Environmental Parameters Regulating Gaseous Nitrogen Losses from Two Forested Ecosystems via Nitrification and Denitrification†

ERIC A. DAVIDSON[1]‡* AND WAYNE T. SWANK[2]

Department of Forestry, North Carolina State University, Raleigh, North Carolina 27695-8002,[1] and U.S. Department of Agriculture Forest Service Southeastern Experiment Station, Coweeta Hydrologic Laboratory, Otto, North Carolina 28763[2]

Gaseous N losses from disturbed and reference forested watersheds at the Coweeta Hydrologic Laboratory in western North Carolina were studied by in situ N_2O diffusion measurements and laboratory incubations throughout a 10-month period. Soil temperature, percent base saturation, and water-filled pore space accounted for 43% of the variation in in situ N_2O diffusion measurements. Laboratory incubations distinguished the gaseous N products of nitrification and denitrification. Nitrifying activity, ambient NO_3^-, and nitrification N_2O were positively correlated with percent base saturation. However, differences between watersheds in soil N substrate caused by presence of leguminous black locust in the disturbed watershed were confounded with differences in soil acidity. Denitrification was most strongly affected by soil moisture, which in turn was determined by precipitation events and slope position. Gaseous N losses from well-drained midslope and toeslope landscape positions appeared to be minor relative to other N transformations. Favorable conditions for denitrification occurred at a poorly drained site near the stream of the disturbed watershed. Laboratory incubations revealed high rates of NO_3^- reduction in these soils. We speculate that the riparian zone is a major site of depletion of NO_3^- from the soil solution via denitrification.

Studies of gaseous nitrogen losses from agricultural systems are abundant, but few studies have addressed losses from forested ecosystems (5, 12, 17, 21). Difficulty in carrying equipment into forested sites has hampered these efforts, but the paucity of studies in forested relative to agricultural ecosystems also results from differences in the economic value of determining the fate of N. However, as intensive silviculture emulates agriculture by becoming increasingly reliant on N fertilizers, an understanding of the processes regulating nitrification and denitrification in forested ecosystems will become valuable.

Environmental parameters which affect nitrification and denitrification have been identified in laboratory studies (4, 6, 16). The relative importance of these parameters has been investigated in field studies of agricultural and grassland systems (14, 18, 19). The objective of this study was to examine the relative importance of selected environmental parameters on gaseous N losses in forested ecosystems. Specifically, the effects of soil temperature, acidity, redox potential, moisture, inorganic N, total N, available C, and total C were examined.

MATERIALS AND METHODS

Study sites and sampling regime. Study sites at the U.S. Department of Agriculture Forest Service Coweeta Hydrologic Laboratory are described in detail in the accompanying paper (2). Two watersheds (WSs) were studied. (i) WS18 (reference WS) supported an uneven-aged, aggrading, mixed-hardwood forest that had not undergone major disturbance since the chestnut blight in the late 1920s. (ii) WS6 (disturbed WS) supported an 18-year-old mixed hardwood

forest dominated by declining black locust (*Robinia pseudoacacia* L., Fabaceae); disturbance history on WS6 includes clear cutting, liming, fertilization, conversion to grassland, herbicide treatments, and a recent infestation by the locust stem borer (*Megacyllene robiniae* Forster). Streambank and toeslope positions were identified on both WSs, and a midslope area dominated by black locust was also studied in the disturbed WS. Within each of these study areas, three soil sampling sites and adjacent frames for measuring N_2O diffusion in situ were established. Because of spatial heterogeneity, the three sampling sites within each area were not considered true replicates in statistical analyses.

Soil sampling and in situ N_2O measurements were carried out on a routine bimonthly basis from September 1984 through July 1985. More intensive sampling before and after a major precipitation event was conducted at the midslope locust site during July 1985.

Gaseous N determinations. In situ N_2O diffusion was measured with closed covers, and estimates of nitrification N_2O, denitrification N_2O, and denitrification N_2 were determined from laboratory incubations under three levels of C_2H_2 partial pressure and at field soil temperatures, as described in the companion paper (2). At each date and sampling site, 12 cores (2.5-cm diameter, 6 cm deep) were composited in plastic bags, returned to the laboratory on ice, and stored at 4°C. All analyses on field-moist soils were conducted within 1 week of sampling. Root fragments and pebbles were removed by hand to the extent practical.

Edaphic parameters. Soil temperature was measured with soil thermometers inserted to 6 cm below the mineral soil surface. Redox potential (E_h) was determined in situ by constructing platinum electrodes (10), inserting the electrodes 3 cm below the mineral soil surface, placing a calomel reference electrode in contact with the soil, reading E_h from a portable pH meter, and adding 244 mV to correct for the redox potential of the reference electrode. Measurements

TABLE 1. Multiple regression models[a]

Dependent Variable	Independent variable[b]	Cumulative R^2
In situ N_2O[c]	$-0.326 + 0.047\text{Temp} + \epsilon$	0.25
	$-0.588 + 0.047\text{Temp} + 0.004\text{BS} + \epsilon$	0.32
	$-1.034 + 0.055\text{Temp} + 0.005\text{BS} + 0.006\text{WFPS} + \epsilon$	0.43
Nitrification N_2O[c]	$-1.045 + 0.011\text{BS} + \epsilon$	0.51
	$-1.402 + 0.010\text{BS} + 0.028\text{Temp} + \epsilon$	0.59
Denitrification N_2O[c]	$-1.455 + 0.022\text{WFPS} + \epsilon$	0.66
	$0.249 + 0.021\text{WFPS} - 0.003E_h + \epsilon$	0.71
Denitrification N_2[c]	$-1.325 + 0.020\text{WFPS} + \epsilon$	0.44
	$0.849 + 0.019\text{WFPS} - 0.004E_h + \epsilon$	0.50
NP	$-29.22 + 0.92\text{BS} + \epsilon$	0.44
	$-65.93 + 0.98\text{BS} + 0.10\text{available C} + \epsilon$	0.73
Ambient NO_3^-	$0.653 + 0.091\text{NP} + \epsilon$	0.58
	$-1.388 + 0.090\text{NP} + 0.164\text{Temp} + \epsilon$	0.62

[a] All models are statistically significant at $\alpha = 0.01$.

[b] All independent variables included are significant at $\alpha = 0.01$.

[c] Gaseous N estimate data are log transformed.

from seven electrodes were made per site. Electrodes were removed and cleaned between sampling dates.

All other measurements were made in the laboratory on the composite soil samples described above. Soil moisture was determined gravimetrically by drying for 24 h at 105°C. Ambient NH_4^+ and NO_3^- were determined by duplicate extraction of 10-g field-moist soil samples in 50 ml of 2 M KCl and colorimetric analysis of filtered extracts with a Technicon Autoanalyzer. Available C was estimated by measuring CO_2 liberated during a 7-day aerobic incubation of triplicate 10-g field-moist soil samples at 20°C (E. A. Davidson, L. F. Galloway, and M. K. Strand, Commun. Soil Sci. Plant Anal., in press). Nitrogen mineralization potentials and nitrification potentials were estimated from changes in NH_4^+ and NO_3^- concentrations after 30-day aerobic incubations of duplicate 10-g field-moist soil samples at 20°C. Water-filled pore space (WFPS) was determined from gravimetric moisture content, bulk density, and an assumed 2.65 particle density (23). Standing water caused WFPS to exceed 100% on two occasions.

The remaining soil was air dried and passed through a 2-mm sieve. The air-dried, sieved samples collected throughout a year from a given site were then composited. pH was measured with a glass electrode, and exchangeable acidity, cation exchange capacity (CEC), and percent base saturation (BS) were determined with Mehlich III by the North Carolina Department of Agriculture, Agronomic Division, Soil Testing Laboratory. Total N was determined by using a micro-Kjeldahl digestion procedure (Coweeta files, unpublished manuscript). Total C was determined by combustion in a Leco total C analyzer, which uses infrared spectroscopy to measure liberated CO_2.

Statistical analyses. Multiple regression models were evaluated by PROC STEPWISE of SAS (20). The three laboratory estimates of gaseous N production and in situ N_2O measurements were considered as dependent variables. The edaphic parameters listed above were considered as independent variables. The factors regulating nitrifying activity were also examined by considering ambient NO_3^- and nitrification potential as dependent variables with the remaining edaphic parameters as independent variables. Four criteria were employed for selecting the best models: (i)

maximizing the R^2 value, (ii) requiring significance at $\alpha = 0.05$ for each independent variable, (iii) minimizing covariation among independent variables, and (iv) affording meaningful interpretations.

Site variability was investigated by analysis of variance with PROC GLM of SAS (20). Only data from the toeslope, mixed hardwood and midslope, locust areas of the disturbed WS were considered, using the following model: $Y = \beta_0 + \text{date} + \text{area} + \beta_1 X(\text{area}) + \epsilon$, where Y is one of the estimates of gaseous N, the date is the class variable for sampling date; the area is the class variable for sampling area (i.e., slope position), $X(\text{area})$ is a continuous variable for an environmental parameter (X) nested within the sampling area, and ϵ is the error term.

RESULTS

In situ N_2O diffusion. Soil temperature, BS, and WFPS accounted for 43% of the variation in in situ N_2O diffusion rates (Table 1). Exchangeable acidity and pH were strongly correlated with BS ($r = -0.91$ and $r = 0.98$, respectively; significant at $\alpha = 0.01$) and could be substituted for BS in all of the models in Table 1 with only a minor effect on the R^2 values. Reference WS sites, where BS was low, generally exhibited low N_2O diffusion rates, and low temperatures generally reduced rates within sites (Fig. 1). Temperature reflects seasonal variation, whereas BS (or acidity) reflects site variation. Rates of N_2O diffusion also increased as soil moisture increased across both sites and dates.

Nitrification N_2O. Temperature and BS also accounted for 59% of the variation in the laboratory estimate of nitrification N_2O (Table 1). In contrast to the model for in situ N_2O, BS accounted for most of the variation; temperature was also significant, but WFPS did not significantly contribute to reduction in sums of squares. Nitrification N_2O also showed significant positive correlations with ambient NO_3^-, nitrification potential (NP), and mineralization potential (Table 2).

Denitrification N_2O and denitrification N_2. WFPS and E_h accounted for 71% of the variation in denitrification N_2O and 50% of the variation in denitrification N_2 (Table 1). The maximum observed rates of gaseous N production in the laboratory differed among processes, with denitrification

TABLE 2. Correlation coefficients (r) among gaseous N estimates and edaphic parameters

Parameter	WFPS	E_h	BS	Temp	NO_3^-	NH_4^+	NP	Mineralization potential	Available C	Total C	Total N
In situ N_2O	0.19	−0.04	0.33^a	0.54^a	0.51^a	−0.09	0.39^a	0.37^a	0.01	−0.14	−0.09
Nitrification N_2O	0.18	−0.35^a	0.73^a	0.36^a	0.75^a	−0.32^a	0.54^a	0.50^a	−0.06	0.02	0.09
Denitrification N_2O	0.81^a	−0.35^a	0.20	0.02	0.17	0.07	0.33^a	0.30^a	0.23^b	0.06	0.08
Denitrification N_2	0.67^a	−0.36^a	−0.03	−0.03	−0.16	0.12	0.05	0.02	0.03	−0.11	−0.12
WFPS		−0.17	0.11	−0.18	0.18	0.19	0.37^a	0.36^a	0.35^a	0.14	0.15
E_h			−0.45^a	−0.00	−0.19	0.10	−0.29^a	−0.25^b	−0.04	−0.10	−0.17
BS				0.06	0.71^a	−0.16	0.67^a	0.63^a	−0.06	−0.11	0.08
Temp					0.24^b	−0.09	0.10	0.11	0.06	−0.07	−0.07
NO_3^-						−0.19	0.77^a	0.74^a	0.26^b	0.25^b	0.33^a
NH_4^+							0.15	0.19	0.42^a	0.10	0.09
NP								0.98^a	0.24^b	0.33^a	0.44^a
Mineralization potential									0.59^a	0.35^a	0.48^a
Available C										0.73^a	0.72^a
Total C											0.92^a

^{a} Statistically significant at $\alpha = 0.01$.
^{b} Statistically significant at $\alpha = 0.05$.

N_2O and denitrification N_2 being 1 and 2 orders of magnitude higher than nitrification N_2O, respectively. Denitrification N_2O was positively correlated with ambient NO_3^-, with the exception of one site that exhibited the highest laboratory denitrifying activity and low levels of ambient NO_3^- (Fig. 2).

Nitrifying activity. Most of the observed variation in NPs could be accounted for by variation in BS and available C (Table 1). Disturbed WS soils, which were high in BS, exhibited high NPs. However, large residuals in the NP versus BS regression for disturbed WS samples (Fig. 3A, sites A through I) indicate that another variable related to seasonal differences also affected NP. Variation in available C reflected both slope position (stream site soils having higher levels) and seasonal changes in soil moisture (available C increased with increasing soil moisture at all sites). The reference WS soils (sites J through O) exhibited low NP regardless of available C, whereas the disturbed WS soils (sites A through I) exhibited a significant correlation between NP and available C (Fig. 3b). Temperature and NP accounted for 62% of the variation in ambient NO_3^- (Table 1).

Site variability. Understory vegetation and ground cover varied within each sampling area. Patches of fescue, appar-ently residual from grassland conversion, were particularly notable on the disturbed WS. In both the midslope, locus and the toeslope, mixed hardwood sampling areas, one of the three sampling sites was located on patches of fescue. These fescue sites (sites C and E in all figures) consistently exhibited the highest in situ diffusion measurements and the highest laboratory N_2O estimates for both areas. When variation due to season and overstory vegetation were partitioned out, variation in BS within these two sampling areas was significantly correlated ($\alpha = 0.05$) with both in situ N_2O and denitrification N_2O variation. Soils supporting patches of fescue had the highest BS of all sites studied.

Effects of precipitation. The effects of a major precipitation event were studied after a dry period in July at the midslope, locust area, where high rates of N_2O diffusion had been observed during other seasons. In situ N_2O diffusion was determined before the rain, the morning after 11 mm of precipitation, 6 days later after 51 mm more precipitation
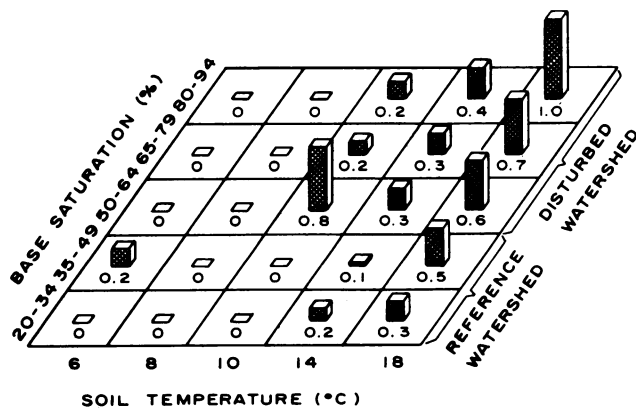

FIG. 1. Effects of temperature and base saturation on rates of in situ N_2O diffusion. Bars represent means of transformed [log (X + 1)] diffusion rates for temperature-BS combinations.
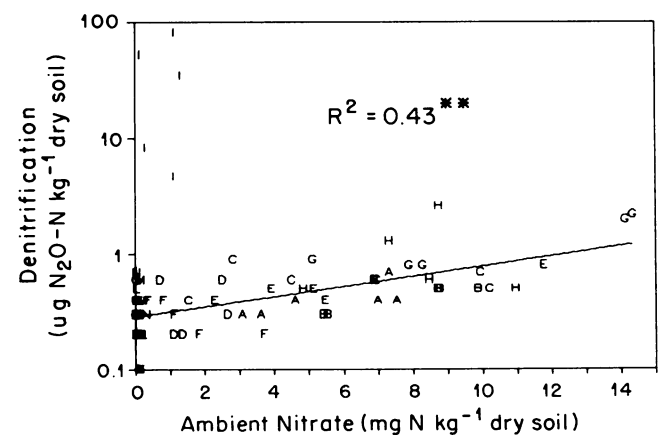

FIG. 2. Regression of denitrification N_2O estimate versus ambient NO_3^- concentration. Measurements were taken from September 1984 through July 1985 from the midslope, locust area of the disturbed WS (sampling sites A, B, and C), toeslope, hardwood area of the disturbed WS (D, E, and F), stream area of the disturbed WS (G, H, and I), toeslope area of the reference WS (J, K, and L), and the stream area of the reference WS (M, N, and O). R^2 was significant at $\alpha = 0.01$.
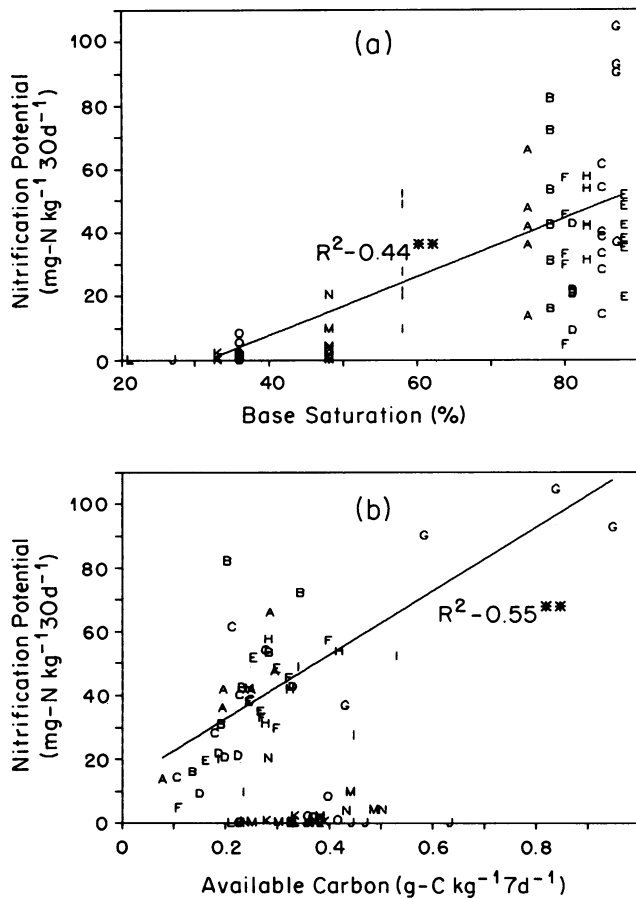
FIG. 3. Regressions of NP versus BS (a) and available carbon (b). The regression line for NP versus available C was calculated for disturbed WS samples only (sites A through I). Symbols are the same as in Fig. 2. R^2 was significant at $\alpha = 0.01$ for both panels.

have demonstrated a similar dominating effect of soil moisture as affected by slope position in a forested ecosystem.

Regardless of WS management history, the highest rates of N loss due to denitrification are likely to be found in riparian zones. Not only are soils wetter near the stream than upslope (9), but also cumulization enriches upper horizons of riparian zone soil with organic matter and thus increases the potential for microbial respiration and oxygen depletion. Although E_h and WFPS are usually related, E_h can reflect differences in O_2 consumption as well as O_2 diffusion. Therefore, both WFPS and E_h were included in the models accounting for most of the variation observed in denitrification estimates (Table 1).

The overwhelming effect of WFPS may have masked the effect of NP on denitrifying activity which has been previously observed (17). Although well-drained sites exhibited a wide range of NPs, we observed very low laboratory denitrification rates in these soils. Therefore, the opportunity to correlate these two parameters across this data subset was poor. The correlation between NP and denitrification N_2O was significant, but the r value was low (Table 2).

Soil moisture also affected many other edaphic parameters that relate to microbial activity. Significant positive correlations between WFPS and available C, NP, and mineralization potential (Table 2) suggest that soil moisture not only affects O_2 diffusion, but also directly stimulates microbial activity. The September 1984 sample date followed a long dry period, resulting in the very low values observed for these parameters. In light of this covariation of edaphic parameters, it is difficult to identify regulating mechanisms for microbial processes. For example, the inclusion of available C in the model for NP (Table 1) may result from sensitivity of the available C bioassay to moisture differences rather than any particular role that available C plays in the nitrification process.

The importance of black locust in the N cycle of successional eastern hardwood forests has been demonstrated by symbiotic N fixation estimates of 30 kg of N ha^{-1} year^{-1} (1). Presumably, rapid turnover of N-rich black locust tissue caused by the stem borer infestation would also influence microbial N transformations. Evidence for this effect can be seen in an 80-fold increase in mean annual hydrologic export of NO_3^- from the disturbed WS relative to the reference WS. Mineralization of black locust tissue probably provides sufficient NH_4^+ to permit high rates of nitrification in the

during that period, and 3 days after the rain stopped. Rates of N_2O diffusion increased dramatically immediately after the precipitation. The high rate remained through the following 6-day rainy period and declined to prerain levels within 3 days after the rain ceased (Fig. 4). Laboratory estimates of both nitrification N_2O and denitrification N_2O were also higher for soils sampled immediately after the precipitation.

DISCUSSION

Observational data must be interpreted in light of the range of sites and variables considered. For example, Melillo et al. (12) found a correlation between ambient NO_3^- and denitrification potentials across a series of well-drained sites that represented a successional chronosequence. We found a similar relationship across well-drained sites that exhibited low denitrification rates, but the highest denitrification rates occurred at a poorly drained site with low ambient NO_3^- (Fig. 2). Although NO_3^- is important as a denitrification substrate, soil aeration appears to be extremely important in controlling the rate at which NO_3^- is reduced. Therefore, we suggest that slope position and its effect on soil drainage within a WS must be considered in addition to differences among WSs. The regulating influence of soil moisture as affected by precipitation (19) and irrigation (18) has been well demonstrated for denitrification in agricultural systems. We
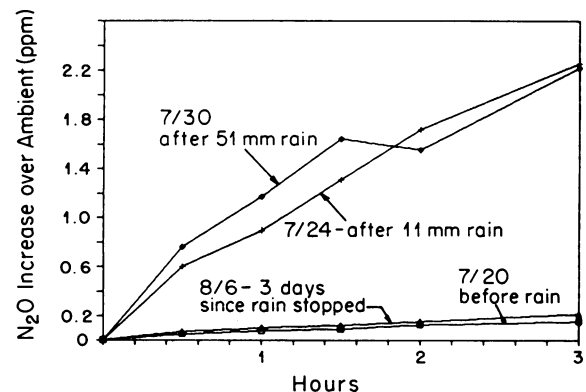

FIG. 4. Intensive sampling of in situ N_2O diffusion before and after a precipitation event in July 1985 at the midslope, locust area of the disturbed WS. Concentrations of N_2O within the soil cover are plotted against the time the cover was in place.

DENITRIFICATION –N_2O

NITRIFICATION–N_2O

PLANT UPTAKE

LYSIMETER
$[NO_3^-] = 5.4$ mg L^{-1}

LEACHING BELOW MAJOR ROOTING ZONE (60 cm.)

$N_2 + N_2O$ DIFFUSION FROM SOIL

N_2O DEGASSING

60 cm

NO_3^-

NH_4^+

PLANT UPTAKE

STREAM $[NO_3^-] = 0.8$ mg L^{-1} , N_2O

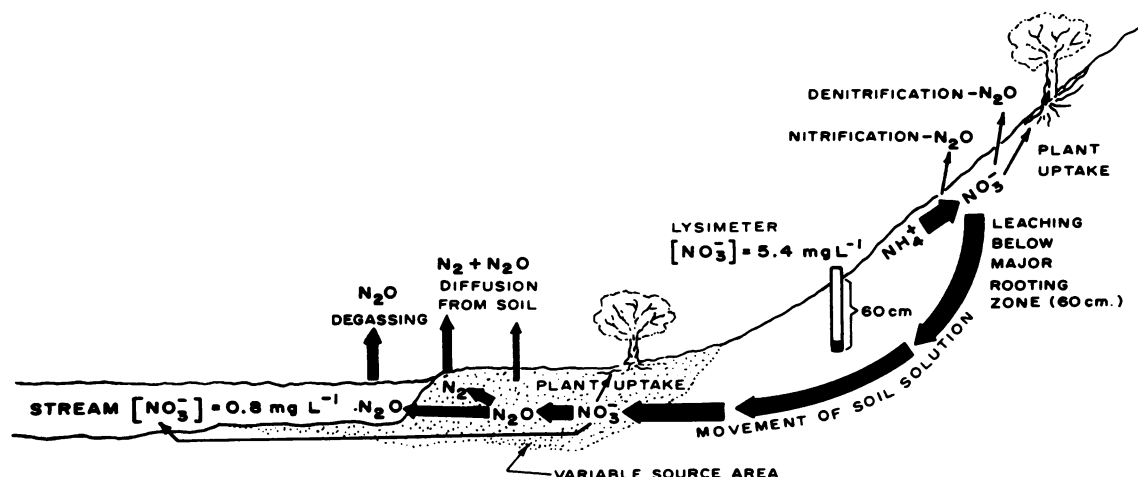N_2O　NO_3^-

MOVEMENT OF SOIL SOLUTION

VARIABLE SOURCE AREA

FIG. 5. Proposed relative importance of gaseous N loss pathways in the disturbed WS. Thickness of arrows corresponds to relative flux magnitude. Data for lysimeter NO_3^- solutions are from Montagnini (Ph.D. thesis).

disturbed WS, whereas intense competition among plants and microorganisms for inorganic N probably precludes nitrification in the mature, aggrading reference WS (13, 22). However, differences in BS across sites could also account for most of the observed variability in nitrifying activity (Table 1). Indeed, acidity appears to be important both between and within WSs, since variation in BS across sampling sites within the well-drained areas of the disturbed WS was correlated with in situ N_2O measurements and denitrification N_2O estimates. Unfortunately, differences in successional development and vegetation type between the two WSs are confounded with differences in soil acidity. Therefore, the effects of acidity and black locust mortality upon nitrification and denitrification cannot be separated. Both factors probably affect relative rates of N transformations.

Nitrifying activity and N_2O production from nitrification are obviously related, but the effect of acidity on NO_3^- versus N_2O production by nitrifying bacteria appears to differ. Whereas autotrophic nitrification in general is favored by circumneutral conditions (16), N_2O production by nitrifying bacteria may be enhanced by acidic conditions (11). At first, it appears that the results reported here are contradictory to those of Martikainen (11), since our estimates of nitrification N_2O are positively correlated with BS. However, we again emphasize that our results are observational across soils exhibiting a broad range of nitrifying activity. Nitrification N_2O increased as NPs increased across sites. Differences in nitrifying activity across sites appeared to be more important than differences in factors that affect NO_3^-/N_2O ratios produced by nitrification. In contrast, Martikainen experimentally manipulated a single soil sample, so that only those factors affecting the NO_3^-/N_2O ratio varied.

Similarly, the present study revealed no clear relationship between nitrification N_2O and WFPS, whereas the proportion of NH_4^+ oxidized by nitrifiers which becomes reduced to N_2O should increase with increasing soil moisture (6) and decreasing O_2 partial pressure (8). Again, although this relationship is probably true for a given soil sample, differences in overall nitrifying activity across sites in the present study appeared to affect N_2O production more than did differences in factors affecting ratios of NO_3^- production to N_2O production.

In situ N_2O diffusion was strongly affected by soil temperature, but laboratory estimates of denitrification were not correlated with incubation temperature. The temperature effect, however, is confounded with moisture differences. Winter months at Coweeta provide both the lowest temperatures and the wettest soil conditions. Diffusion of gases is restricted by water-saturated pore spaces, and N_2O solubility increases with decreasing temperature, thus contributing to the low diffusion rates observed in winter. Denitrification, however, is enhanced by wet conditions but retarded by low temperatures (3). In situ measurements in the present study cannot distinguish between the processes of N_2O diffusion and N_2O production. In contrast, laboratory incubations of small soil samples at simulated field temperatures provide estimates of biological activity under laboratory conditions with only minimal errors associated with restriction of diffusion. Laboratory rates of biological denitrification in very wet soil samples collected in December and incubated at 8°C were similar to rates observed in drier soil samples collected in July and incubated at 18°C. Apparently, the effects of temperature and moisture roughly cancelled each other. Although we cannot demonstrate that similar high rates of denitrification were occurring in situ during winter months with the N_2O failing to diffuse to the soil surface, this speculation is consistent with observations of high rates of N_2O diffusion during spring thaws in Wisconsin (5, 7).

Diffusion of N_2O from upslope positions increased after a precipitation event, but the effect on these well-drained soils was short lived (Fig. 4). If extrapolated across an entire hectare and throughout an entire year, the highest observed rate of N_2O diffusion from a well-drained site after the precipitation event studied would be equivalent to 15 kg of N ha^{-1} year^{-1}. Since losses are 1 to 2 orders of magnitude lower during drier periods during the summer and colder periods during the winter, annual losses from these well-drained sites via N_2O diffusion are probably at least 1 order of magnitude lower than the highest projected rate, thus rendering N_2O loss by diffusion insignificant relative to other N transformations in this disturbed ecosystem. The highest observed rate of N_2O diffusion from any of the reference WS sites, when similarly extrapolated, was equivalent to 0.4 kg of N ha^{-1} year^{-1}. Actual gaseous N losses from this middle-aged, aggrading forest are also probably at least 1 order of magnitude below this maximum estimate. Laboratory incu-

bations indicated that N_2 production was not important in the reference WS or in well-drained soils of the disturbed WS.

In contrast, gaseous N losses in riparian zones of the disturbed WS are more difficult to quantify and are potentially of greater magnitude. At the wettest sites, N_2 may be the main product of denitrification as it was in our laboratory incubations. Furthermore, diffusion of N_2O may be impeded in wet soils so that N_2O does not escape to the atmosphere until soil water reaches the stream. Quantifying N losses in the riparian zone was not possible, but riparian zone soils from the disturbed WS exhibited high rates of denitrification in the laboratory. Since these same soil samples also exhibited very low ambient NO_3^- levels, denitrification in the riparian zone had apparently depleted soil NO_3^- relative to upslope concentrations.

Although hydrologic export of NO_3^- is elevated in the disturbed WS relative to the reference WS, stream water NO_3^- concentrations are still 1 order of magnitude lower than soil solution concentrations measured by porous cup lysimeters at 60 cm depth at midslope positions in the disturbed WS (F. Montagnini, Ph.D. thesis, University of Georgia, Athens, 1985). Either most of this NO_3^- must be taken up by plants as soil water passes through surface horizons near the stream—an unlikely process due to low oxygen availability for roots when the variable source area is saturated—or it must be reduced before entering the stream (Fig. 5). Low estimates of gaseous N production in toeslope and midslope soils and high estimates in stream-side soils support the hypothesis that the riparian zone is a major site of depletion of soil solution NO_3^- via denitrification. Similar conclusions have been reached for forested riparian zones that receive agricultural drainage (10, 15). The present study suggests that much of the NO_3^- produced within a disturbed forested ecosystem is reduced in the riparian zone.

ACKNOWLEDGMENTS

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