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Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, Vol. 296, No. 1082, The Nitrogen Cycle (Jan. 27, 1982), 445-457.

Stable URL:
http://links.jstor.org/sici?sici=0080-4622%2819820127%29296%3A1082%3C445%3ANIFE%3E2.0.CO%3B2-4

Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences is currently published by The Royal Society.

Phil. Trans. R. Soc. Lond. B **296**, 445–457 (1982)
Printed in Great Britain

Nitrification in forested ecosystems

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Nitrification, the microbial oxidation of NH_4^+-N, plays a key role in the cycling of N in forested and other terrestrial ecosystems. Solution losses of nitrate and gaseous losses of N_2 and nitrous oxides are important vectors of N loss from many forested systems and are directly or indirectly controlled by the activity of the nitrifiers. These losses can also have important consequences for downstream ecosystems, groundwater quality, and atmospheric concentrations of ozone.

Relative nitrification (the proportion of the total mineral N that is nitrate at the end of an incubation period) provides an independent means of evaluating the general importance of site factors thought to regulate nitrification *in situ*. Regressions of relative nitrification against soil pH, C:N, and percentage N, with the use of data from previously published studies, suggest that although these factors may be important regulators of nitrification in particular sites, they are not good predictors of nitrification across a wide range of sites. Reasons for their low predictive ability may include limitations of current measurement techniques or the capacity of nitrifiers to adapt to relatively extreme conditions.

Introduction

The microbial oxidation of NH_4^+-N in soil attracted early attention as a means of producing saltpetre for gunpowder during the Napoleonic wars. More recently, attention has stemmed from a growing awareness of nitrification's key role as gatekeeper for mineral N losses and losses of cations from both cropped and natural ecosystems.

With minor exceptions, the biochemistry of autotrophic nitrification seems to be well understood: nitrifiers mediate the transformation of NH_4^+-N to various less-reduced forms, collectively gaining as much as 440 kJ of energy per mole of NH_4^+-N oxidized when nitrate is the end product. Less clearly understood are important aspects of their ecology, in particular the factors that regulate the rate of NH_4^+-N oxidation *in situ*. The rate of ammonium oxidation can vary strikingly among different systems, however, and has a number of important consequences for these systems. Where nitrification occurs slowly, for example, mineral N remains in the relatively immobile NH_4^+-N form. But where the oxidation is rapid, the ammonium may be quickly transformed to negatively charged NO_3^--N, a form that is substantially more mobile than ammonium and susceptible to loss by both solution and gaseous pathways. Nitrate is easily leached from most soil profiles and can also act as a terminal electron acceptor for denitrifiers, which can subsequently transform it to nitrous oxide or N_2. NH_4^+-N, on the other hand, is not easily leached from most soils because of cation exchange processes, and gaseous losses from unfertilized systems (as NH_3) are not likely to be important where soil pH is below 7 or the plant canopy is intact (Denmead *et al.* 1976).

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Associated with solution losses of nitrate are losses of cations such as K^+, Ca^{2+}, and NH_4^+ that accompany anions in the soil solution to maintain ionic equilibrium. Losses of these nutrient cations are exacerbated by the hydrogen ions produced during nitrification; these can force other cations into solution by displacing them on cation exchange sites.

In addition to the impact that nitrifier-regulated losses can have on local systems, there can also be important consequences for the systems receiving the N lost. Aquatic systems that receive leached nitrate and cations may be significantly affected by the elevated nutrient inputs, and high levels of nitrate in groundwater-derived drinking water is an important health problem in both industrialized and developing countries (Wilkinson & Greene, this symposium). The NO_x-mediated degradation of stratospheric ozone has been another source of recent concern (Crutzen 1982).

A number of recent reviews have synthesized available information concerning nitrifier taxonomy, biochemistry and the various factors that have the potential to regulate nitrifiers on a physiological or population level in the laboratory (see, for example, Focht & Verstraete (1977), Belser (1979) and Verstraete (1981)). Less readily available, however, are quantitative assessments of the importance of these factors *in situ*, and comprehensive analyses on scales larger than a single watershed have apparently not yet been attempted. Only with the increased use of similar techniques for measuring nitrification have comparisons across studies become possible. Their potential for providing significant insight into the factors that regulate the process under field conditions seems considerable.

In this paper I use published data to review the relation between nitrification and some of the principal factors that are thought to regulate nitrate production *in situ*. A better understanding of these factors is essential if we are to be able to predict the effects of disturbance on the N status of terrestrial systems and to understand the processes controlling its cycling well enough to utilize both native and fertilizer N efficiently.

Nitrification and N loss in forested systems

The widespread application of watershed techniques for studying nutrient cycling in forested systems has revealed a number of interesting features of the nitrogen cycle in these systems. One of the more intriguing of these is the diversity with which the various systems so far studied release nitrate to groundwater after clear-cutting or other severe disturbance. While NO_3^--N losses from some systems have remained unchanged after devegetation, losses from other systems have been considerable, in some cases more than two orders of magnitude greater than the nitrate lost from adjacent, undisturbed control sites (Likens *et al.* 1969; Vitousek & Melillo 1979; Vitousek *et al.* 1979). Differential nitrification rates among soils of the various sites is one of the major mechanisms identified by Vitousek *et al.* (1979) that could account for these intersite differences. In fact, when soils or forest floors from 17 of their control sites were incubated in the laboratory, net nitrate production ranged from less than 0.1 to over 800 mg NO_3^--N kg^{-1} dry soil per 8 weeks (Vitousek *et al.* 1982). In general, sites with large, active populations of nitrifiers tend to lose the most nitrate when the site is disturbed.

Even in the absence of severe disturbance, nitrification can lead to considerable N losses. Bormann & Likens (1979), for example, estimated that 19% of the N entering a 55 year old northern hardwood forest in the northeastern U.S. is lost as nitrate annually, and Melillo *et*

al. (1981) suggested that as much as another 27 kg N ha^{-1} may be lost annually through gaseous pathways.

Substantially different rates of nitrate production during laboratory incubations of soils from a wide variety of forested and other systems have been extensively documented during the past 50 years. Six major factors have been identified that appear to affect nitrate production in most well drained soils. The evidence for the importance of these factors has come principally from correlations of site characteristics with rates of nitrate production in soil incubations, and from experimental manipulation of incubated soils. These factors are moisture, temperature, C:N ratio, pH, the presence of plant-produced allelochemicals, and the supply of essential nutrients, e.g. phosphorus. Low nitrifier populations have also been suggested to limit nitrate production in certain situations, but this factor is attributable to the factors that keep the natural population in these sites low in the first place.

In general, increasing the moisture and temperature of soils which actively nitrify tends to stimulate nitrification up to a point beyond which rates become substantially reduced; widening the C:N ratio with oxidizable carbon (effectively decreasing the availability of NH_4^+-N as it becomes immobilized in rapidly expanding heterotroph populations) inhibits nitrate production; increasing the pH of acidic soils with $CaCO_3$ stimulates nitrate formation; adding various plant, litter and soil extracts and washings to soils from some sites can decrease nitrate production; and several investigators have reported increased nitrate production in some soils following the addition of phosphate.

However, experiments of this nature may yield a misleadingly simple picture of nitrification in most soils. Changes in absolute rates of nitrate production in response to experimental perturbations of a soil – the means by which the importance of these factors is most commonly evaluated – provide little insight into the factors that regulate nitrification *per se* in unfertilized soils. Absolute nitrate production is at least partly a function of N mineralization, the rate at which organic N is transformed to a form available to the nitrifiers. Consequently, it is not possible to separate the effects of a treatment on nitrification from its effects on mineralization unless simultaneous information regarding ammonium production is also made available. For example, what is often interpreted as a $CaCO_3$-effected increase in nitrification during incubation can in many cases be more accurately described as a $CaCO_3$-effected increase in *mineralization*, with a concomitant increase in nitrate formation due to elevated ammonium availability rather than to effects of $CaCO_3$. This is quite a different conclusion from that often drawn from such evidence, namely that low pH depresses nitrifier activity. The distinction is critical for the development of mechanism-based models for predicting nitrate production in soil.

An alternative measure of nitrification in non-fertilized soils might consider nitrate production in relation to the ammonium-supplying capacity of the soil. Such a measure of relative nitrification (NO_3^--N/(NH_4^+-N + NO_3^--N) at the end of an incubation) can considerably enhance the power of the incubation technique. In the example above, nitrification might be concluded to be stimulated by liming or be pH-constrained only if the $CaCO_3$ treatment caused an increase in the proportion of total mineral N (NH_4^+-N + NO_3^--N) that appears as nitrate at the end of the incubation. (Since all of the nitrate produced must at some point have been ammonium, summing ammonium and nitrate yields total net nitrogen mineralization or total net ammonium availability

In addition to providing improved insight into the mechanisms controlling nitrification in particular soils, studies that report relative nitrification values in addition to absolute values of nitrate production provide the additional advantage of allowing one to make meaningful cross-system comparisons. These comparisons can be used to evaluate the general *in situ* relevance of factors that have been suggested to be important in a particular system.

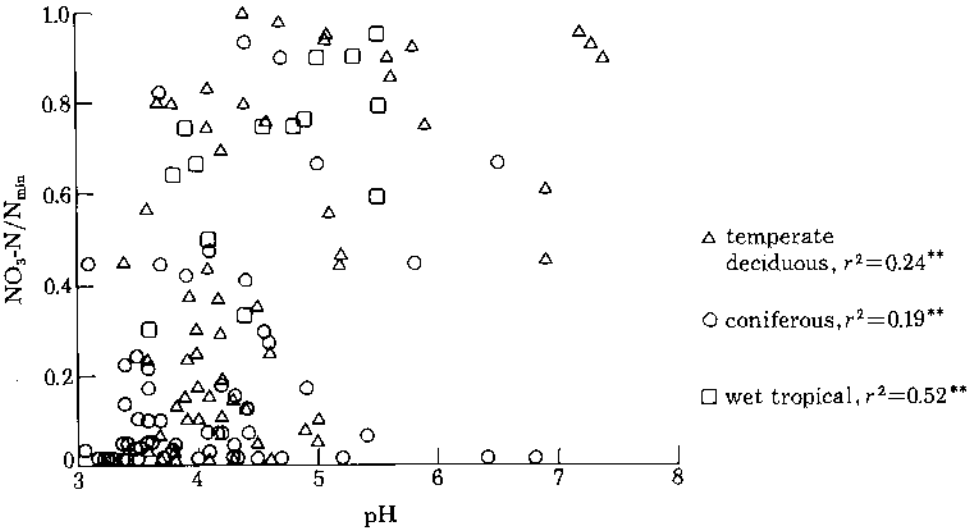

FIGURE 1. Relative nitrification in incubated soils plotted against soil pH for temperate deciduous, coniferous and wet tropical forest sites. Asterisks after regression coefficients indicate significance levels of $p < 0.05$ (*) and $p < 0.01$ (**). Data for regressions were taken from studies referenced in table 1.

LANDSCAPE PATTERNS OF RELATIVE NITRIFICATION

By comparing rates of relative nitrification with specific soil characteristics for a variety of different systems, one can evaluate the general importance of many of the factors so far demonstrated to affect nitrification under experimental conditions. If a factor such as pH is in general an important regulator of nitrification in terrestrial systems, independently of its effect on mineralization, then a regression of relative nitrification against soil pH should reveal that pH is a good predictor of relative nitrification. Although a significant correlation would not necessarily imply a causal relation, a lack of significance would suggest that it is not an important relation in general.

This approach for examining the *in situ* importance of factors that appear to regulate nitrification has apparently not yet been used for large-scale quantitative comparisons, perhaps because until recently sufficient data have been lacking. Only in the past few years have studies reporting values for the production of both NO_3^--N and NH_4^+-N become common. Such an approach has long been possible for absolute nitrate production, but the diversity of incubation methods would make its interpretation difficult. Length of incubation period and temperature and moisture conditions during incubation can substantially alter absolute rates of ammonium and subsequently nitrate production, but evidence so far published suggests that within a relatively broad range of conditions the *relative* rates of production will not significantly differ for most sites.

Regressions of soil pH, C:N, and total N against relative nitrification are shown in figures 1–3 for deciduous temperate, coniferous and wet tropical forest sites at least 20 years old. Data for these regressions were extracted from studies in the literature that reported both NH_4^+-N and NO_3^--N production or accumulation in freshly collected, non-dried soils incubated for 3–6 weeks at moisture contents of 50–100% water-holding-capacity. Most soils were incubated in

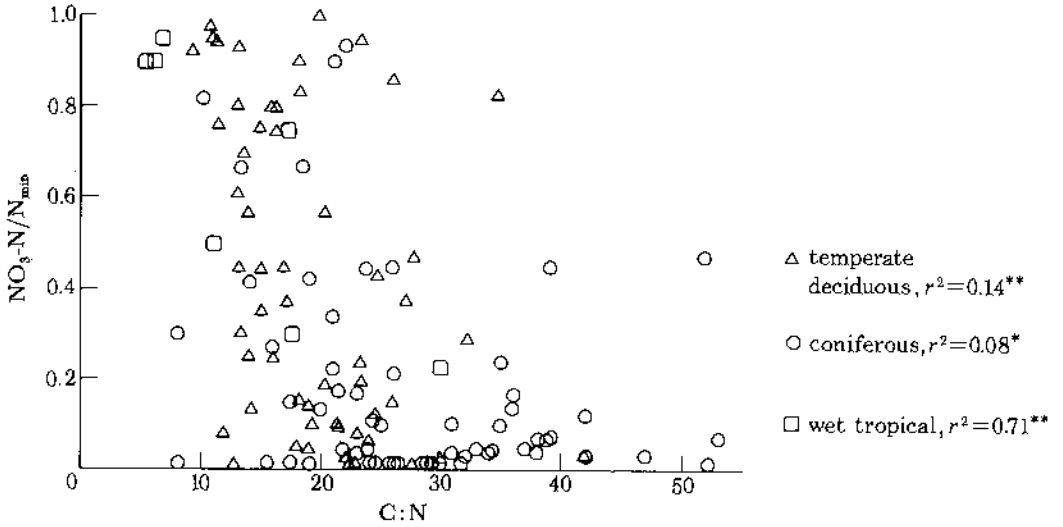

FIGURE 2. Relative nitrification in incubated soils plotted against soil C:N ratios. See legend to figure 1 for further explanation.

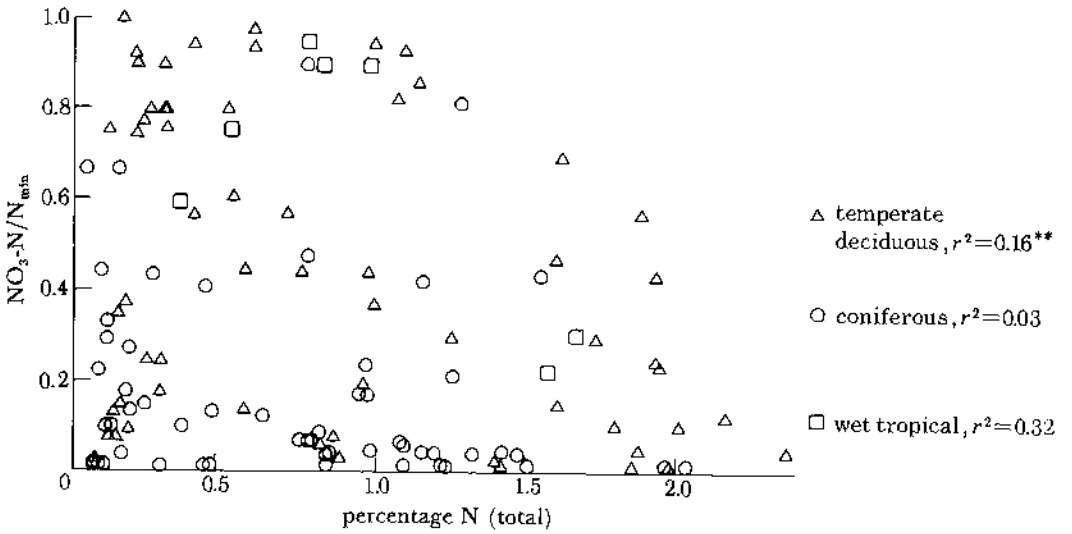

FIGURE 3. Relative nitrification in incubated soils plotted against total percentage N in the soils. See legend to figure 1 for further explanation.

constant-temperature rooms (20–30 °C), though some were incubated in the field in buried bags. When results for several incubation conditions for the same soil were reported, I chose data from these conditions nearest a 4 week incubation period, a constant 20 °C, a 60% water holding capacity, and a mid-growing-season collection date. Incubations of different parts of the soil profile (usually F + H and mineral soil to 15 cm or less) were treated independently,

TABLE 1. DATA SET USED FOR REGRESSIONS OF RELATIVE NITRIFICATION AGAINST SELECTED SITE CHARACTERISTICS

(Final N values have been adjusted to a 4-week incubation period for comparative purposes by the formula $[((N_{tf}-N_{ti})/t_t)t_4]+N_{ti}$, where N_{ti} is N (milligrams per kilogram dry soil) at the beginning of the incubation, N_{tf} is N at the end, t_t is the length of the original incubation period, and $t_4 = 28$ days. See text for further explanation. n.g. = not given.)

	final N/(mg/kg)		soil characteristics (initial)						
forest	NO_3-N	$N_{mineral}$	pH	C:N	%N	NO_3-N	NH_4-N	t_t	reference
temperate deciduous sites									
mixed oak, SE U.S.	< 1	24	n.g.	30	0.08	n.g.	n.g.	60	Coile (1940)
Alsatian lowland, France									
Querceto-Carpinetum	14	57	4.0	16	0.29	n.g.	n.g.	42	Lemée (1967)
Pruneto-Fraxinetum	44	55	4.4	13	0.30				
Quercetum media-europaeum	9	150	3.7	24	0.82				
Querceto-Molinietum	3	180	3.8	22	1.4				
Alnus + Fraxinus, 30 years	83	110	4.6	12	0.31				
Betula, 25 years	24	68	4.5	15	0.15				
mixed oak, Virelles, Belgium	18	40	6.9	13	0.57	1.1	18	28	Froment & Mommaerts-Billiet (1969)
mixed oak, Belgium	23	38	6.9	13	0.53	12	2.5	42	Remacle & Froment (1972)
beech forest, Belgium									
acid mull, A_{11}	130	360	4.2	17	1.01	16	46	42	van Praag & Weissen (1973)
A_{12}	50	63	3.7	16	0.51	9	8		
moder, L	6.3	22	4.2	32	1.74	3	17		
F_1	6.7	720	4.3	28	1.99	10	95		
F_2	6.3	750	4.1	23	2.77	3	181		
A_{11}	61	420	3.9	18	1.61	14	83		
A_{12}	37	82	3.4	17	0.76	10	19		
mulious moder, L	18	150	4.4	25	2.17	19	93		
F_2	28	625	4.5	19	2.37	15	180		
A_{11}	54	180	4.0	13	1.26	1	12		
A_{12}	16	21	4.1	17	0.21	3	4		
beech forest,									
Solling, F.R.G.; F_1	130	300	4.1	25	1.94	n.g.	n.g.	35–49	Runge (1974*a*, *b*)
F_2	85	370	3.6	23	1.95				
H	83	150	3.6	20	1.89				
A_h	51	64	3.8	16	0.25				
beech forest, Belgium									
F	22	87	n.g.	n.g.	1.94	n.g.	n.g.	42	van Praag *et al.* (1974)
0–5 cm	16	28	n.g.	n.g.	0.71				
5–15 cm	13	17	n.g.	n.g.	0.24				
beech forest, France;									
+ herbs	0	280	4.6	13	1.86	n.g.	n.g.	42	Lemée (1975)
− herbs	200	280	4.2	14	1.62				
central Europe									
Caria-Fagetum	6.9	7.7	7.4	18	0.3	n.g.	(1.8)†		von Gadow (1975)
Melico-Fagetum 1	31	34	7.3	13	1.1		(3.9)		
Aceri-Fraxinetum 1	32	33	7.2	11	1.0		(1.8)		
Aceri-Fraxinetum 2	50	51	4.7	11	0.6		(2.0)		
Melico-Fagetum 2	63	66	5.1	23	0.4		(6.5)		
Aceri-Fraxinetum 3	51	55	5.1	11	0.6		(6.9)		
northern hardwoods, NE U.S.; F–H	29	160	4.2	23	0.96	6	48	30	Melillo (1977)
oak–hickory, SE U.S.; Mineral	2.6	2.9	5.6	18	0.20	0.5	1.3	30	Montes & Christensen (1979)
brown forest soils, Japan									
Kuragari-4, HA less F	10	330	3.6	42	0.89	9	130	35	Ohta & Kumada (1979)
AB	2	26	4.9	23	0.14	0	9		
Owase-6, F + H	440	520	5.6	26	1.15	180	120		
A	41	72	5.1	14	0.40	11	10		
Owase-2, HA less F	44	910	5.0	18	1.88	22	550		
A_h	46	104	5.2	15	0.98	12	11		
Owase-7, A_1	11	81	4.3	19	0.57	7	32		
central U.S.									
oak–hickory 1; A	5.3	14	3.9	27	0.17	n.g.	n.g.	30	Matson & Vitousek (1981)
oak–hickory 2; A	4.6	31	4.1	27	0.15				
oak–hickory 3; A	0.9	9.5	3.9	22	0.18				
northern hardwood, NE U.S.									
30 years	0	160	3.7	n.g.	n.g.	0	5	28	Melillo *et al.* (1981)
50+ years	87	380	3.9			2	44		
oak–hickory, NC U.S.									
mid-successional, FF + A	12	17	5.9	15	0.11	0	3	30	Robertson & Vitousek (1981)
old growth, FF + A	1.3	16	4.2	12	0.11	0	2.5		
mixed oak, E U.S.; FF + A	29	29	4.4	20	0.16	2	2		
central U.S.									
maple; FF	430	520	5.7	34	1.07	26	120	28	Vitousek *et al.* (1982)
A	23	25	5.8	9	0.20	3	4		
oak; FF	220	470	5.2	28	1.60	84	84		
A	1.9	14	3.8	14	0.13	0	2		
northeastern U.S.									
oak–maple; FF	0	150	3.8	22	1.42	0	78		
A	1.6	8.7	4.0	20	0.29	0	0		
northern hardwoods; FF	89	900	4.0	21	2.01	6	120		
A	85	100	4.1	18	0.86	5	13		
aspen, Rocky Mountains, U.S.; FF	33	320	5.0	19	1.80	0	210		
A	16	63	4.6	14	0.24	1	29		

TABLE 1 (*cont.*)

forest	final N/(mg/kg) NO_3-N	final N/(mg/kg) $N_{mineral}$	soil characteristics (initial) pH	C:N	%N	NO_3-N	NH_4-N		reference
			coniferous forest sites						
spruce, Norway									
Dryopteris understory	0	230	4.5	n.g.	n.g.	0	76	28	Mork (1938)
Vaccinium understory	0	370	4.3	n.g.	n.g.	0	92		
loblolly pine, SE U.S.									
young 1	< 1	41	n.g.	19	0.07	n.g.	n.g.	60	Coile (1940)
young 2	< 1	17	n.g.	23	0.06				
70 yrs	01	33	n.g.	21	0.11				
Picea excelsa, planted, France	10	210	3.6	24	1.16	n.g.	n.g.	42	Lemée (1967)
spruce, Sweden									
Frodeparken 1; H	100	250	3.9	19	1.16	8	95	28	Popović (1967)
A_1	11	72	4.3	17	0.24	2	10		
Haboskogen; H	1.8	7.5	3.5	35	0.97	2.5	4.0		
A_1	0.6	2.7	3.4	21	0.09	1.0	0.6		
Brattforsheden; H	2.2	12.9	3.6	23	0.95	2.2	14.4		
A_1	1.0	5.5	4.2	21	0.18	1.3	4.7		
Frodeparken 2; H	29	71	4.4	14	0.44	4	9		
A_0	6	22	4.6	16	0.19	1	5		
Douglas fir, NW U.S.; F	320	340	4.4	22	1.02	240	2	28	Bollen & Lu (1968)
FF + A	120	130	4.7	21	0.77	79	2		
spruce, S Sweden									
Skarhult; H	36	170	3.6	26	1.26	5	62	42	Popović (1971)
$A_{0-6\,cm}$	4	41	3.6	25	0.36	2	18		
Fulltofta; H	5	190	3.8	32	1.41	3	140		
$A_{0-6\,cm}$	1	28	3.8	22	0.16	1	14		
Tönnersjöheden 1; H	3	73	3.5	34	1.33	3	19		
A	1	10	3.7	35	0.13	2	3		
Tönnershöheden 2; H	2	40	3.4	37	1.20	2	14		
A	1	7.7	3.4	36	0.19	1	4		
Tönnershöheden 3; H	3	83	3.5	31	1.48	3	24		
A	1	10	3.5	31	0.12	1	4		
Pinus sylvestris, Scotland; H	9	290	3.0	47	2.8	n.g.	n.g.	62	Williams (1972)
spruce, planted, Belgium; F_1	4	640	4.3	28	1.97	13	120	42	van Praag & Weissen (1973)
F_2	0	300	3.5	26	2.04	0	110		
H-A_{11}	< 1	67	3.3	26	1.23	1	30		
A_{12}	0	15	3.3	29	0.45	0	8		
spruce, Belgium; F	13	270	3.6	33	1.43	n.g.	n.g.	42	Froment & Remacle (1975)
H	9	180	3.4	34	0.99	n.g.	n.g.		
A_1 (0–5 cm)	6	44	3.8	20	0.46	n.g.	n.g.		
Pinus radiata, S Australia; FF									
sand podzol 1	6	23	6.1	n.g.	n.g.	n.g.	n.g.	90	Lamb (1975)
2	6	71	6.2						
3	8	72	6.0						
4	79	94	5.7						
humus podzol + gleyed podzolic 1	120	140	6.2						
2	9.6	69	6.2						
3	180	350	5.5						
terra rossa/sand podzols 1	190	280	6.0						
2	220	300	6.1						
3	160	210	6.1						
terra rossa 45 cm deep	75	92	6.2						
100 cm deep	150	240	6.0						
Pinus banksiana, Ontario; F + H	38	460	4.4	24	0.82	n.g.	n.g.	28	Morrison & Foster (1977)
northern boreal, N Sweden									
site 1	0.5	7.3	4.2	39	0.79	< 1	< 1	42	Popović (1977)
2	0.5	7.2	4.2	38	0.79	< 1	6		
3	0.5	7.2	4.1	54	0.75	< 1	6		
4	0.5	13	4.3	38	0.85	< 1	2		
5	0.5	20	4.1	42	0.84	< 1	3		
6	0.5	4.2	4.4	42	0.63	< 1	1		
Pinus taida, SE U.S.; A	0.36	0.54	5.0	13	0.15	0.42	0.51	30	Montes & Christensen (1979)
Pinus spp. NC U.S.; FF + A	8.5	13	6.5	19	0.04	0.5	1.4	30	Robertson & Vitousek (1981)
Pinus sp., planted, c. U.S.; FF	0	77	3.4	52	0.84	0	14	28	Vitousek *et al.* (1982)
A	0	0.5	3.7	15	0.07	0	0.7		
northeastern U.S.									
red pine; FF	0	72	3.2	26	1.22	0	26		
A	2.9	6.6	3.7	24	0.26	0	0		
balsam fir; FF	32	73	3.1	26	1.55	0	188		
A	0	400	3.2	17	0.43	4	13		
Rocky Mountains, S c. U.S.									
ponderosa pine; FF	0	42	6.4	29	1.10	0	62		
A	0	3.4	6.8	30	0.08	2.1	2.2		
mixed conifer; FF	10	150	5.4	39	1.09	24	190		
A	4.7	10.5	5.8	39	0.09	0	11		
spruce fir; FF	0	120	5.2	25	1.51	0	220		
A	0	21	4.7	8	0.29	0	12		
northwestern U.S.									
hemlock rainforest; FF	54	110	4.1	52	0.78	5	54		
A	14	17	3.7	10	1.29	1	6		
douglas fir; FF	14	83	4.9	36	0.98	0	87		
A	2.5	8.7	4.3	8	0.11	0	1.3		
silver fir; FF	0	31	3.4	32	1.10	0	25		
A	0	1.7	4.0	24	0.10	0	1.7		

TABLE 1 (*cont.*)

forest	final N/(mg/kg) NO_3-N	final N/(mg/kg) $N_{mineral}$	soil characteristics (initial) pH	C:N	%N	NO_3-N	NH_4-N	t	reference
wet tropical sites									
tropical rainforest, Jamaica									
mor ridge; 0–10 cm	100	460	3.0	30	1.58	31	360	40	Tanner (1977)
mull ridge; 0–10 cm	110	370	3.6	18	1.67	17	240		
wet slope; 0–10 cm	71	150	4.1	11	0.35	0	180		
gap forest: 0–10 cm	280	380	4.3	17	0.52	44	210		
lowland rainforest, Australia									
43 years	65	68	5.5	7	0.78	15	3	20	Lamb (1980)
53 years	61	68	5.3	6	0.83	11	3		
> 53 years	88	98	5.0	5	0.98	15	3		
Ivory Coast, West Africa									
lowland rainforest, Banco 1	5.7	8.5	4.0	n.g.	n.g.	0.0	5.1	42	de Rham(1970)
2	7.3	9.8	3.9			0.8	3.1		
3	11	17	3.8			2.7	4.7		
lowland rainforest, Yapo 1	11	15	4.8			5.1	3.2		
2	36	48	4.9			8.3	4.1		
3	6.1	18	4.4			0.0	9.0		
semi-deciduous forest 1	11	19	5.5			8.3	4.3		
2	13	16	5.5			9.1	1.7		

† Numbers in parentheses indicate absolute values of negative production values.

as long as chemical characteristics of the profile components were also reported separately. The data used for the regressions are presented in table 1. Nitrogen accumulation (final N) values rather than production (final N minus initial N) values were used to calculate relative nitrification whenever possible to avoid interpretational and statistical difficulties associated with negative production values (which can occur when net immobilization exceeds net nitrification or net ammonification). In cases where only production values were reported, initial ammonium and nitrate values were assumed to equal zero or the absolute value of the lowest negative production value. Arcsine transformations of relative nitrification values were used in the regression analysis.

The most striking feature of these regressions is the relative lack of coherent pattern: contrary to conventional wisdom, only in the wet tropical forest sites do soil pH, C:N or percentage N explain a large portion of the variance in relative nitrification. In these sites the C:N ratio apparently explains 71% of the variance ($n = 7$, $p < 0.01$), although the extremely small sample size makes any judgement tenuous. In neither the temperate deciduous nor the coniferous sites are such relations evident. In the deciduous forests pH can explain as much as 24% of the variance ($n = 56$, $p < 0.01$), and in the coniferous as much as 19% ($n = 56$, $p < 0.01$). Taken together (table 2), pH, C:N and percentage N can explain up to 38% of the variation in relative nitrification in temperate deciduous sites ($n = 56$, $p < 0.01$), but only 13% in the coniferous sites in which all four factors were measured ($n = 56$, $p < 0.10$).

There are a number of possible explanations for the relatively poor ability of these factors to explain the pattern of relative nitrification in these systems. The first and most obvious is that relative nitrification (as defined here) is a poor indicator of nitrifier activity. This argument is difficult to evaluate fully with information currently available. The index seems to make conceptual sense and appears to offer a useful means for evaluating nitrification independently of mineralization in incubation studies, but it could be inappropriate for multi-study comparisons, especially if relative nitrification is more variable under different moisture and temperature incubation conditions than the data currently available indicate.

A second reason for the poor fit may be that the incubation technique in general yields a misleading picture of nitrification or mineralization in soils. Particularly open to criticism is the standard practice of mixing and sieving soil before incubation. Increased mineralization

and nitrate production after mixing and sieving of various incubated soils – especially mor types of humus – is well documented (Romell 1935; Tamm & Pettersson 1969; Melillo 1977). Effects on relative nitrification, however, are not well documented. In the absence of information to the contrary, though, it seems plausible that the measure is as robust for this perturbation as it is for the usual moisture and temperature range. In any case, mixing and sieving may not affect the ability of these soil factors to predict relative nitrification because the soils upon which the conventional predictions are based were also mixed and sieved. Unless the artificial

TABLE 2. MULTIPLE-REGRESSION COEFFICIENTS FOR RELATIVE NITRIFICATION IN INCUBATED SOILS AGAINST SELECTED SOIL CHARACTERISTICS AS REPORTED IN THE STUDIES LISTED IN TABLE 1

(Values for wet tropical forest sites are not shown, owing to the small sample size ($n = 7$).)

	temperate deciduous forests		coniferous forests	
factors	r^2	n	r^2	n
pH, C:N	0.29**	56	0.12*	56
pH, %N	0.36**	56	0.06	56
C:N, %N	0.23**	57	0.08	59
pH, C:N, %N	0.38**	56	0.13	56

*, $p < 0.05$; **, $p < 0.01$.

TABLE 3. REGRESSION COEFFICIENTS FOR RELATIVE NITRIFICATION IN INCUBATED SOILS AGAINST THE PERCENTAGE OF TOTAL N MINERALIZED IN THE SOILS DURING THE INCUBATION PERIOD ($100 \times N_{mineral}/N_{total}$)

(See table 1 for references.)

system	r^2	n
temperate deciduous forest	0.04	60
coniferous forests	0.001	58
wet tropical forests	0.09	7
temperate agriculture	0.003	58

*, $p < 0.05$; **, $p < 0.01$.

disturbance associated with incubation causes treated soils to react qualitatively differently to a treatment than if they had not been disturbed, this application of the technique should be valid.

A third incubation effect that could also affect the relative nitrification rate is the quick degradation of highly labile plant-produced allelochemicals in soils removed from the influence of living roots and throughfall (Rice 1979; Moleski 1976). However, such effects are very difficult to assess, given the ambiguity of the information currently available (Robertson & Vitousek 1981), and evidence for even recalcitrant nitrification inhibitors is weak (Robertson 1982).

If the nitrification index used is reasonable, there remain at least two explanations for the patterns observed in these analyses. The first is that the factors known to affect nitrification in the laboratory may not be accurately characterized in the field. For example, the limitations of bulk soil pH measurements have long been recognized (Romell & Heiberg 1931): the appropriate measure may be microsite pH, and the techniques for making such measurements are not practical. C:N ratios and percentage N data are used mainly as indicators of the

availability of N at a site, though both may bear little relation to the rate at which N is mineralized (Keeney 1980). An alternative measure might be the proportion of the total N in a soil that is mineralized over an incubation period of several weeks, though this measure no better predicts relative nitrification in soils than do the others analysed above (table 3). A better index of the N status of a forested site could be the C:N ratio of freshly fallen litter (Vitousek 1982): where N is in short supply, perennial vegetation might be expected to conserve as much N as possible from one season to the next by withdrawing it from senescing leaves (Turner 1977) or by increasing the efficiency of use of the nitrogen taken up. Consequently, in stressed sites, litter has a high C:N ratio. The effects of potential allelochemical compounds in soils may also be inadequately measured as yet. Many of the techniques so far used to indicate their presence and importance possess fundamental flaws (Robertson 1982), but such inhibitors could be important in some sites. They may be mainly important in sites that are nutrient-poor, since plants might be expected to invest in nitrifier-specific toxins only where N availability could be enhanced or H^+ production deleterious.

The remaining explanation for the inability of these factors to explain more than a small amount of the variation in relative nitrification is that the techniques used to evaluate the potential importance of a site factor – nitrification rates along an experimentally induced environmental gradient – may overrate the factor's importance. There is mounting evidence of the capacity for nitrifiers to adapt to conditions *in situ* (Ulyanova 1961, 1962; Mahendrappa *et al.* 1966; Thiagalingam & Kanehiro 1973; Monib *et al.* 1979), so that the inability of a nitrifier population developed under one set of conditions (e.g. high pH) to nitrify under another (e.g. low pH) may have little bearing on the ability of a population *developed* under the different conditions to nitrify. This means that in most forests, nitrification *per se* may be relatively unaffected by pH, C:N, and percentage N conditions. Rather, in most sites N availability may be the principal factor regulating rates of nitrification (Romell 1935; Robertson & Vitousek 1981).

Relative nitrification in agricultural systems

Conventional wisdom regarding the factors that regulate nitrification is based principally on experimental results from agricultural soils, but re-examination of these data by using relative nitrification rather than absolute nitrate production to indicate the general importance of a factor is also interesting (figure 4). Soil pH can explain 41 % of the variation in relative nitrification across different sites ($n = 58$, $p < 0.01$), and active nitrification occurs in some soils at pH < 4.5. None of the other factors examined appear significantly related to relative nitrification rates (table 4). The soils used in these regressions were dried before incubation and the results should therefore be interpreted cautiously (Birch 1960), but the regressions indicate that nitrification in agricultural soils may also be more complex than conventional wisdom often implies.

Conclusions

Rates of nitrification vary widely among forested and other terrestrial ecosystems, and these rates can have important consequences for site fertility and for N enrichment of downstream ecosystems. Relative nitrification (the proportion of mineral N that is nitrate at the end of an incubation period) can provide significant insight into the factors that regulate nitrification

TABLE 4. REGRESSION COEFFICIENTS FOR RELATIVE NITRIFICATION IN INCUBATED TEMPERATE AGRICULTURAL SOILS AGAINST SELECTED SOIL CHARACTERISTICS

(See legend to figure 4 for references.)

factors	r^2	n
pH	0.41**	58
C:N	0.07	51
%N	0.001	58
pH, C:N	0.39**	51
pH, %N	0.42**	58
C:N, %N	0.08	51
pH, C:N, %N	0.39**	51
%N mineralized	0.003	58

*, $p < 0.05$; **, $p < 0.01$.

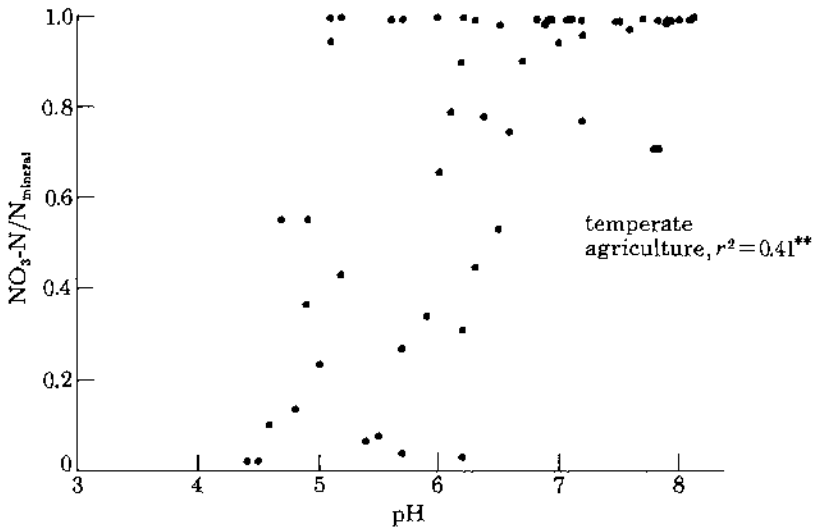

FIGURE 4. Relative nitrification in incubated temperate agricultural soils plotted against soil pH. **, $p < 0.01$. Data for regressions were extracted from Ahrens (1977), Brar & Giddens (1968), Cornfield (1952), Ekpete & Cornfield (1966), Jones & Hedlin (1970), Justice & Smith (1962), Kowalenko & Cameron (1976), McCormick & Wolf (1980), Nyborg & Hoyt (1978), Reichman *et al.* (1966), Soulides & Clark (1958), Vlassak (1970), and Westerman & Tucker (1974).

independently of mineralization. Additionally, such an index provides the opportunity to make cross-study evaluations of the factors that appear to regulate nitrification.

Regressions of relative nitrification against soil pH, C:N, and percentage N for a wide variety of forested sites suggest that, while these factors may be locally important regulators of nitrification in some sites, in general they are not good predictors of relative nitrification. This may be because current measurement techniques are inadequate or because nitrifiers can adapt to relatively extreme conditions. A better understanding of the factors that regulate nitrification at a mechanistic level will allow better predictions of the rates of nitrification in the field, and subsequently permit better predictions of the effects of disturbance on N loss and more efficient utilization of native and fertilizer N.

I thank P. M. Vitousek for helpful discussions during the preparation of the manuscript, and T. Rosswall for reading and commenting on an earlier draft. I also thank E. Wishinsky for help

with the statistical computations. Financial support was provided by a SCOPE–Mellon Foundation postdoctoral fellowship and the SCOPE/UNEP International Nitrogen Unit, Royal Swedish Academy of Sciences, Stockholm.

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