corresponding increase in field denitrification rates was not found (Table 1). While several studies have found that NO_3^- concentration is strongly linked with denitrification (Myrold, 1988; Schipper et al, 1993) others have found opposite results (Parsons et al, 1991). Most likely NO_3^- will be linked to denitrification rates if all other requirements are met for denitrification to occur. In my study factors other than NO_3^- concentrations were limiting field denitrification rates. The lack of a response to fertilizer addition in the pasture and poplar soils was due to a C limitation and in native forest soils to low denitrifyer populations.

Vegetative Uptake

Vegetative uptake, as measured by litterfall N concentrations, was greatest in the native riparian oak forest (Table 12). The poplar stand and the native riparian forest had equal amounts of litter material, but the oak forest litter had higher N content. Most likely the higher N content was due to the variety of understory species that were sampled throughout the year (Mahendrappa, et al., 1986).

The method used to measure uptake was simplistic. In small herbaceous plants such as grasses, the nutrients are concentrated in the leaves and roots. In woody plants, nutrients are spread throughout the tree, but most N is stored in the

woody tissues (Hauck and Tanji, 1982). So to measure uptake in a grass sward, simply clipping the leaves provides an adequate estimate of uptake.

Assessing uptake in trees is a much more difficult task and in fact can not be directly measured (Waring and Schlesinger, 1985). Some of the complicating factors include "absorption and release of nutrients by the tree canopy, translocation of nutrients among tree tissues, fine-root turnover, and difficulties in measurement of annual woody increment in cases where it represents a small proportion of the total biomass."(Bockheim and Leide, 1990) The long-lived woody tissues of a tree contain the bulk of the stored nutrients. But it is the leaves and fines roots with their higher concentration of N and rapid turnover rates that are more accurate indices of annual nutrient cycling rates in trees (Waring and Schlesinger, 1985).

In the pasture, uptake values were quantified in a fairly straight-forward manner. The grass was clipped, dried, weighed, and analyzed. Values obtained ranged from 0.91% TKN in the fall to 2.4% TKN in the spring (Table 13). I collected 238 g·sq m^{-1} of herbage that contained 2.56 g·sq m^{-1} of nitrogen. Prairie grass litter collected in the fall from a site in Saskatchewan, Canada had N values of 1.07% (Kochy and Wilson, 1997). Whitehead (1995) reports annual yields of herbage for an intensively managed temperate grassland of 8000 to 15,000 kg dry weight per hectare with N contents of 200 to 550 kg N per hectare. While there is a large capacity for uptake in some grasslands (Whitehead, 1995) my study site produced yields that were only about 13% of reported values.

In the poplar stand, both poplar leaves and understory grass were collected. The grass component was smaller than in pasture plots due to crown closure which shaded out the understory. However exact amounts are unknown since grass and leaf mass were measured as one. Uptake from the trees was estimated from N in litterfall (Table 12). I collected 403 g·sq m^{-1} of litter that contained 3.74 g·sq m^{-1} of nitrogen. Lodhiyal and Lodhiyal (1997) determined that in 1 to 4-year-old *P. deltoides* Marsh plantations in the central Himalayan Tarai, 65-68% of N is retranslocated in poplar leaves and 61-67% of the annual uptake is allocated to the foliage. Using these values, the total uptake for my study would have been 176 kg N per hectare per year. Heilman and Stettler (1986) measured the annual leaf fall in 4-year-old hybrid poplars (*P. trichocarpa* x *P. deltoides* Bartr.) in western Washington. They reported values of 5.9 - 6.6 Mg per ha per year of annual leaf fall, with an N concentration of 1.21-1.42%, and a total weight of 80-84 kg N per ha. Kochy and Wilson (1997) found that *P. tremuloides* litter from a site in Saskatchewan, Canada had N values of 0.62%. In my study, litter mass was slightly lower than (Table 12) and N concentrations (Table 13) fall within those in the literature.

In the native riparian oak forest, as in the poplar stand, the understory vegetation was clipped and litterfall was collected. I collected 407 g·sq m^{-1} of litter that contained 5.47 g·sq m^{-1} of nitrogen (Table 12). In a northern Michigan forest, Zak et al. (1986) measured litter weights of 276 and 153 kg/ha, N concentrations of 0.76 and 0.88%, and N contents of 1.90 and 0.88 kg/ha in *Q. rubra* and *Q. alba*,

respectively. Scott and Binkley (1997) reported litterfall characteristics from several previously published studies, including 5182 and 2946 kg per ha per year with 8.5 and 7.8 g N per kg for *Q. rubra* and *Q. alba*, respectively, from the University of Wisconsin Arboretum (as published by Nadelhoffer et al., 1983). Nitrogen concentrations in *Q. garryana* found in my study were almost double those reported in the literature for *Q. rubra* and *Q. alba*. However, the quantity of litterfall collected for *Q. garryana* (Table 12) was comparable to that reported by Scott and Binkley.

Seasonal effects

Denitrification seasonal patterns were the same in all three vegetation types: highest in the winter and lowest in the summer (Table 1). These patterns reflect variation in soil moisture content (Figure 5) and thus soil O_2 depletion. Myrold (1988) found the same strong seasonal pattern of denitrification in western Oregon ryegrass and wheat fields. He measured the highest rates of denitrification in March, which corresponds with my winter sampling, with secondary peaks in the fall. Numerous others (Groffman and Tiedje, 1989; Struwe and Kjoller, 1989; Parsons et al., 1991; Whitehead, 1995) have also reported similar seasonal denitrification trends linked with seasonal soil moisture.

An interesting illustration of the importance of soil temperature was provided during the winter sampling where there was a significant increase in field denitrification corresponding to a soil temperature increase from 4.5 to 9.8° C

(Figure 4). This demonstrates that once soils become anaerobic, all other conditions being favorable, a spike in temperature can lead to increased denitrification rates. Ryden (1983) found that for denitrification to occur, soil temperatures needed to be greater than 5-8° C. Hixson, et al. (1990) concluded that soil temperature had the most important long-term effect on denitrification because denitrification rates decreased with decreasing fall soil temperatures. However others (Myrold, 1988; Parsons et al., 1991) have found no strong relationships between soil temperature and denitrification rates, most probably due to the inverse relationship of temperature with soil moisture.

Denitrification potentials were highest during the fall (Figure 8) even though field denitrification rates were not. Field denitrification rates peaked in the winter in response to a temporary warming trend (Figure 4). However the high denitrification potentials in the fall reflect long-term favorable conditions. Potentials have been shown to be a good relative index of suitable conditions for denitrification over a scale of weeks (Griffiths et al., 1982; Griffiths et al., 1983; Sinsabaugh, 1992). Thus they function as a "memory" for conditions favoring denitrification. Because potentials are assessed with no limitations, the rate of N_2O produced is proportional to the denitrifying enzyme content (Tiedje et al., 1989). Therefore potentials reveal whether denitrifying enzymes have been built up by denitrifier populations, in the recent past. Groffman and Tiedje (1989) described it as a "long-term, integrative product of multiple physical and biological factors." From this it can be concluded that high potentials in the fall reveal that conditions

have been favorable for denitrification. Most likely this is due to the release of C from litter fall and N trapped in the summer-dried soils after the first autumn rains. Alfani et al. (1983) and Groffman and Tiedje (1989) suggest that pulses of denitrification are higher in the spring and fall because there is less competition from trees for the N. They found strong links between tree activity and denitrification rates. High spring denitrification rates ended once trees leafed out and fall denitrification rates increased once leaf drop began. Groffman and Tiedje (1989) suggest that the substantial vegetative uptake of N may limit denitrification due to increased competition for nitrate. At my site, when the soil temperature increased after soils become saturated, the conditions for denitrification were optimal. Nitrate and degradable C had been accumulating in the soil and the availability of oxygen was reduced because of high moisture content. Under these conditions, a sufficient increase in temperature produced an increase in denitrification rates.

Other factors potentially limiting denitrification

pH (Table 3), moisture content and temperature were the same for all three vegetation types. This suggests that because pH, moisture, and temperature conditions were the same for all plots, these factors did not contribute to the differences in denitrification rates between the three vegetation systems. Groffman, et al. (1991) hypothesized that differences in soil pH between a forest (pH <4.5)

and grassland (pH =5.9) may have contributed to variation in denitrification rates but no such differences were measured in this study.

A slight difference in soil type exists between the pasture and poplar stand and the native riparian forest, as described in the soil survey (Knezevich, 1975). The pasture and poplar stand are on a Bashaw clay. The Bashaw soils are poorly drained and have very slow permeability. They have an apparent water table at a depth of 1 foot above the surface to 0.5 foot below the surface from November to May. Common flooding for long periods of time occurs from December to April. ("Bashaw series," 1997) Whereas the native riparian forest is on a Waldo silty clay loam. Waldo soils are also poorly drained but have slow permeability. Their apparent high water table fluctuates between the soil surface and 0.5 foot below the surface from November to May. Waldo soils are subject to occasional flooding for brief periods from January to April. ("Waldo series," 1998) So even though both soils have poor drainage, the Waldo silty clay loam has just slightly better permeability.

Sexstone, et al. (1985) found that denitrification rates were double in a clay loam soil with lower permeability and poorer drainage than in a sandy loam. Interestingly there was no denitrification response in the clay loam soil following repeated rainfall events even though NO_3^- was present in the soil. This may have been due to a lack of available carbon. Ambus and Lowrance (1991) found higher denitrification potentials in the more poorly-drained of two riparian soils. Groffman and Tiedje (1989) believe the high correlation between soil texture and denitrifying

activity were due to the water holding capacity of the smaller pored fine-textured soils.

The differences between the pasture and poplar Bashaw clays and the native forest Waldo silty clay loams were in fact very apparent in the field. The Bashaw clays were very difficult to sample. They were very sticky and very to extremely firm. In the winter, some the pasture and poplar plots were partially ponded. The Waldo silty clay loams were always much easier to sample than the Bashaw clays. They were very friable and were seemingly better aerated. From these field observations, it would seem that while infiltration would be slower in the pasture and poplar soils, anaerobic conditions would occur more frequently. Thus the pasture and poplar soils could be better sites for denitrification activity.

Conclusions

Denitrification was greatest in the pasture and poplar soils with mean extrapolated annual rates of 8.3 and 9.1 kg N/ha·yr, respectively. Native oak forest soils only removed 0.23 kg N/ha·yr. Granted, these rates probably could not be maintained for extended periods because ultimately some limiting factor would be reached. Conversely, nitrogen uptake was greatest in the native forest plots. Annual uptake rates were 54.7, 37.4, and 25.6 kg N/ha·yr in the native forest, poplar stand, and pasture, respectively. Thus uptake was greater than denitrification in all vegetation types.

Denitrifying populations may be more prevalent in the pasture and poplar stand soils, resulting in higher field denitrification rates and higher denitrification potentials than the native riparian oak forest. Even though DOC concentrations were significantly higher in the native forest soils, the forest soils still had significantly lower denitrification potentials. There are several possible explanations for these differences: (1) the availability of readily degradable organic matter, (2) denitrifying populations may be lower in these plots, or (3) the native forest soils are less likely to become anaerobic. The fact that the same patterns hold throughout the year argues against the last alternative. DOC concentrations were actually higher in forest soils than in other treatments but it is not known what fraction of this carbon is readily degradable by microorganisms. A comparison between denitrification potentials in soils amended with nitrate and nitrate plus glucose showed that glucose stimulated denitrification to a greater extent in the pasture and poplar soils than in the native forest soils. This led me to conclude that lower denitrification rates in the native forest soils were due to depressed denitrifying populations.

Differing limitations may have been the cause for no significant denitrification response to fertilization. The pasture and poplar soils were C limited and the native forest soils were limited by inadequate denitrifying populations.

Vegetative uptake of N was greatest in the native oak forest. However, simply measuring leaf production, while providing a relative comparison, vastly underestimated actual uptake rates especially on the forested sites. Further research

with greater sample size and measurement of wood production is necessary to more accurately quantify uptake rates.

A possible lack of readily available C in the organic C rich native riparian oak forest emphasized the need for maintaining appropriate vegetation in a riparian buffer zone. To optimize nutrient removal rates, vegetation in buffer zones should be able to take up entering excess nutrients as well as provide a preferred C source for denitrifying organisms. Because the native oak forest took up more N and the pasture and poplar sites denitrified more N, an integrated, multi-zone riparian buffer area with all three vegetation types may serve as the best riparian nutrient removal solution.

Management Implications

My study has examined two of the more important mechanisms utilized in the prevention of N enriched stream water, vegetative uptake and denitrification. I had only one site at the Oregon State University dairy farm, therefore my scope of inference should be limited to similar sites, with similar soils in the Willamette Valley, Oregon. What can be learned from this study to help in the design of riparian buffer zones for the Willamette Valley? First, a coupled system of denitrification and vegetative uptake is necessary to provide maximum year round nitrate removal capabilities. The woody vegetation grows primarily in the spring and early summer to remove nutrients. Grasses can grow almost year round, except for late summer, to remove nutrients. Denitrification occurs primarily in the fall and

winter. The combination of the two mechanisms provides for year-round complementary nutrient removal.

Secondly, poplar can work very well in riparian buffer strips. In my study, the poplar presumably provided a better carbon source than the oak trees, since denitrification rates were higher in the poplar stand. Haycock and Pinay (1993) found that poplar (*P. italica*) riparian strips retained more NO_3^- in the winter than grassed riparian strips. They hypothesized that the poplar provided a better source of C for soil microbes. Besides being fast-growing, and therefore able to take up a considerable amount of nutrients, poplars are adapted to riparian soils, and can provide economic benefits (Withrow-Robinson et al., 1994). Establishment in riparian areas can be difficult however, if proper precautions are not followed. Beaver, deer, livestock, and voles will browse or girdle the young trees so control strategies, such as fencing, will need to be implemented. Also, aggressive weed control, normally required to establish poplar stands, will need to be applied with caution so as to prevent possible stream contamination with herbicides. Alternatively, other weed control strategies, such as mechanical methods, could be used. If there will be any slope within the poplar buffer zone, bands of grass or other erosion control materials may be necessary to prevent stream siltation. During the first two years of stand establishment, the poplar will not consume appreciable amounts of N (McLaughlin et al., 1985; Heilman and Fu-Guang, 1993). Alternative control strategies to limit leaching, such as grass strips, may need to be enacted

until the stand ages. Once established however, poplar seems to be an ideal tree species component for riparian buffer strips.

Vegetation on a site is essential to provide a carbon source for denitrification. As seen in my study, the carbon must be an available form for the denitrifiers. Sites can be managed to provide suitable forms of C. Besides poplar and grass litter, addition of alfalfa, straw and fresh crop residues (Beauchamp et al., 1989) have been shown to increase denitrification rates.

Finally, and most importantly, choosing where to locate riparian buffer zones is critical. Fortunately many riparian areas provide ideal sites for denitrification, with frequent flooding and high water tables creating anaerobic conditions. Fine textured soils, like those commonly found in the Willamette Valley, also tend to create anaerobic micro-sites. Ultimately however, location is determined by a water quality limitation in the stream.

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