High rates of nitrification and nitrate turnover in undisturbed coniferous forests

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THE importance of nitrate (NO_3^-) in the internal nitrogen cycle of undisturbed coniferous ecosystems has not been widely recognized[1,2]. Nitrate concentrations in soils from these forests tend to be low, and assays measuring net nitrification usually show exceedingly slow rates[3,4]. It may be, however, that microbial assimilation of NO_3^- is substantial in these soils, and that net nitrification rates greatly underestimate gross rates[5]. Here we use a ^{15}N isotope-dilution technique in intact soil cores to measure gross rates of nitrification and microbial assimilation of NO_3^- in eleven undisturbed forest ecosystems of New Mexico and Oregon. We found that gross nitrification rates were surprisingly high in all of the forests examined. Net nitrification rates poorly predicted gross rates because the soil microbial communities had the capacity to assimilate almost all of the NO_3^- produced. To our knowledge, this is the first report of gross nitrification and NO_3^- assimilation rates in intact soil samples from a large number of contrasting forest ecosystems. Our results contradict previous assumptions that nitrification rates are low in mature coniferous forests and suggest that current models greatly underestimate the role of the microbial community in preventing NO_3^- loss.

Studies examining nitrogen retention in forest ecosystems have focused on net nitrification, net mineralization, microbial assimilation of ammonium (NH_4^+), and plant uptake; however, microbial assimilation of NO_3^- has been largely ignored. Early studies showed that soil microbial communities prefer NH_4^+ to NO_3^- as a source of nitrogen[6], and measurable quantities of NH_4^+ are almost always present in soils. Therefore, it has generally been assumed that NH_4^+ will be the nitrogen source for microbes, and that microbial assimilation of NO_3^- will be minimal[7,8].

Microbial assimilation of NO_3^- has been discounted as a significant process controlling NO_3^- pool sizes and as a mechanism of nitrogen retention following disturbance in forest ecosystems[3,9,10], but we considered that substantial amounts of microbial assimilation of NO_3^- might occur in these systems because: high rates of carbon addition to soils are likely to result in nitrogen limitation to the microbial biomass; high spatial variability in carbon inputs is likely to result in microsites of mineralization and nitrification adjacent to microsites of intense immobilization; and fungal populations dominating these soils are capable of translocating NO_3^- from microsites with high mineralization and nitrification to microsites with high carbon availability.

We evaluated the importance of nitrification and microbial assimilation of NO_3^- by measuring rates in eleven forest soils along an elevational transect in the Tesuque watersheds of northern New Mexico[3,9,10] and a latitudinal transect (at about 44° N) extending 220 km from the Oregon coast to the east side of the Cascade Mountains in central Oregon[11,12] (Table 1). The ecosystems along these two transects represent a wide range of forest ecosystems and span almost the entire range of above-ground net primary production that occurs in forests of North America (1 to 13 Mg ha^{-1} yr^{-1})[11,12].

Gross rates of nitrification and NO_3^- consumption were measured in late spring (May and June) and late summer (August) using $^{15}NO_3^-$ isotope dilution[13]. Rates were measured during *in situ* incubation of intact core samples and homogenized samples from the 0–15-cm mineral soil layer. Homogenized samples were incubated with and without acetylene (at 10 kPa): to verify the validity of isotope dilution measurements; to evaluate the relative importance of autotrophic compared with heterotrophic nitrification; and to determine how much NO_3^- consumption was due to denitrification. Rates of microbial assimilation of NO_3^- were also verified by measuring microbial biomass ^{15}N and total soil organic ^{15}N at the end of the incubations.

Gross nitrification rates in intact soil cores were high at all eleven forest sites (Table 2), ranging from 25 mg N m^{-2} d^{-1} in the New Mexico ponderosa pine site during summer, to >300 mg N m^{-2} d^{-1} in the Douglas-fir site during spring. These rates are one to two orders of magnitude higher than rates of nitrogen input from litterfall[3,11], indicating that cycling of NO_3^- through the soil microbial community is extremely rapid relative to plant nitrogen uptake. High nitrification rates occur in these forests in spite of low soil pH (Table 1), low nitrogen deposition rates, and low availability of nitrogen. Wet deposition of nitrogen at each of these sites averaged <2 kg N ha^{-1} yr^{-1} during the past decade[14].

Comparison of nitrification rates determined by isotope dilution in homogenized samples with rates determined by acetylene inhibition verified that rate estimates from isotope dilution are reliable ($k_a = -0.08 + 0.97 k_N$, where k_N is the gross nitrification rate determined by ^{15}N isotope dilution (in mg N kg^{-1} d^{-1}), and k_a is the rate calculated from the difference between net NO_3^- consumption with and without acetylene; $r^2 = 0.67$; $n = 34$). Acetylene inhibition also showed that, in spite of low soil pH, almost all of the nitrification was due to the activity of autotrophic

rather than heterotrophic nitrifier populations. Only soil at the Oregon ponderosa pine site had significant gross nitrification rates following exposure to acetylene ($0.30\ mg\ N\ kg^{-1}\ d^{-1}$; $P < 0.025$).

In spite of high nitrification rates, NO_3^- concentrations were low in almost all of the forest soils examined (Table 1). With the exception of the pinyon/juniper and red alder/Douglas-fir sites, ambient soil NO_3^- concentrations were $<0.6\ mg\ N\ kg^{-1}$; NO_3^- concentrations in more than half of the plots at the Oregon ponderosa pine and western hemlock/sitka spruce sites were below detection limits ($<0.05\ mg\ N\ kg^{-1}$). Because of small NO_3^- pools and high flux rates, mean residence times for NO_3^- pools ranged from <1 h in the Oregon ponderosa pine site in spring and the western hemlock/sitka spruce site in summer, to 1.47 days in the western juniper site in summer (Table 2).

Net nitrification rates provided little indication of the high rates of nitrification that were occurring at the sites. Mean net nitrification rates were negative in 13 of 19 cases (Table 2). These net rates, determined during 1-day incubations, encompass the range of net nitrification rates determined over longer incubation periods in other undisturbed mature temperature forests (-2 to $41\ mg\ N\ m^{-2}\ d^{-1}$) (calculated from data in ref. 15, assuming a 180-day active period). Net nitrification poorly predicted gross nitrification rates because in most soils all of the NO_3^- produced was rapidly assimilated by microorganisms.

Measurements made of extractable microbial ^{15}N, soil organic ^{15}N, and denitrification verified that the NO_3^- consumption in these soils was almost completely due to microbial assimilation. Isotope dilution estimates of NO_3^- consumption were strongly correlated with rates of accumulation of ^{15}N in the chloroform-labile microbial biomass nitrogen pool and in the soil organic nitrogen fraction ($r^2 > 0.65$; slopes of both regression lines were not significantly different from 1.0 at $P \leq 0.05$). Denitrification, measured in homogenized samples exposed to C_2H_2, accounted for <4% of NO_3^- consumption at all sites except the Douglas-fir site in spring, where it accounted for 17%.

In intact core samples, NO_3^- consumption was tightly coupled to gross nitrification rates (Fig. 1), suggesting that NO_3^- assimilation was limited by NO_3^- availability. At low and moderate nitrification rates, NO_3^- consumption exceeded nitrification (as indicated by points above the 1:1 line). Addition of $^{15}NO_3^-$ may have stimulated consumption rates in these samples[13], and thus consumption rates in unamended soils may be lower than the rates shown here. Nevertheless, our results demonstrate that the microbial communities in most of the ecosystems have the capacity to assimilate even more NO_3^- than is produced by nitrification.

Rates of NO_3^- consumption were consistently lower than nitrification only when nitrification rates were very high (Fig. 1). These data apparently represent soils with high NH_4^+ availability relative to carbon availability, which stimulates nitrification rates and suppresses NO_3^- assimilation. For example, soils tended to have higher rates of NO_3^- production than consumption at the red alder/Douglas-fir site, where nitrogen fixation increased the availability of NH_4^+, and at the western juniper site, where low carbon availability reduced assimilatory demands for nitrogen.

The high rates of microbial assimilation at these sites raise an important question regarding carbon availability: is sufficient carbon fixed in these ecosystems to sustain the high assimilation rates throughout the active season? Whether or not the rates shown in Table 2 can be sustained depends on: the length of the active period; the amount of above-ground and below-ground net primary production (ANPP and BNPP); the amount of NH_4^+ assimilated; the C:N ratio of the microbial biomass; and the carbon-use efficiency of the microbial biomass. We used a model describing secondary production processes[16] to calculate

TABLE 1 Selected characteristics of study sites

Ecosystem	Symbol	Elevation (m)	MAT (°C)	MAP (mm)	ANPP* ($Mg\ ha^{-1}\ yr^{-1}$)	Soil texture†	Soil pH‡	Extractable inorganic N§		$^{15}NO_3^-$ added
								NH_4^+	NO_3^-	
								($mg\ N\ kg^{-1}$)		
Tesuque watershed, New Mexico										
Pinyon/juniper (*Pinus edulis/Juniperus osteosperma*)	Y	2,410	8.5	480	ND¶	SL	6.1	3.29	1.04	1.18
Ponderosa pine (*Pinus ponderosa*)	P	2,740	6.5	550	ND	SL	5.0	1.39	0.19	1.06
Mixed conifer (*Pseudotsuga menziesii/Abies concolor*)	C	2,720	5.0	550	ND	SL	5.1	2.65	0.23	1.47
Aspen (*Populus tremuloides*)	A	3,110	2.5	625	5.7	L	5.1	4.41	0.24	1.24
Spruce/fir (*Picea engelmanii/Abies lasiocarpa*)	S	3,415	0.0	700	ND	L	4.6	1.32	0.25	0.77
Oregon transect										
Western juniper (*Juniperus occidentalis*)	J	930	9.0	220	1.2	SL	5.9	1.32	0.50	1.02
Ponderosa pine (*Pinus ponderosa*)	O	1,030	7.5	540	2.2	SL	5.5	0.98	0.05	1.27
Mountain hemlock (*Tsuga mertensiana*)	M	1,460	6.0	1,800	5.1	SL	4.8	0.97	0.18	2.06
Douglas-fir (*Pseudotsuga menziesii*)	D	170	11.0	1,000	11.6	SiL	5.0	2.59	0.54	1.30
Red alder/Douglas-fir (*Alnus rubra/Pseudotsuga menziesii*)	R	200	10.0	2,400	10.7	L	3.5	4.11	1.24	3.23
Western hemlock/sitka spruce (*Tsuga heterophylla/Picea sitchensis*)	H	240	10.0	2,400	13.0	SiL	3.8	4.53	0.08	2.02

Soil characteristics are for the 0–15-cm mineral soil layer. ND, not determined; MAT, mean annual temperature; MAP, mean annual precipitation.
* Above-ground net primary production (in Mg biomass $ha^{-1}\ yr^{-1}$) from refs 3, 11, 12, 29 and 30.
† L, loam; SL, sandy loam; SiL, silt loam.
‡ Soil pH was measured in 0.01 M $CaCl_2$ (2:1 solution:soil wt ratio).
§ Mean 2 M KCl-extractable N from spring and summer sampling dates; $n = 10$ for all sites, except for the spruce/fir and red alder/Douglas-fir sites, where $n = 5$.

the microbial carbon-use efficiencies that would be necessary to allow the nitrogen-assimilation rates to be sustained throughout the active periods at the sites along the Oregon transect. The length of the active period was estimated on the basis of the amount of time that the surface soil was moist but not frozen (periods estimated from data in refs 11 and 12 ranged from 96 to 335 days). Because no BNPP data are available for these sites, we assumed that BNPP was equal to ANPP (ratios of BNPP/ANPP estimated for forests typically range from 0.3 to 4, with the highest values obtained when the NPP translocated to mycorrhizal fungi is included in estimates[17,18]). In addition, we summed mean NH_4^+ assimilation rates, measured in separate soil cores using $^{15}NH_4^+$ isotope dilution (data not shown), with mean NO_3^- assimilation rates for spring and summer to obtain rates of microbial $NH_4^+ + NO_3^-$ assimilation. We also assumed that two thirds of all microbial nitrogen assimilation occurs in the 0–15-cm soil layer. Finally, we used microbial C:N ratios that we had measured

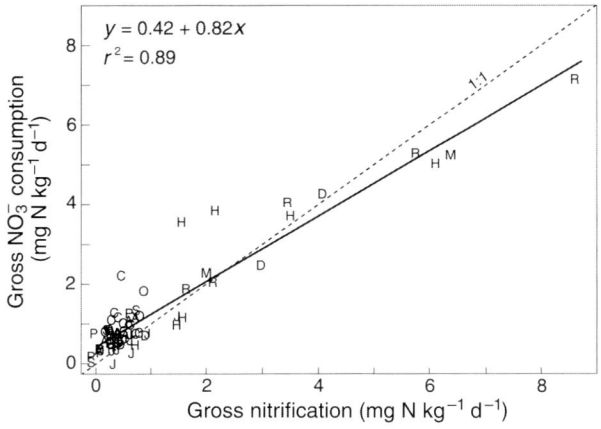

FIG. 1 Relationship between NO_3^- production and consumption in intact soil cores. Points represent gross rates in individual cores measured by ^{15}N-isotope dilution during late spring and late summer in the 0–15-cm mineral soil layer of forests in New Mexico and Oregon ($n = 70$). See Table 1 for key to symbols.

following isotope dilution experiments at each site. Modelling results showed that assimilation rates could be sustained throughout the active periods if microbial carbon-use efficiencies at each site were as follows: juniper, 0.50; ponderosa pine, 0.33; mountain hemlock, 0.44; Douglas-fir 0.25; red alder/Douglas-fir, 0.57; and western hemlock/sitka spruce, 0.53. These carbon-use efficiencies are all within the range of values previously reported for soil microorganisms utilizing NO_3^- and NH_4^+ as N sources[19].

The high rates of microbial assimilation of NO_3^- shown in these forests may have resulted from the activity of both saprophytic microorganisms and mycorrhizal fungi. In other coniferous forests of the northwestern coast of the United States, however, mycorrhizal fungi have been estimated to process <25% of the NPP[17,20], indicating that the major portion of the NPP is decomposed by saprophytic organisms. Therefore, the NO_3^- assimilation rates shown in Table 2 are most likely to be due to the activity of saprophytic microorganisms. It is also likely that the small amount of nitrogen assimilated by mycorrhizal fungi is used to produce fungal biomass rather than plant biomass. Plant demand for nitrogen, estimated on the basis of litterfall data[3,11], is more than an order of magnitude lower than the rates of NO_3^- assimilation that we measured.

The results of our study contradict two assumptions commonly made regarding nitrogen cycling in forest ecosystems: (1) that nitrification is insignificant in undisturbed coniferous forests; and (2) that microbial assimilation of NO_3^- is unimportant in controlling nitrogen retention in forests. Our results demonstrate that even in mature ecosystems with relatively 'tight' nutrient cycles[21], large amounts of NO_3^- can be produced internally without subsequent nitrogen loss. In these systems, microbial assimilation of NO_3^- constitutes an important mechanism for nitrogen retention.

We propose a modification of the existing paradigm for nitrogen retention in forest ecosystems that accounts for high rates of microbial assimilation of NO_3^-. In ecosystems where soil carbon and nitrogen are accumulating, the microbial biomass will be a net sink for inorganic nitrogen, including NO_3^-. In mature ecosystems, however, where annual increases in microbial biomass are relatively small, microbial biomass nitrogen accretion is unlikely to cause rates of NO_3^- assimilation as high as those shown here. Instead, we propose that rapid turnover of the microbial biomass promotes nitrogen retention. Microbial assimilation of NO_3^-

TABLE 2 Gross rates of nitrification and NO_3^- consumption, net rates of nitrification, and mean residence times for NO_3^- pools in mature forest ecosystems

	Gross nitrification ($mg\,N\,m^{-2}\,d^{-1}$)		Gross NO_3^- consumption ($mg\,N\,m^{-2}\,d^{-1}$)		Net NO_3^- accumulation ($mg\,N\,m^{-2}\,d^{-1}$)		NO_3^- mean residence time (d)	
Ecosystem	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer
Tesuque watershed, New Mexico								
Pinyon/juniper	39*	125 (33)*	28*	107 (20)*	−22 (48)*	66 (36)*	1.46*	0.27 (0.17)*
Ponderosa pine	29 (13)	25 (11)	60 (20)	80 (13)	−30 (12)	−54 (20)	1.08 (0.67)	0.88 (0.52)
Mixed conifer	62 (5)	44 (4)	86 (9)	164 (26)	−24 (11)	−120 (23)	0.42 (0.11)	0.45 (0.10)
Aspen	46 (7)	35 (10)	75 (10)	76 (11)	−29 (5)	−41 (2)	0.78 (0.48)	1.08 (0.40)
Spruce/fir	ND†	27 (13)	ND	66 (21)	ND	−39 (10)	ND	0.80 (0.10)
Oregon transect								
Western juniper	82 (18)	127 (37)	97 (14)	85 (36)	−15 (10)	42 (13)	1.47 (0.66)	1.31 (0.64)
Ponderosa pine	41 (22)	79 (21)	84 (44)	112 (37)	−58 (26)	−66 (21)	0.00 (0.00)	0.28 (0.25)
Mountain hemlock	ND	198 (119)	ND	189 (84)	ND	−65 (50)	ND	0.11 (0.04)
Douglas-fir	304 (132)	82 (25)*	304 (128)	42 (12)*	1 (29)	102 (53)*	1.16 (0.79)	0.34 (0.13)*
Red alder/Douglas-fir	270 (90)	ND	251 (70)	ND	19 (21)	ND	0.35 (0.11)	ND
Western hemlock/ sitka spruce	112 (12)	145 (54)	224 (5)	111 (53)	−109 (7)	34 (13)	0.07 (0.03)	0.00 (0.00)

Values are means and (standard errors); $n = 5$ for all net rates; $n = 5$ for gross rates and mean residence times at all sites, except: $n = 1$ where no standard error is listed; $n = 2$ at the western hemlock/sitka spruce site in spring and the Oregon ponderosa pine site in summer; $n = 3$ at the Oregon ponderosa pine site in spring and at the pinyon/juniper, Douglas-fir, and mountain hemlock sites in summer; and $n = 4$ at the western hemlock/sitka spruce site in summer. Gross nitrification rates were significantly greater than zero at all sites except the mountain hemlock site ($P = 0.12$ for the mountain hemlock site, $P \leq 0.10$ for the Oregon ponderosa pine site, and $P \leq 0.05$ for all other sites with $n > 1$).

* Rates could not be determined in intact cores because the soil was either too rocky or too hard; rates from homogenized samples are provided instead.

† Rates not determined.

followed by release of biomass nitrogen as organic nitrogen and NH_4^+ results in conversion of the highly mobile NO_3^- ion into less mobile nitrogen forms. Therefore, NO_3^- assimilation and rapid microbial turnover will continually deplete NO_3^- pools, and minimal NO_3^- leaching will occur in spite of significant rates of nitrification.

Although increased rates of nitrogen loss from ecosystems following disturbance are usually attributed to increased rates of nitrification, greater availability of NH_4^+ and reduced inputs of plant carbon following disturbance are likely to decrease microbial assimilation of NO_3^-. Therefore, the increased nitrogen loss observed in a large number of forest ecosystems following vegetation removal[10] and increased nitrogen deposition[22] may be largely due to a reduction in NO_3^- assimilation by soil microorganisms. □

Methods

On each sampling date, $^{15}NO_3^-$ isotope dilution measurements[13] were made in intact soil cores at five plots distributed over 0.3 ha at each site. Each intact mineral soil core (4.8 cm diameter by 15 cm deep) received eight 2-ml injections of a solution containing 1.7 mM $K^{15}NO_3$ (99 atom% ^{15}N), resulting in an increase of 30 to 150 g H_2O kg^{-1} oven dry soil and 0.77 to 3.23 mg NO_3^--N kg^{-1} (Table 1), depending on soil bulk density. After injection of two core samples from each plot, one sample was immediately homogenized and a subsample was extracted in 2 M KCl to determine ^{15}N extraction efficiency[13]. Intact soil cores and homogenized samples were sealed in separate one-litre canning jars. Acetylene was added to half of the jars containing homogenized samples (creating 10 kPa C_2H_2). The jars were buried at the original location and soil depth for 24 h. After incubation, head-space samples were collected for N_2O analysis[23], and soil subsamples were analysed for NO_3^--^{15}N (refs 24, 25), microbial biomass ^{15}N (refs 26, 27), and total organic ^{15}N (ref. 28). All analyses of microbial biomass ^{15}N and total organic ^{15}N included procedures for eliminating NO_3^- to prevent contamination of organic N by residual $^{15}NO_3^-$. Gross nitrification and NO_3^- consumption rates were calculated from isotope dilution equations[13]. Mean residence times were calculated assuming that ambient NO_3^- pools were at steady state and that fluxes were equal to gross nitrification rates.

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